FAO Species Catalogue for Fishery Purposes No. 4 Vol. 2

ISSN 1020-8682

CEPHALOPODS OF THE WORLD

AN ANNOTATED AND ILLUSTRATED CATALOGUE OF CEPHALOPOD SPECIES KNOWN TO DATE

Volume 2. Myopsid and Oegopsid Squids

FAO Species Catalogue for Fishery Purposes No. 4, Vol. 2 FIR/Cat. 4/2

CEPHALOPODS OF THE WORLD

AN ANNOTATED AND ILLUSTRATED CATALOGUE OF CEPHALOPOD SPECIES KNOWN TO DATE

Volume 2

Myopsid and Oegopsid Squids

edited by

P. Jereb
Istituto Superiore per la Protezione e la Ricerca Ambientale
Rome, Italy

and

C.F.E. Roper
Smithsonian Institution, National Museum of Natural History
Washington, DC, United States of America

with the support of the
Government of Italy
(Ministero per le Politiche Agricole e Forestali,
Direzione Generale per la Pesca e l’Acquacoltura)

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

Rome, 2010

The designations employed and the presentation of material in this information product do not imply the expression of any opinion whatsoever on the part of the Food and Agriculture Organization of the United Nations (FAO) concerning the legal or development status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. The mention of specific companies or products of manufacturers, whether or not these have been patented, does not imply that these have been endorsed or recommended by FAO in preference to others of a similar nature that are not mentioned.

The views expressed in this information product are those of the author(s) and do not neccessarily reflect the views of FAO.

ISBN 978-92-5-106720-8

All rights reserved. FAO encourages the reproduction and dissemination of material in this information product. Non-commercial uses will be authorized free of charge, upon request. Reproduction for resale or other commercial purposes, including educational purposes, may incur fees. Applications for permission to reproduce or disseminate FAO copyright materials, and all queries concerning rights and licences, should be addressed by e-mail to

copyright@fao.org

or to the

Chief, Publishing Policy and Support Branch
Office of Knowledge Exchange, Research and Extension
FAO, Viale delle Terme di Caracalla, 00153 Rome, Italy

© **FAO 2010**

The Second Volume of this New Edition of the Cephalopods of the World Catalogue

is heartily dedicated to the

Worldwide Cephalopod Scientific Community.

May our knowledge continue to improve with time and this contribute to a wiser use of the World Oceans. We feel there is no better way to honour the memory of all our colleagues who have passed away.

PREPARATION OF THIS DOCUMENT

This document has been prepared by the Marine and Inland Fisheries Service, Fisheries and Aquaculture Resources Use and Conservation Division, FAO Fisheries and Aquaculture Department. It is part of the regular programme activities and a partial fulfilment of the Organization's role with regards to the marine fisheries resources identification and biodata (FAO Programme Element 232A3). It received support through contributions from the Ministry of Agriculture and Forestry Policies of the Government of Italy and from the Ministry of Foreign Affairs of the Kingdom of Norway to the FAO Global Partnerships for Responsible Fisheries (FISHCODE).

This publication is the second of three volumes of the second edition of the original FAO Catalogue of Cephalopods of the World (Roper *et al.*, 1984), and it constitutes Volume II of Number 4 in the new series: *FAO Species Catalogue for Fisheries Purposes*, that evolved as an independent series in 2001 from the former *FAO Fisheries Synopsis* No. 125.

Because the new Catalogue has expanded apace with recent research and fisheries information and revisions, it now is necessary to publish it as three free-standing volumes. Each volume has separate pagination, terminology/glossary, systematic sections, list of species and a volume-specific bibliography. This allows readers to use each volume independently without having to consult the other volumes for technical terms, measurements or bibliographic purposes. We hope that this added flexibility will provide convenience and utility for users of the Catalogue.

Programme coordinators: Jordi Lleonart and Michel Lambouef (former FAO, Rome).

Programme manager: Johanne Fischer (FAO, Rome).

Scientific and technical editors: Patrizia Jereb (ISPRA, Rome) and Clyde F.E. Roper (Smithsonian Institution, NMNH, Washington DC, USA).

Scientific reviser: Nicoletta De Angelis (FAO, Rome).

Technical, editorial assistance: Ingrid Roper (Smithsonian Institution, NMNH, Volunteer, Washington DC, USA).

Scientific assistance: Michael J. Sweeney (formerly Smithsonian Institution, NMNH, Washington DC, USA).

Scientific illustrator: Emanuela D'Antoni (FAO, Rome).

Page composition and indexing: Michèle S. Kautenberger-Longo (FAO, Rome).

Digitization of distribution maps: Fabio Carocci (FAO, Rome).

Cover illustration: Emanuela D'Antoni (FAO, Rome).

Jereb, P.; Roper, C.F.E. (eds)

Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 2. Myopsid and Oegopsid Squids.

FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. 2010. 605p. 10 colour plates.

ABSTRACT

This is the second volume of the entirely rewritten, revised and updated version of the original FAO Catalogue of Cephalopods of the World (1984). The present Volume is a multiauthored compilation that reviews 28 families, i.e. (in alphabetical order), *Ancistrocheiridae, Architeuthidae, Australiteuthidae, Bathyteuthidae, Batoteuthidae, Brachioteuthidae, Chiroteuthidae, Chtenopterygidae, Cranchiidae, Cycloteuthidae, Enoploteuthidae, Gonatidae, Histioteuthidae, Joubiniteuthidae, Lepidoteuthidae, Loliginidae, Lycoteuthidae, Magnapinnidae, Mastigoteuthidae, Neoteuthidae, Octopoteuthidae, Ommastrephidae, Onychoteuthidae, Pholidoteuthidae, Promachoteuthidae, Psychroteuthidae, Pyroteuthidae* and *Thysanoteuthidae,* with 83 genera and the 295 species known and named to the date of the completion of the volume. It provides accounts for all families and genera, as well as illustrated keys. Information under species accounts includes: valid modern systematic name and original citation of the species (or subspecies); synonyms; English, French and Spanish FAO names for the species; illustrations of dorsal and ventral aspects of the whole animal (as necessary) and other distinguishing illustrations; field characteristics; diagnostic features; geographic and vertical distribution, including GIS map; size; habitat; biology; interest to fishery; local names when available; a remarks section (as necessary) and literature. The Volume is fully indexed and also includes sections on terminology and measurements, an extensive glossary, an introduction with an updated review of the existing biological knowledge on squids (including fisheries information and main catch data for recent years) and a dedicated bibliography. Due to the conspicuous amount of literature addressing many squid species, an appendix is included in the online version, where those references considered most pertinent to the species are listed, by family and species, in alphabetical order by author; key words, also, are reported.

Distribution

Authors
FAO Fisheries Officers
Regional Fisheries Councils and Commissions
Selector SC

For bibliographic reference the different sections should be quoted as follows:

Jereb, P., Roper, C.F.E. & Vecchione, M. 2010. Introduction. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 1–11.

Jereb, P., Roper, C.F.E. & Vecchione, M. 2010. Family Australiteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 35–37.

Jereb, P., Vecchione, M. & Roper, C.F.E. 2010. Family Loliginidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 38–117.

Roper, C.F.E. & Jereb, P. 2010. Family Ancistrocheiridae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 118–120.

Roper, C.F.E. & Jereb, P. 2010. Family Architeuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 121–123.

Roper, C.F.E. & Jereb, P. 2010. Family Bathyteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 124–126.

Roper, C.F.E. & Jereb, P. 2010. Family Batoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 127–128.

Roper, C.F.E. & Jereb, P. 2010. Family Brachioteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 129–134.

Roper, C.F.E. & Jereb, P. 2010. Family Chiroteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 135–145.

Roper, C.F.E. & Jereb, P. 2010. Family Chtenopterigidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 146–147.

Roper, C.F.E. & Jereb, P. 2010. Family Cranchiidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 148–178.

Roper, C.F.E. & Jereb, P. 2010. Family Cycloteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 179–182.

Roper, C.F.E. & Jereb, P. 2010. Family Enoploteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 183–200.

Roper, C.F.E. & Jereb, P. 2010. Family Histioteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 223–236.

Roper, C.F.E. & Jereb, P. 2010. Family Joubiniteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 237–238.

Roper, C.F.E. & Jereb, P. 2010. Family Lepidoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids.* FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. n239–240.

Roper, C.F.E. & Jereb, P. 2010. Family Lycoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 241–246.

Roper, C.F.E. & Jereb, P. 2010. Family Magnapinnidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 247–249.

Roper, C.F.E. & Jereb, P. 2010. Family Mastigoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 250–256.

Roper, C.F.E. & Jereb, P. 2010. Family Neoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 257–261.

Roper, C.F.E. & Jereb, P. 2010. Family Octopoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 262–268.

Roper, C.F.E. & Jereb, P. 2010. Family Onychoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 348–369.

Roper, C.F.E. & Jereb, P. 2010. Family Pholidoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 370–373.

Roper, C.F.E. & Jereb, P. 2010. Family Promachoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 374–376.

Roper, C.F.E. & Jereb, P. 2010. Family Psychroteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 377–378.

Roper, C.F.E. & Jereb, P. 2010. Family Pyroteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 379–383.

Roper, C.F.E. & Jereb, P. 2010. Family Thysanoteuthidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 384–387.

Roper, C.F.E., Nigmatullin C. & and Jereb P. 2010. Family Ommastrephidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 269–347.

Roper, C.F.E., Jorgensen, E. M., Katugin O. N. & Jereb, P. 2010. Family Gonatidae. *In* P. Jereb & C.F.E. Roper, eds. *Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. No. 4, Vol. 2. Rome, FAO. pp. 200–222.

Acknowledgements

The authors are pleased to heartily acknowledge the contributions of colleagues who have supplied information or read drafts of this Second Edition of the Cephalopod Catalogue. Without their good efforts this work would have been a less comprehensive, and consequently a less useful tool.

In particular, for this Volume, we want to thank: **Louise Allcock** (Co-editor, Journal of Natural History, Martin Ryan Marine Science Institute, Galway, Ireland), **Freddy Arocha** (Instituto Oceanografico, Universidad de Oriente, Cumana, Venezuela), **Giambattista Bello** (Mola di Bari, Italy), **John Bower** (Northern Biosphere Field Science Center, Hokkaido University, Hakodate, Hokkaido, Japan), **Norma E. Brunett**i (Instituto Nacional de Investigacion y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina), **Naritoshi Cho** (National Research Institute of Fisheries Science, Fisheries Research Agency, Nagai, Yokosuka, Japan), **Cherdchinda Chotiyaputta** (Department of Marine and Coastal Resources, Ministry of Natural Resources and Environment, Bangkok, Thailand), **Angel F. Gonzalez** and **Angel Guerra** (ECOBIOMAR, Instituto de Investigaciones Marinas, Vigo, Spain), **Eugenia Lefkaditou** (Institute of Marine Biological Resources-NCMR, Athens, Greece), **Marek Lipinski** (Marine and Coastal Management-DEAT, Cape Town, South Africa), **Chung-Cheng Lu** (Victoria, Australia), **Pilar Martínez** (Servicio de Biología, Instituto Nacional de Toxicología, Madrid, Spain), **Rodrigo S. Martins** (Marine and Coastal Management, University of Cape Town, South Africa), **Ana Moreno** and **Joao M.F. Pereira** (Instituto Nacional De Investigacao Agroria e das Pescas, INIAP/IPIMAR, Lisbon, Portugal), **José A. Alvarez Perez** (Centro de Ciências Tecnológicas da Terra e do Mar, Vale do Itajai University, Brazil), **Uwe Piatkowski** (Leibniz-Institut fuer Meereswissenschaften, Kiel University, Kiel, Germany), **Antoni Quetglas** (IEO-Centre Oceanogràfic de Balears, Palma de Mallorca, Spain), **Rui Rosa** (Laboratório Marítimo da Guia, Centro de Oceanografia, Lisbon University, Cascais, Portugal), **Toshie Wakabayashi** (Oceanic Squid Section, National Research Institute of Far Seas Fisheries, Fukuura, Yokohama, Japan), **José Xavier** (Centre of Marine Sciences, University of Algarve, Faro, Portugal), and **Karsten Zumholz** (Fisheries School Rendsburg, Rendsburg, Germany).

Very special thanks are due to **Nancy Voss** (Director of the Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, USA), for her knowledgeable help in solving systematic problems, with reference to species of the Cranchiidae, and to **Richard E. Young** (Professor Emeritus, Department of Oceanography, University of Hawaii at Manoa, Honolulu, Hawaii), for his continuous help and support in addressing and solving systematics and nomenclatural problems throughout the last phase of our work.

In the earliest phase of this work, **Michael J. Sweeney** (formerly Smithsonian Institution, National Museum of Natural History, WA, DC, USA) provided technical support, nomenclatural listing and literature searches, for which we all are grateful.

We gratefully acknowledge **Joerg Loetze**, Director of the Humboldt Field Research Station at Eagle Hill, Steuben, Maine (USA), for his support and generosity during our several visits to this collegial retreat.

Michel Lamboeuf (formerly Programme Manager at FAO, now retired) and **Jordi Lleonardt** (formerly Programme Manager at FAO, now back to the Institut de Ciències del Mar, CSIC, Barcelona, Spain), were our principal administrative contacts at FAO until 2008. This publication would not have been forthcoming without their very much appreciated support and encouragement.

We especially want to thank **Michel** for his help and constant support during all the years dedicated to this project.

Of course, a compilation of this nature must rely heavily on already-published works: these, we acknowledge with gratitude. In particular, we acknowledge here that many illustrations from these works have been used for the purposes of this Catalogue, for which we are most appreciative.

We also acknowledge with deep thanks the members of the FAO technical staff who so efficiently contributed to the preparation of this Volume: **Emanuela d'Antoni** for her excellent job in creating the many illustrations needed for the Catalogue and for greatly enhancing many illustrations from the literature; **Nicoletta De Angelis** and **Michèle Kautenberger-Longo** for their skilful collaboration in completing this highly technical and complex document; **Fabio Carocci** for the preparation of the distribution maps. All are premier representatives of their professions.

We especially want to thank **Nicoletta**, for her constant, collegial support and faith that this volume would be completed.

Colour photographs are included in this new edition of the Catalogue to enrich the quality and utility of the book. Therefore we acknowledge with deep gratitude those who contributed with great generosity by offering photographic material: **Howard** and **Michele Hall** (Howard Hall Production, USA), **Roger T. Hanlon** (Marine Biological Laboratory, Woods Hole, USA), **Tsunemi Kubodera** (National Museum of Nature and Science, Department of Zoology, Tokyo, Japan), **Mark Norman** (Museum of Victoria, Australia), **Malcolm Smale** (Port Elizabeth Museum, Bayworld Centre for Research and Education, Port Elizabeth, South Africa), **Isamu Soyama** (Tsuru-Shi, Yamanashi-Prefecture, Japan), **Michael Vecchione** (National Systematic Laboratory, National Museum of Natural History, Washington, DC, USA), **Peter Wirtz** (Madeira, Portugal), and **Richard E. Young** (Department of Oceanography, University of Hawaii at Manoa, Honolulu, Hawaii).

Last, but not least, very special thanks are due to **Ingrid H. Roper,** for her technical assistance and invaluable support during all stages of the preparation of this Catalogue. Without her technical and linguistic skills and her perseverance, this volume would not have been so well accomplished.

In the years that have elapsed between the publication of the first and the second Volumes of this new Edition, three highly esteemed colleagues and cherished friends have passed away: **Peter R. Boyle**, **Martina Compagno-Roeleveld** and **Martin J. Wells**. Our knowledge of the cephalopod world has benefitted greatly by their universally acknowledged and valued contributions. We all have gained from their collegiality and have enjoyed greatly their friendship.

Our special thanks to them for their lifetime service.

Table of Contents

1. INTRODUCTION

Patrizia Jereb, Clyde F.E. Roper and Michael Vecchione

The increasing exploitation of finfish resources, and the depletion of a number of major fish stocks that formerly supported industrial-scale fisheries, forces continued attention to the once-called 'unconventional marine resources', which include numerous species of cephalopods. Cephalopod catches have increased steadily in the last 40 years, from about 1 million metric tonnes in 1970 to more than 4 million metric tonnes in 2007 (FAO, 2009). This increase confirms a potential development of the fishery predicted by G.L. Voss in 1973, in his first general review of the world's cephalopod resources prepared for FAO. The rapid expansion of cephalopod fisheries in the decade or so following the publication of Voss's review, meant that a more comprehensive and updated compilation was required, particularly for cephalopod fishery biologists, zoologists and students. The FAO Species Catalogue, 'Cephalopods of the World' by C.F.E. Roper, M.J. Sweeney and C.E. Nauen was published in 1984 to meet this need.

The number of cephalopod species that enter commercial fisheries has continued to grow significantly since 1984, as a result of a still-growing market demand and the expansion of fisheries operations to new fishing areas and to deeper waters. It has been suggested that the cephalopod 'life-strategy' may guarantee survival against environmentally stressful conditions, including those caused by heavy fishing. However, as cephalopod fisheries experienced further extensive development, parallel concern developed regarding potential overexploitation. Thus, a broad consensus emerged among fishery biologists to apply the experience gained from errors made in finfish management to avoid possible failures in cephalopod exploitation. To help prevent potential failures, refined species identification capabilities are required, as well as a more detailed and accurate compilation of information on cephalopod species, distribution, biology, fisheries and catch statistics. Consequently, FAO recognized that a new edition of the 'Cephalopods of the World' catalogue was required. To achieve this expanded goal, several authors with particular areas of specialization were assembled to enhance the accuracy, coverage and utility of this revised catalogue.

In our attempt to make this document as comprehensive and as useful as possible, the taxonomic coverage of this edition of the catalogue is organized into 3 levels of interest:

Level 1: species of cephalopods currently exploited commercially and species utilized at the subsistence and artisanal levels;

Level 2: species of occasional and fortuitous interest to fisheries; this includes species considered to have a potential value to fisheries, based on criteria such as edibility, presumed abundance, accessibility, marketability, etc.; species of actual or potential interest to research museums also are considered under this level.

Level 3: species with no current interest to fisheries, which are listed only with the basic information available.

The inclusion of such a wide range of species is necessary to provide the most comprehensive inventory of species potentially useful to mankind, regardless of their current commercial status. For example, this work should be useful for the ever-expanding search for development and utilization of 'natural products', pharmaceuticals, etc.

The catalogue is based primarily on information available in published literature. However, yet-to-be-published reports and working documents also have been used when appropriate, especially from geographical areas where a large body of published information and data are lacking. We are particularly grateful to colleagues worldwide who have supplied us with fisheries information, as well as bibliographies of local cephalopod literature.

The fishery data reported herein are taken from the FAO official database, now available on the Worldwide web: FISHSTAT Plus 2009. This information is supplemented by field observations made by the authors in many parts of the world, both in preparation of the 1984 volume, as well as for the current edition. These field visits provided opportunities to examine fresh material at landing sites, markets and laboratories, as well as to obtain first-hand information about local cephalopod fisheries from regional fisheries workers. Additional examinations of preserved specimens occurred in museums.

During the 20-plus years separating the two editions, the rapid development of cephalopod fisheries worldwide and the simultaneous increase in the population of fisheries scientists, their research and publications, made available an enormous amount of new data and research results. Sometimes it is difficult to evaluate the reliability of published data, especially with regard to the identification of species in areas where the cephalopod fauna has not been sufficiently studied taxonomically. It is entirely understandable that field workers isolated from good library and museum/collection facilities find it difficult to correctly identify the species they encounter in the field. Moreover, the discovery of new species, the more accurate delimitation of known species, or even the introduction of nomenclatural changes, may cause confusion and lead to the use of scientific names that are incorrect by modern standards. Although great care was exercised to evaluate and correct such published information used in the preparation of this catalogue, some incorrect interpretations may have occurred. Another potential limitation, in the taxonomic literature especially, is that information on the economic importance of species is rather scarce or of a very general nature. Also, important information may have been overlooked if published only in local fisheries literature that is unavailable on an international scale. All of these potential limitations, however, have been significantly mitigated during the preparation of the new edition because of the availability of on-line fisheries databases and bibliographic search capabilities.

With regard to the limitations mentioned above, we heartily request that readers who detect any errors in the information presented, or who have additional information and data that will enhance the accuracy and utility of this book, please contact and inform one of the authors or the Species Identification and Data Programme (SIDP) of the Marine Resources Service, Fisheries Resources Division, Fisheries Department, FAO Rome.

For further reading and information on cephalopod biology, fisheries and resources, several references and websites are listed at the end of references.

1.1 Plan of the Catalogue

This catalogue is organized by families and their appropriate genera within major cephalopod groups. The type genus within each family is treated first, then all remaining genera are listed alphabetically. The type species within each genus is treated first, then all species are listed alphabetically.

Level 1 includes the most important species for fisheries utilization, and it consists of detailed information in all 12 categories listed below. **Level 2**, which comprises those species of occasional or potential interest to fisheries, consists of whatever information is available and appropriate for the 12 categories. **Level 3**, those species for which there is no current direct or indirect interest to fisheries, consists of basic information (i.e. scientific name, size, geographical distribution, literature). The format within the species sections includes the first two levels of treatment (Level 1 and Level 2) presented together. Species included in Level 3 are presented at the end of each family.

Consequently, each major group and family is introduced with general descriptive remarks, illustrations of diagnostic features, highlights of the biology and relevance to fisheries. The information that pertains to each species in Levels 1 and 2 is arranged by categories as follows: (1) scientific name; (2) synonymy; (3) misidentifications; (4) FAO names; (5) diagnostic features with illustrations; (6) maximum known size; (7) geographical distribution with map; (8) habitat and biology; (9) interest to fisheries; (10) local names; (11) remarks (12) literature.

(1) Scientific Name: Reference to author, date and publication citation is given for the original description of each species.

(2) Frequent Synonyms: Principal synonyms and name combinations are listed. Due to the complex situation/evolution of Myopsid and Oegopsid squid systematics in the last decades, this section is particularly detailed in this volume; even synonyms not “frequent” in a common language usage and/or different names used for species by different authors are reported, as an additional tool/information to the users.

(3) Misidentifications: Misidentifications as other species are reported here and discussed in detail when appropriate under section 11, Remarks, along with other nomenclatural points.

(4) FAO Names: English, French and Spanish names for each species, used primarily within FAO, are selected on the basis of the following criteria: (i) each name must apply to one species only, in a worldwide context; (ii) the name must conform to FAO nomenclatural spelling; (iii) the name should apply only to a cephalopod species, and should not lead to confusion with species names in other major animal groups. Wherever possible, these names are selected based on vernacular names (or parts of names) already in existence within the areas where the species is fished. FAO species names, of course, are not intended to replace local species names, but they are considered necessary to overcome the considerable confusion caused by the use of a single common name for many different species, or several names for the same species.

(5) Diagnostic Features: Distinctive characters for the species are given as an aid for identification, accompanied by pertinent illustrations. Species identifications should be attempted only after verification of the family through use of the illustrated key to families. Reference to FAO Species Identification Guides is given wherever relevant.

(6) Size: The known mantle length (or total length in some cases) of both males and females is provided where possible. Sizes or measurements might not be completely comparable because they were taken mostly from preserved or fixed specimens, but measurements of commercially important species often come from fresh material. Because of the elasticity of tentacles and arms, total length is not a very accurate measurement. Where both total length and mantle length are given, the respective figures do not necessarily pertain to the same specimen but may have been obtained from different sources. The available information on the size attained by some species often is very meagre, so the maximum reported size cited here might be considerably smaller than the actual maximum size. Maximum weight is given when available.

(7) Geographical Distribution: The entire known geographic range of the species, including areas of seasonal occurrence, is given in the text and shown on a map. In cases where only scattered records of occurrence are available, question marks have been used to indicate areas of suspected or unconfirmed distribution.

(8) Habitat and Biology: The known depth range of the species and information on salinity and temperature of its habitat are given where available. For the sake of exactness actual depth data are reported, as given in the referenced literature. Information on biological aspects, such as migration, spawning season and area, longevity, prey, and predators, also is included. Due to the dominant role of squids in the marine environment, this section is especially detailed in this volume.

(9) Interest to Fisheries: This paragraph gives an account of the areas where the species is fished and of the nature of the fishery; its importance either is qualitatively estimated (minor, moderate, major or potential) or actual figures of annual landings are provided. Data on utilization (fresh, dried, cooked, frozen, canned, etc.) also are given where available. Here, too, the quality and quantity of the available information varies considerably among the species, and it is reported in as much detail as possible in relation to the squid’s significance to the fisheries.

(10) Local Names: These are the names used locally for the topic species. The present compilation is necessarily incomplete, since only a fraction of the local names applied to specific entities actually is published. In many cases, local names are available only for species that support traditional fisheries. Apart from possible omissions due to limitations of literature available, some of the names included may be somewhat artificial, i.e. through transliteration of indigenous words into English. The local species name is preceded by the name of the country concerned in capital letters and, where necessary, by geographical specifications in lower case letters.

(11) Remarks: Important information concerning the species, but not specifically linked to any of the previous categories, is given here. For example, in some cases the taxonomic status of certain scientific names requires further discussion. Other nomenclatural problems are discussed in this section, such as the use of subspecies names.

(12) Literature: This includes references to the most important publications relevant to the species, particularly on biology and fisheries. Additional references are included in the bibliography. In the case of a few uncommon species, only systematic papers are available. The massive amount of literature relevant to fisheries for many species of squids required that appendices be compiled for this Volume. The appendix includes a list of publications useful to gain an understanding of the species biology, ecology and fisheries. Publications are listed by author's name, date of publication and key words for the publication's contents.

1.2 General Remarks on Cephalopods

The group known as cephalopods (class **Cephalopoda**) is the most complex in the phylum Mollusca, and indeed, in all of the invertebrate phyla. Cephalopods include exclusively marine animals that live in all oceans of the world with the exception of the Black Sea, from the Arctic Sea to the Antarctic Ocean and from the surface waters down into the deep sea.

Cephalopods first appeared as a separate molluscan taxonomic entity, the nautiloids, in the Upper Cambrian period (over 500 million years ago), but more than half of these ancestors were already extinct by the end of the Silurian, 400 million years ago, when only the nautiluses survived. Meanwhile, other forms arose in the late Palaeozoic (between 400 and 350 million years ago), including those of the Subclass Coleoidea, but most of them became extinct by the end of the Mesozoic, about 150 million years ago. The only members of the subclass Coleoidea that exist today are the forms that developed in the Upper Triassic and Lower Jurassic (between 200 and 150 million years ago).

Although there is a long fossil record of many different groups, all living cephalopods belong to two 'subclasses': the **Coleoidea**, which includes the major groups known as squids, cuttlefishes *sensu lato*, octopods and vampires, and the **Nautiloidea**, containing two genera, ***Nautilus*** and ***Allonautilus***, the only surviving cephalopods with an external shell.

At the present time the status and understanding of the **Systematics** and **Classification** of the Recent Cephalopoda is under considerable discussion. The families of living cephalopods are, for the most part, well resolved and relatively well accepted. Species-level taxa usually can be placed in well-defined families. The higher classification, however, still is not resolved. The classification above the family level is controversial and a broad consensus still needs to be achieved. This situation is not unexpected for a group of organisms that has undergone explosive research attention in recent decades.

Consequently, rather than accept and promote any particular scheme of classification, before consensus and stability are achieved, we will use an 'operational breakdown' that is satisfactory for the objectives of this Catalogue. For practical purposes we separate the cephalopods into several groups, without assigning or implying taxonomic relationships. **Figure 1** diagrams several of the classification schemes currently under discussion.

In this work the following groups are used, as illustrated in **Figure 2**[1/]:

Nautiluses
Cuttlefishes
Bobtail squids
Bottletail squids
Pygmy squids
Ram's horn squid
Myopsid squids
Oegopsid squids
Vampires
Cirrate octopods
Incirrate octopods

Unresolved taxa:

Spirula
Idiosepius
Bathyteuthis
Chtenopteryx
Sepiadariidae

Plural versus singular usage of cephalopod common group names is standardized as follows:

squid, cuttlefish, octopod, octopus, vampire, nautilus refer to one individual or one species;

squids, cuttlefishes, octopods, octopuses, vampires, nautiluses refer to two or more individuals and/or species. These terms are also used to indicate the major groups.

The term '**cuttlefishes**' also is used '*sensu lato*' to indicate the following groups: Cuttlefishes, Bobtail squids, Bottletail squids, Pygmy squids and the Ram's horn squid. Cuttlefishes, along with Nautiluses were treated in Volume 1 (Jereb and Roper, 2005).

We differentiate between the members of the family Octopodidae, which are called **octopus/octopuses**, and the members of the whole group (Incirrate and Cirrate or any combination of non-Octopodidae taxa), which are called **octopod/octopods**. Octopods will be treated in Volume 3.

This second volume of the Catalogue is focused on Squids.

1.3 General Remarks on Squids

Squids occur in almost all marine habitats of the world. Salinity is considered to be a limiting factor in squids distribution; they are generally restricted to salinity concentrations between 27 and 37‰. However, ***Lolliguncula brevis***, which lives and reproduces in waters of 17‰, demonstrates a capacity for a higher degree of salinity tolerance (Hendrix *et al*., 1981). Some species

---

[1/] The endings used in the group names do not imply any level of classification.

Roper *et al*. (1984)

Order	Suborder
Teuthoidea	Myopsida
Sepioidea	
Vampyromorpha	
Octopoda	Cirrata
	Incirrata

Engeser and Bandel (1988)

Superorder	Order	Suborder
Decapoda	Spirulida	
	“higher decapods” (name not given)	Teuthina
		Sepiina
Vampyromorphoidea	Vampyromorpha	
	Octopoda	Cirrata
		Incirrata

Clarke (1988b)

Order	Suborder
Sepioidea	
Sepiolioidea	
Teuthoidea	Myopsida
	Oegopsida
Vampyromorpha	
Octopoda	

Sweeney and Roper (1998)

Superorder	Order	Suborder
Decabrachia	Spirulida	
	Sepiida	
	Sepiolida	
	Teuthida	Myopsina
		Oegopsina
Octobrachia	Vampyromorphida	
	Octopodida	Cirrina
		Incirrina

Young *et al*. (1998a)

Division	Superorder	Order	Suborder
Neocoleoidea	Decapodiformes	Oegopsida	
		Myopsida	
		Sepioidea	Sepiida
			Sepiolida
			Spirulida
			Incertae sedis
	Octopodiformes	Vampyromorpha	
		Octopoda	Cirrata
			Incirrata

Boletzky (1999)

Grade	Superorder	Order
	Decabrachia	Spirulida
		Sepiida
		Sepiolida
		Idiosepiida
		Teuthida
Vampyropoda	Pseudooctobrachia	Vampyromorpha
	Octobrachia	Cirroctopoda
		Octopoda

Haas (2002)

1	2	3	4	5
Neocoleoidea	Decabrachiomorpha	Oegopsida		
		Uniductia	Spirulida	
			Myopsida	Loliginida
				Sepiida
	Octobrachiomorpha	Vampyromorpha		
		Octopoda	Cirrata	
			Incirrata	

Fig. 1 Some conflicting suprafamilial classifications of living coleoid cephalopods

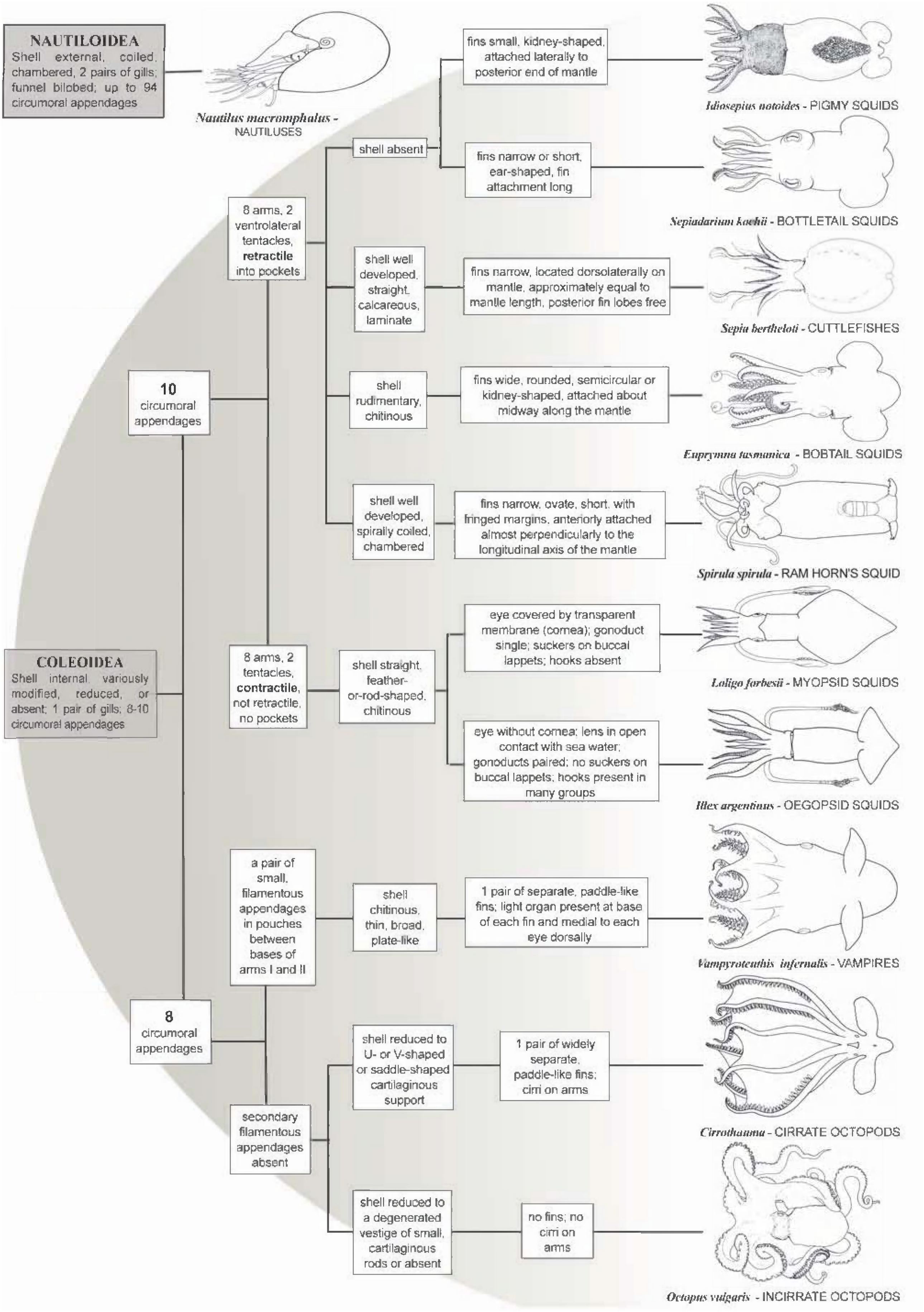


Fig. 2 Living cephalopods

inhabit the Red Sea and the southern coasts of the Iberian Peninsula (Guerra, 1992), where the salinity is higher than 37‰ and other species have been found in waters where salinity ranges between 25 and 18‰ (Sea of Marmara; Unsal *et al*., 1999). The habitat depth range extends from the intertidal to over 5 000 m. Many species of oceanic squids undergo diel vertical migrations: they occur at depths of about 200 to 700 m during the day, then at the onset of twilight and increasing darkness, they ascend into the uppermost 200 m for the night. A deeper-living layer of diel migrators occurs from about 1 000 m to 600 m during the daytime. The abundance of squids varies, depending on genera, habitat and season, from isolated individuals, small schools with a few dozen individuals, to huge schools of neritic and oceanic species with millions of specimens.

General charcteristics

The size of adult squids ranges from less than 10 mm mantle length (e.g. some members of the family Pyroteuthidae) to the giant squid ***Architeuthis*** sp. and the colossal squid ***Mesonychoteuthis hamiltoni***, at well over 2 m mantle length. The largest specimens may weigh over 500 kg, but the average size of commercial species is 200 to 400 mm mantle length and about 0.1 to 2.0 kg total weight.

Squids are easily distinguished by external characteristics: they have an elongate, cylindrical body with posterolateral fins on the mantle (rarely, the fins extend for the length of the mantle); 10 circumoral appendages anteriorly on the head, not connected at bases with a web (except Histioteuthidae); 8 arms with 2 (occasionally 4 or more) series of stalked suckers with chitinous rings (and/or chitinous hooks in some groups) that extend along the entire arm length; 2 longer tentacles with an organized cluster of 2 or more series of stalked suckers (and/or hooks) at the distal section (tentacular club); the proximal tentacular stalks usually are devoid of suckers or hooks.

Squids are soft-bodied, bilaterally symmetrical animals with a well-developed head and a body that consists of the muscular mantle, the mantle cavity that houses the internal organs, and the external fins. The head bears an anterior circum-oral (surrounding the mouth) crown of mobile appendages (arms, tentacles). Arms and tentacles bear suckers and/or hooks, which are powerful tools to seize prey. The mouth, at the interior base of the arm crown, has a pair of chitinous jaws (the beaks) and, as in other molluscs, a chitinous tongue-like radula (band of teeth).

The ancestral mollusc shell is reduced to a rigid structure composed of chitin, the gladius or pen, sometimes quite thin and flexible.

The loss of the external shell allowed the development of a powerful muscular mantle that became the main locomotory organ for fast swimming, via water jettisoned from the funnel. The funnel (also known as siphon, an archaic term correctly applied to some other molluscs, but not to modern, extant cephalopods) is a unique, multifunctional, muscular structure that aids in respiration and expulsion of materials, in addition to locomotion. Oxygenated water is drawn through the mantle opening around the head (neck) into the mantle cavity, where it bathes the gills for respiration. Muscular mantle contraction expels the deoxygenated water from the mantle cavity through the ventrally located funnel. The discharge jet serves to eliminate nephridial and digestive wastes, as well as to complete the respiratory cycle and for locomotion. Female reproductive products (eggs, egg masses) also are discharged through the funnel. Squids produce ink, a dark, viscous fluid also expelled through the funnel. The ink may take the form of a mucoidal 'pseudomorph' (false body) to decoy potential predators, or of a cloud to obscure the escaping cephalopod.

One pair of gills (ctenidia) is present, for respiration, i.e. to extract the oxygen from the water. Squids may use anerobic muscle layers, and cutaneous respiration also occurs.

The circulatory system

The circulatory system is distinctive within the Mollusca. It is a closed system (blood contained within vessels), similar in many respects to that of vertebrates, that fulfills the demand for the more efficient circulation required by an active locomotory system. The system is composed of a principal, or systemic, heart, two branchial hearts and developed arterial, venous and capillary systems that supply blood to the muscles and organs. The oxygenated blood passes from the gills through the efferent branchial vessels to the systemic heart, where it is expelled from the ventricle through three aortas: the cephalic or dorsal aorta, which supplies the head and the anterior part of the gut; the posterior, minor or abdominal aorta that supplies the mantle and fins along with the posterior part of the gut and the funnel; and the gonadal aorta that develops gradually with sexual maturation of the animal. The blood is collected through sinuses and capillaries into the veins, through which it passes to the branchial hearts that pump it through the filaments of the gills. The circulating respiratory pigment used for oxygen transport is copper-containing haemocyanin, a system of rather lower efficiency than the iron-containing haemoglobin of vertebrates. Blood sinuses in living squids are much reduced and replaced functionally by muscles. The circulatory system therefore has to work against the peripheral muscle-induced pressure, which increases with increasing activity (maximum during jet-swimming). It also has to cope with the resistance of the small diameter of the final capillary blood vessels, and the low oxygen carrying capacity of the blood (less than 4.5% by volume). In spite of these limitations, the system has other functional modifications (see for example Wells and Smith, 1987; Martin and Voight, 1987) that achieve the capacity to deliver oxygen at a rate comparable to that of active fishes, enabling squids to accomplish extraordinary swimming, attack and escape performances.

The excretory system

The excretory system also differs markedly from that of other molluscs and, along with the closed circulatory system and the branchial circulation, enables unique relationships between blood and the final secretion, the urine. The excretory system consists basically of the renal sac with the renal appendages (organs comparable to vertebrate kidneys), the pericardial glands, the branchial hearts and the gills. Squids are ammoniotelic, whereby ammonium ions are continuously released by the gill epithelium and by renal appendages into the surrounding water. Ammonium ions are used by buoyant squids to replace denser chloride ions in fluids in the coelom and in the body tissues. Because this solution is less dense (and hence more buoyant) than seawater, it provides lift for neutral or positive buoyancy.

The nervous system

The nervous system is highly developed, with a large brain and peripheral connections, contrasting with the original molluscan circumesophageal nerve ring. Among its most remarkable features is the giant fibre system that connects the central nervous system with the mantle muscles. This system consists of three orders of cells and fibres and ensures the immediate and simultaneous contraction of mantle, fins and retractor muscles of both sides, rather than an anterior to posterior sequential contraction that would be counter-productive for water movement (expulsion). Also remarkable is the eye development of squids, for which vision plays a major role in life. Their eyes are large, have a design generally similar to that of fishes and other vertebrates (e.g. a lens focuses images on the retina), and all the available evidence suggests that the ocular/visual performance is comparable to that of vertebrates. Squids also have developed a system to keep the focused image stationary on the retina while the animal turns, by moving the eyes in coordination with the head/body movement. This is extremely important for hunters that rely on sight, and it is accomplished by connections of the eye muscles with the statocysts, a bilateral mechanism similar to the vestibulo-optic system of fishes. The statocyst system provides squids with information on their orientation, as well as changes in position and direction of movement. It is a highly developed system that consists of two separate cavities located bilaterally in the cartilaginous skull, posteroventral to the brain. The statocysts contain nervous cells and receptors differentiated to detect both linear acceleration, with the aid of calcareous stones called statoliths, and angular acceleration. Some squids also have extra-ocular photoreceptors (photosensitive vesicles) about which little is known; in mesopelagic squids they appear to monitor light intensity in order to enable the animals to match their counter-illumination with the ambient light with their own photophores (light-producing organs). Squids are provided with numerous mechano- and chemoreceptors and recent evidence indicates that in some species, e.g. ***Loligo vulgaris***, ciliate cells form lines in several parts of the body, a system analogous to the lateral-line system in fishes.

Squids are able to change colour by using a complex system of chromatophores under nervous control. The chromatophores are pigment-filled sacs present in the skin, and capable of remarkable expansion and contraction. This system responds virtually instantaneously to contemporary situations in the environment, and it is critical for survival. Squid species also have iridocytes (shiny, reflective platelets) in the skin. Squids' behaviour includes rapid changes in overall colour and colour pattern and many deep-sea forms camouflage themselves by producing bioluminescent light from photophores which eliminate their silhouettes against the down-welling sunlight in the dimly-lit mid-depths.

Locomotion

Locomotion is achieved by a combination of jet propulsion and flapping or undulating the fins on the mantle. The fins on the mantle also provide balance and steering during jet propulsion. Many families of midwater squids have evolved to 'low energy life styles' and achieve neutral buoyancy by producing and storing in tissues or in different organs substances/elements with specific properties, such as oils or solutions of ammonium ions. This capability enables squids to inhabit open water, even in the great depths in the ocean, the greatest volume of living space on earth.

Feeding

Squids are voracious, active predators that feed upon crustaceans, fishes and other cephalopods. The speed of squids, their high mobility and powerful visual systems, along with strongly-muscled arms and tentacles, both equipped with suckers and/or hooks, make them extremely efficient hunters. A common hunting technique involves extremely rapid shooting forward of the tentacles to capture the prey, while in some oegopsid squids the tentacles may be used like long, sucker-covered fishing lures. The captured prey is brought to the mouth and killed by bites of the strong, chitinous beaks, equipped with powerful muscles. Digestion is rapid and efficient and squid metabolism is essentially proteinic: there is little or no digestion/assimilation of carbohydrates and lipids. Food conversion is highly efficient but such active animals like squids can eat from 3 to 15% of their body weight each day.

Reproduction

Squids are dioecious (separate sexes) and many species, though not all, exhibit external sexual dimorphism, either in morphological or morphometric differences. Females frequently are larger than males and males of most species possess one, occasionally two, modified arm(s) (the hectocotylus) for transferring spermatophores to females during mating. The males of some species also exhibit modifications to other arms, in addition to the hectocotylus. The hectocotylus may be simple or complex and can consist of modified suckers, papillae, membranes, ridges and grooves, flaps. The one or two "nuptual" limbs function to transfer the spermatophores (tubular sperm packets) from the male's reproductive tract to an implantation site on the female. The spermatophores may be implanted inside the mantle cavity (where they may penetrate the ovary), into the oviducts themselves, around the mantle opening on the neck, on the head, in a pocket under the eye, around the mouth or in other locations. Females of a few species also develop gender-specific structures (e.g. arm-tip photophores) when mature.

Mating often is preceded or accompanied by courtship behaviour that involves striking chromatophore patterns and display.

Copulatory behaviour varies significantly among species, in colour and textural display, proximity of male and female, duration of display and spermatophore transfer, and the location of implantation of the spermatophores on the female.

The gonads form a single mass at the posterior end of the mantle cavity, and female gonoducts may be paired (in oegopsids) or single, as in other squids. The reproductive systems are highly complex structures with ducts, glands and storage organs. Female squids have nidamental glands and loliginids have accessory nidamental glands, as well. Spermatophores are produced in the multi-unit spermatophoric gland and stored in the Needham's sac, from which they are released through the terminal part of the duct, the "penis". This term is not strictly accurate, because the spermatophores are passed to, or taken by, the hectocotylized arm(s), which in turn transfer(s) the spermatophore(s) to the female. The number and size of spermatophores vary greatly, depending on the species and group (for reviews on spermatophore structures and function see Mann *et al*., 1966, 1970; Mann, 1984; Nigmatullin *et al*., 2003). Once in contact with seawater, the so called 'spermatophoric reaction' begins. The spermatophores evert, with the resultant extrusion of the sperm packet caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher. The resulting extruded sperm packet is named spermatangium (or sperm bulb or body). Sperm are able to survive several months once stored in the female, at least in some species, and fertilization of mature ova may take place either in the ovary, the mantle cavity or the arm cone formed by the outstretched arms while the eggs are laid. Fertilized eggs are embedded in one or more layers of protective coatings produced by the nidamental glands and generally are laid as egg masses. Egg masses may be benthic or pelagic.

Eggs of neritic, inshore squids, except in ***Sepioteuthis***, generally are very small (only a few millimetres in diameter) and frequently are laid in finger-like pods each containing from a few to several hundred eggs. Deposited in multi-finger masses (sometimes called 'sea mops'), these eggs are attached to rocks, shells or other hard substrates on the bottom in shallow waters. Many oceanic squids lay their eggs into large sausage-shaped or spherical gelatinous masses containing tens or even hundreds of thousands of eggs that drift submerged in the open sea.

Growth and life history

Development of squid embryos is direct, without true metamorphic stages. However, hatchlings undergo gradual changes in proportions during development and the young of some species differ from the adults. Thus, the term 'paralarva' has been introduced for these early stages of cephalopods that differ morphologically and ecologically from older stages. The paralarvae of many deep-sea species of squids occur in the upper 100 m of the open ocean; then they exhibit an ontogenetic descent, gradually descending to deeper depths with increasing size until the adult depth is attained. Time of embryonic development varies widely, from a few days to many months, depending on the species and the temperature conditions. Hatching may occur synchronously from a single clutch or be extended over a period of 2 or 3 weeks.

In spite of the large number of studies and research carried out on squids, especially in recent decades, the life history of many species still is unknown, and our knowledge of the life cycles of the members of this interesting group remains fragmentary. Information comes from studies in the field as well as from observations in the laboratory. However, little is known of life history for species that are not targets of regular fisheries, and only a few squid species have been reared successfully in the laboratory. Studies and monitoring of growth are complicated by the high variability in individual growth rates. This makes it difficult to apply conventional methods, e.g. length frequency analysis, used for more traditional resources such as fishes and crustaceans. Determination of age also is difficult, because squids have few hard structures that show daily marks (rings) that enable direct estimates of age. In the last 20 years, progress has been made on the study and analysis of squid statoliths that has resulted in an increased knowledge of age. This has led to changes in our conceptions about the physiology and ecology of many species, but more research is required before a full understanding is achieved (see Jereb *et al*., 1991; Okutani *et al*., 1993; Jackson, 1994a, Lipinski and Durholtz, 1994 for reviews and discussions). Principal results obtained from the research generally confirm a very high growth rate in squids, comparable to that of the fastest-growing fishes.

The life expectancy of most squids appears to range from a few months to one or two years, and many small oceanic squids, such as pyroteuthids may complete their life cycles in less than six months. Recent evidence, however, suggests that larger species of squids, for example the giant squid (***Architeuthis*** spp.), as well as those that live in coldest habitats, may live for several years.

A general consensus exists that spawning is a terminal event, in spite of the high variability in the duration of individual spawning periods (5 to 50% of ontogenesis; Nigmatullin, 2002b) as well as the type of spawning, e.g. from one-time, total spawning, to prolonged, intermittent, multiple batches (see Rocha *et al*., 2001 for a review). All squids die after their spawning period.

Systematics status

The total number of living species of squids that currently are recognized is more than 300; 295 are listed in the present volume. The status of the systematics of squids has changed in the last 30 years, as research and associated scientific discussions have increased substantially. However, phylogenetic relationships among many families remain uncertain, and new species are described fairly frequently as new habitats are explored and as families are gradually better-understood.

Conclusions

Squids are important experimental animals in biomedical research with direct applications to human physiology and neurology, for example. Because of their highly developed brains and sensory organs, they are valuable in behavioural and comparative neuro-anatomical studies. In addition, the extremely large single nerve axons of some squids, the largest in the animal kingdom, are used extensively in neuro-physiological research.

The bite of squid can be painful at the least to humans, or secondarily infected, or, rarely, lethal. A documented threat by squids to humans is from the large ommastrephid squid, ***Dosidicus gigas***, which forms large aggressive schools that are known to have attacked fishermen that have fallen in the water, causing several confirmed deaths. Scuba divers also have been attacked. Therefore, squids must be handled carefully.

1.4 Interest to Fishery and Role in the Ecosystem

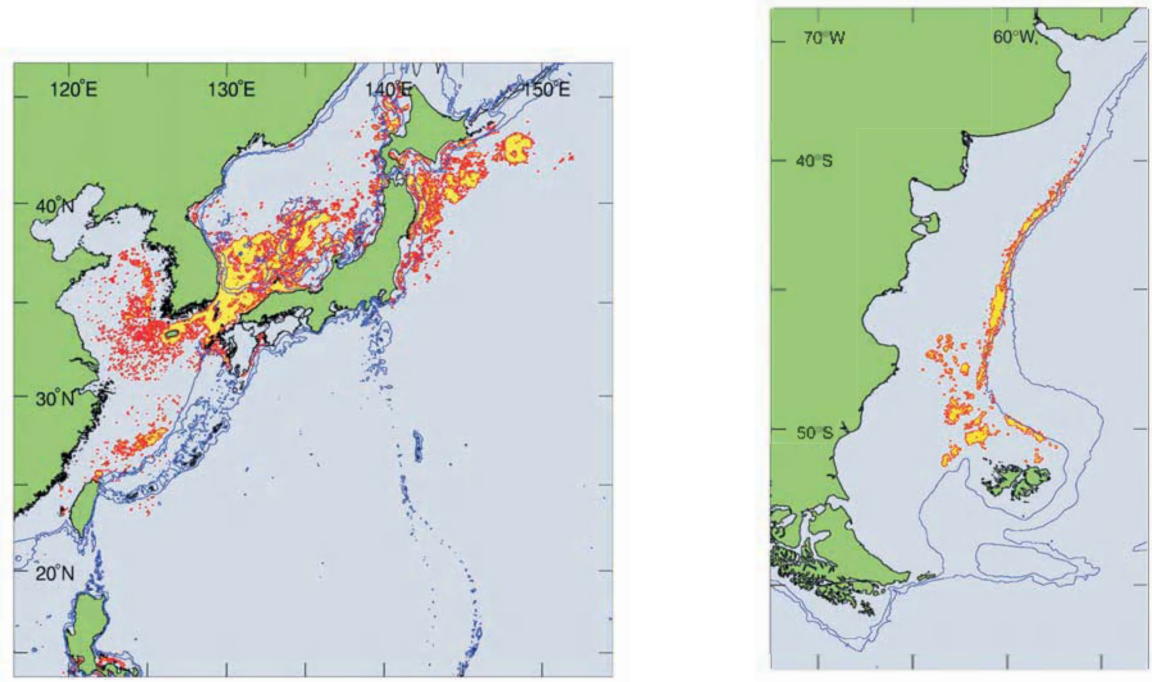
Squids are an important resource for human consumption. Of the total cephalopod catch of over 4 million tonnes reported for 2007 by FAO statistics (FAO, 2009), over 3 million tonnes were squids, i.e. about 74%. The impressive increase in squid production during the last 25 years is due mainly to the 'discovery' and increasing exploitation of squid resources in the southwest Atlantic, principally for ***Illex argentinus***, as well as an increase in the production of other major squid target species, mainly ***Todarodes pacificus*** in the northwest Pacific and ***Dosidicus gigas*** in the eastern Pacific. ***Illex argentinus*** catches exceeded 1 million tonnes in 1999, a record peak which placed this species at the eleventh position in value of the total world marine-species production for that year. Fluctuations in squid catches are responsible for the major fluctuations in total cephalopod landings, changes usually related to a combination of environmental, marketing and/or political causes.

About 30% of world squid catches is taken in the southwest Atlantic; followed by the eastern Pacific, with about 20%, then the Northwest Pacific (about 13%); however, smaller-scale fishing activities in other areas also developed consistently in the last decades (see, for example, the Indian Ocean fisheries).

Numerous fishing techniques and methods to capture squids have been developed over time. These were extensively reviewed, for example, by Rathjen (1984, 1992 [1991]) and Roper and Rathjen (1991). They include lures, jigs, lampara nets, midwater trawls and otter trawls.

Jigging is the most widely used method, which accounts for almost half of the world squid catch, primarily ommastrephids, but also a few loliginids. This technique is employed primarily at night, when many species of squids are attracted to the fishing vessel by lights. **Figure 3** shows the distribution of the world's light fishery for some of the most important squid species. Jigs, which feature numerous, variously-arranged, barbless hooks (Plate I, 6), are lowered and retrieved by jigging machines that simulate the constant swimming behaviour of natural prey, inducing the squids to attack them. While simple hand-jigging machines are still used in small-scale, artisanal fisheries, large modern vessels for industrial fishing activities are equipped with scores of automated, computer-controlled jigging machines, each capable of catching several tonnes per night (Plate I, 1 and 5).

Trawling is the secondmost productive fishery method to catch squids (Plate I, 2). Formerly, almost all squids were caught as bycatch in trawl fisheries for finfishes and shrimps. However, the amount of squids taken as bycatch in bottom trawls for finfish fisheries drove increasing attention to the resource by the 1980s; this led to the development of the (principally) midwater trawl fisheries specifically targeting squids, particularly the South Atlantic/Sub-Antarctic fishery for ***Illex argentinus***. Trawling is a very efficient technique to catch species, but soft-bodied animals like cephalopods are often damaged by the other species in the catch, particularly in benthic and epibenthic otter trawls. Even in fisheries in which squid-specific trawling occurs, the huge catches of squids per tow often result in crushed and damaged product. Consequently, trawled squid product generally is less valuable than jig-caught squids. However, modern oceanic trawlers can process on board many metric tonnes of cephalopods per day, which helps insure a high-quality product. Bottom trawling can be very dangerous for benthic habitats because of the physical damage it causes to the seabed and associated fauna and because of its lack of selectivity. Consequently, less intense exploitation by this traditional fishing technique and an approach toward diversification of methods and redistribution of the fisheries through different areas were encouraged and still are highly recommended, especially in situations where small-scale fisheries still exist and new, more efficient methods can be implemented. Nearshore, neritic squids frequently are caught by purse seines, lift nets, beach seines, etc.



a) Kuroshio Current Province
(*Todarodes pacificus* and *Ommastrephes bartramii*)

b) Southwest Atlantic Province
(*Illex argentinus*)

Fig. 3 Distribution of the world's light fisheries for ommastrephids (illustrations based on night-time satellite imagery) (from Rodhouse *et al*., 2001)

The utilization of squids for human consumption is extensive and diverse. Products range from fresh food, eaten raw as 'sashimi' in Japan and, in recent years, worldwide, and fresh-cooked, as well as various types of processed product (dried, canned, frozen, reduced to meal, etc.). The high protein and low fat content of cephalopods make them an important and healthy element in the human diet. Considering the present level of exploitation of the commercially-fished squid populations, a further increase in such fishery production is likely to occur, first by expansion of the fisheries into the less-fished regions of the oceans, e.g. the Southern Ocean, probably the 'last frontier' in the field of marine fisheries. There, a standing stock of squid biomass as high as 100 million tonnes was estimated by scientists, based on an estimate of 30 million tonnes consumed by vertebrate predators (see Rodhouse *et al*., 1994 for details), even though squid captures are rarely highly successful. Therefore, a priority for the future research in the field of Antarctic cephalopod biology will be to assess the squid biomass there, quantitatively and qualitatively, with the objective of determining and developing a sustainable fishery production. However, polar squids probably are longer living and slower growing than species currently harvested. Therefore, caution must be exercised in assumptions and decisions for management of polar squid fisheries.

In the future, it is likely that attention will be focused on finding other species and families to replace fish stocks that become severely reduced by overfishing. Even though clear evidence reveals the existence of large cephalopod resources available for exploitation in the open oceans, based on the estimated consumption by predators (see Clarke, 1996b; Piatkowski *et al*., 2001a for reviews), many oceanic squids are distasteful for human consumption as their tissues have a high ammonium content. Research is being carried out on how to remove this factor on a commercial scale, but results will take time and catches will need to be processed before marketing and utilization. A number of ommastrephid squids that lack ammonium are considered to be underexploited. These include: ***Sthenoteuthis pteropus***, ***Ommastrephes bartramii***, ***Martialia hyadesi***, ***Todarodes sagittatus***, ***Sthenoteuthis oualaniensis***, ***Nototodarus philippinensis***, ***Dosidicus gigas***, and the circumpolar, sub-Antarctic ***Todarodes filippovae***. Exploitation of these species would provide large tonnages of high quality cephalopods and would require only minor development in catching techniques. However, it will be necessary to determine where these species congregate for feeding and spawning activities. An analysis of biomass, production and potential catch for the Ommastrephidae species is presented in Nigmatullin (2004).

Although a number of other oceanic squid families have large populations and high quality flesh, they are not currently exploited on a commercial scale except for a few seasonal fisheries. These include members of the families Thysanoteuthidae, Gonatidae and Pholidoteuthidae, for example. Increased exploitation of these groups, however, would also require some research and development of catching techniques. Commercial exploitation of the cosmopolitan family Histioteuthidae also could be considered, since at least one large commercial-level catch has been made in the North Atlantic (see Okutani, personal communication, *in* Clarke, 1996a). However, the increased exploitation of these oceanic squid species might have unpredictable, far-reaching negative effects on the mesopelagic ecosystem. Therefore, great caution must be exercised in developing this kind of fishery.

Almost all of our knowledge of the general biology of cephalopods, in fact, is limited to the shelf-living species, as well as to those ommastrephids that move onto the shelf at certain seasons. These represent only about 15% of all cephalopod species. Even so, many gaps still exist in our knowledge about their life cycles, especially as far as the relationships among species are concerned (e.g. prey-predator balances). Some populations of harvested species have shown sudden, occasionally catastrophic, declines before adequate biological data could be gathered and analysed. Squid stocks experienced true collapses at least in two well-known and documented cases. These were the northwest Pacific ***Todarodes pacificus*** fishery failure in the 1970s and the northwest Atlantic ***Illex illecebrosus*** fishery collapse in the 1980s. While the ***T. pacificus*** fishery has recovered, the ***I. illecebrosus*** fishery has remained insignificant. These collapses are thought to have occurred mainly as a consequence of temporarily unfavourable environmental conditions or actual long-term environmental changes, probably aggravated by heavy fishing pressure (Dawe and Warren, 1993).

A significant challenge thus exists to deepen our knowledge and learn the details of distribution, life history and biology of exploited species in order to allow rational utilization of the stocks. The necessity for research as a key factor towards attaining this goal has been stressed by many authors (e.g. Lipinski *et al*., 1998b) and it is especially important in the fields of life-cycle clarification, stock structure and genetics, role in the food web and interactions with the environment. The last topic seems of particular interest within the more general context of global climate/environmental changes, since the unusual biological characteristics and short life cycles of squids are strongly linked to immediate, temporal environmental circumstances. Therefore, squids are potentially very good 'indicator species' to predict or reflect changes in environmental conditions, both locally and on a broader scale (see Pierce *et al*., 2008b for a review).

Perhaps even more significant is the challenge that exists for future exploitation of new species or populations. The role of squids in the ecosystem, in fact, is more complex than it was thought to be only a few decades ago. Squids can be considered subdominant predators that tend to increase in biomass when other species, particularly their predators and competitors for food, become depleted, as a result of a combination of heavy or excessive fishing, other human impacts, oceanographic fluctuations and competition for food (see Caddy, 1983, and Caddy and Rodhouse, 1998 for a detailed analysis of the transition from finfish-targeted fisheries to cephalopod-targeted fisheries). In turn, squids are major food items in the diets of innumerable species of fishes, toothed whales (e.g. sperm whales, beaked whales, dolphins, porpoises), pinnipeds (seals, sea lions) and seabirds (penguins, petrels, albatrosses).

Muscular squids derive their energy from crustaceans, fishes and other cephalopods. At the same time, they are a very efficient food storage for the large, oceanic predators, by rapidly converting oceanic resources into high energy food. On the other hand, neutrally buoyant ammoniacal squids, which probably greatly outnumber the muscular squids in biomass, also provide food to many of the same predators, but not over the continental shelf and with consistently lower energy per unit body mass. We know virtually nothing about the details of feeding, growth, life cycles, periodicities, distribution and spawning in ammoniacal species.

In spite of our relatively incomplete knowledge, it is now clear that squids are a dominant component within marine ecosystems and that their abundance ultimately may influence the abundance of their predator and prey populations. Studies of the effects of consumption of important pelagic squids and fishes by predatory fishes on the northeastern shelf of the United States (Overholtz *et al*., 2000), concluded that changes in predator abundance may have important implications for the long-term fishery yields of pelagic species. Consistent with our present knowledge is the concept that removal of squids through fisheries would have a continuous impact on the environment: populations of small midwater fishes would increase, while top predators like cetaceans, seabirds, seals and even some fish populations, would decrease.

Taking into consideration these factors, increasing effort should be focused on improving scientific knowledge of this group. Squid catches need increased monitoring, especially in those areas of major environmental fluctuations and where fisheries management is complicated by multiple countries exploiting the same resource. Cooperation, collaboration and commitment are required to better understand these important and fascinating animals.

1. 5 Illustrated Glossary of Technical Terms and Measurements

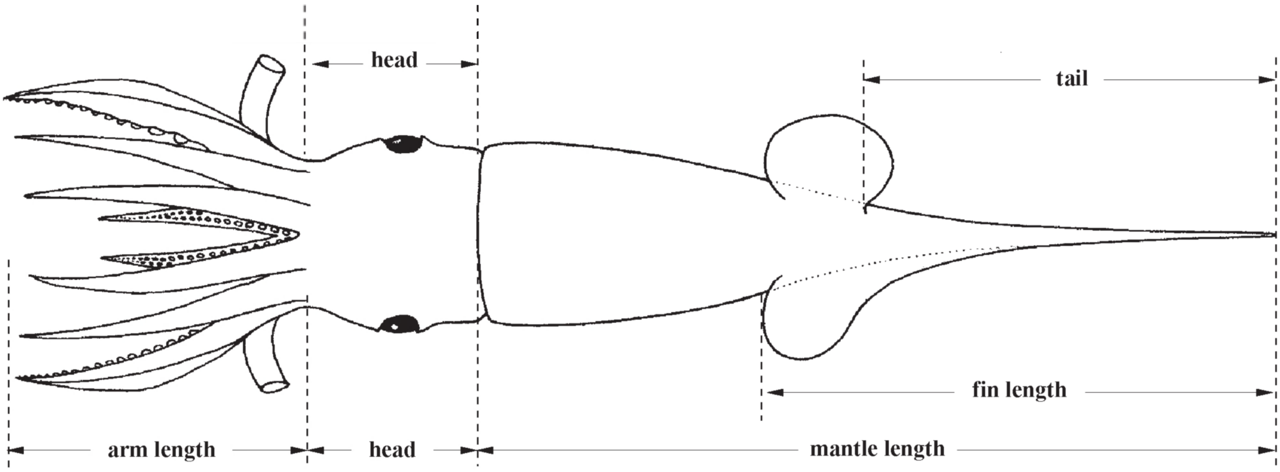


Fig. 4 Schematic illustration of a squid

Aboral – Away from or opposite to the mouth.

Abyssal – The great depths of the ocean: from 2 000 to 6 000 m.

Accessory nidamental glands – Glands of unknown function; consist of tubules containing symbiotic bacteria. Found in all **decapodiformes** except oegopsid squids.

Adult – A female that has mature eggs (these frequently are stored in the oviducts), or a male that has produced spermatophores (these are stored in Needham's sac).

Afferent blood vessel – Artery vessel carrying blood toward an organ.

Afferent nerve – Nerve carrying impulses toward the brain or specific ganglia.

Anal flaps – A pair of fleshy papillae involved in directing releases of ink, 1 flap situated at each side of the anus (Fig. 5).

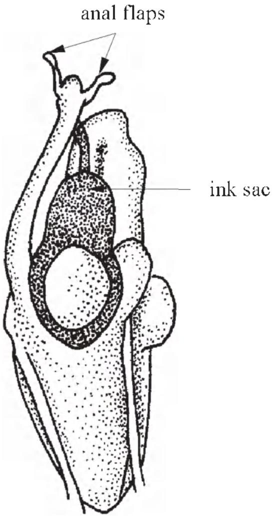


Fig. 5 Terminal portion of the digestive track

Anal pads – Ovoid pads of unknown function, apparently glandular, one located on each side of the anus in some squids (e.g. bobtail squids).

Anterior – Toward the head-end or toward the arm-tips of cephalopods.

Anterior salivary glands – Glands on or in the buccal mass that aid in preliminary digestion.

Anterior suboesophageal mass – See **Brachial lobe**.

Antitragus – Knob that projects inward from the posterior surface of the central depression in the funnel-locking apparatus of some squids (Fig. 6).

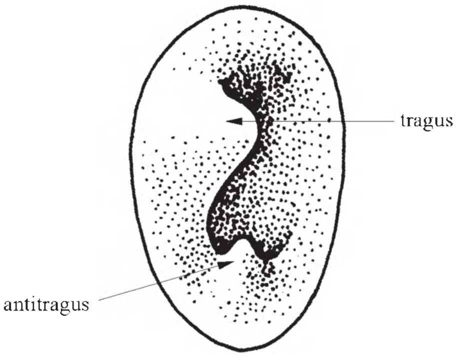


Fig. 6 Funnel-locking cartilage

Anus – Terminal opening of the digestive tract, in the anterior mantle cavity, sometimes extending to inside the funnel, through which digestive waste products, as well as ink, are expelled.

Apomorphic – Derived from a more ancestral condition. Loosely considered the 'advanced' condition.

Arm – One of the circumoral appendages of cephalopods. Arms are designated by the numbers I to IV, starting with I as the dorsal (or upper) pair. In squids each appendage of the fourth ancestral pair is modified to form a tentacle.

Arm formula – Comparative length of the 4 pairs of arms expressed numerically in decreasing order: the largest arm is indicated first and the shortest last, e.g. IV>III>II>I. If IV>III=II>I, then arm IV is the largest, followed by arm III which is the same size as arm II and both are larger than arm I.

Armature – The grappling structures of the arms and tentacular clubs, including suckers and/or hooks.

Bathypelagic – The deep midwater region of the ocean.

Beak – One of the 2 chitinous jaws of squids bound in powerful muscles. The dorsal beak is referred to as the 'upper' beak and it inserts within the 'lower' (ventral) beak to tear tissue with a scissors-like cutting action.

Belemnoidea – A fossil group of cephalopods that is thought to be the sister group of the Coleoidea. Belemnoids are distinguished by the presence of hook-like structures on the arms rather than suckers.

Benthopelagic – A free-swimming animal that lives just above the ocean floor but rarely rests on the ocean floor.

Bilateral symmetry – The symmetry exhibited by an organism or an organ if only one plane can divide the animal structure into 2 halves that are mirror images of each other.

Bioluminescence – The production of light by living organisms, sometimes called 'living light'. The light is produced through a chemical reaction that generally takes place in complex organs called photophores or light organs.

Brachial – Pertaining to the arms.

Brachial crown – The combination of arms and tentacles that surround the mouth.

Brachial lobe (of the brain) – The anteriormost part of the brain located ventral to the oesophagus. The large axial nerve cords that run down the centres of the arms connect to this lobe. The proper name is 'anterior suboesophageal mass'.

Brachial photophore – Photophore located on the arms.

Brachial pillar – A narrow, elongate anterior region on the paralarval or juvenile head of some families, between the eyes and the base of the brachial crown; especially well developed in young cranchiid squids.

Brain – Medial portion of the central nervous system that includes the suboesophageal and supraoesophageal masses but generally does not include the large optic lobes.

Branchial – Pertaining to the gills.

Branchial canal – A large opening at the base of each gill lamella and between the primary afferent and efferent blood vessels of the gill.

Branchial gland – Elongate or spheroidal gland adjacent and parallel to the gill attachment to the mantle wall.

Branchial heart – A gland at the base of the gill through which afferent blood is pumped to the gill. It also is the site of hemocyanin (the blood respiratory pigment) synthesis.

Brooding – Incubation of eggs by the female. A characteristic feature of incirrate octopods, but also found in some squids (e.g. **Gonatidae**).

Buccal – Pertaining to the mouth.

Buccal connective – Thin muscular band that attaches the buccal support of the buccal membrane to the base of the adjacent arm. The position of attachment of the connective on the fourth arms was recognized in the early twentieth century as an important character for phylogenetic relationships among **decapodiformes** (Fig. 7).

Buccal crown – Umbrella-like structure that surrounds the mouth and in turn is enveloped by the brachial crown. It consists of buccal supports and the buccal membrane.

Buccal lappet – A small, subtriangular flap at the tip of each buccal support of the buccal membrane; thought to be homologous with the inner ring of tentacles that surrounds the mouth of nautiluses. May bear suckers (Fig. 7).

Buccal mass – Muscular bulb at the anteriormost part of the digestive system that consists of the mouth, beaks, radula, muscles and pairs of salivary glands.

Buccal membrane – The muscular membrane that encircles the mouth like an umbrella (Fig. 7). It connects the buccal supports to form the buccal crown. The pigmentation of the buccal membrane often differs from that of the adjacent oral surfaces of the arms.

Buccal membrane connectives – See **Buccal connective** (Fig. 7).

Buccal suckers – Small suckers on the buccal lappets/ membrane of some species (Fig. 7).

Buccal support – Muscular rod fused to buccal membrane as supporting rib; 6 to 8 in number (Fig. 7).

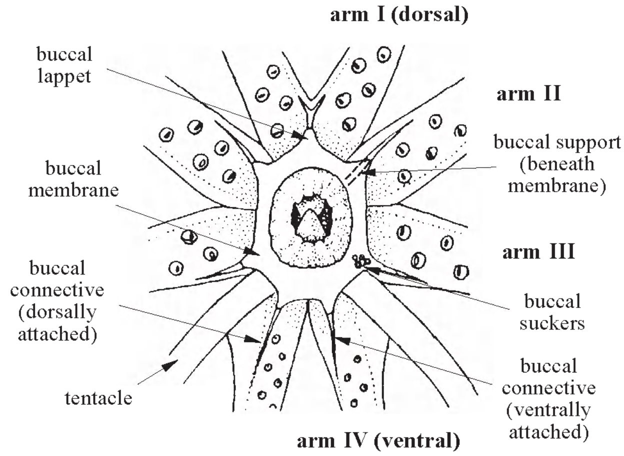


Fig. 7 Buccal anatomy of decapods

Buoyancy (neutral, positive, negative) – The tendency to float in seawater. A neutrally buoyant object does not rise or sink but maintains its position in the water; a positively buoyant object will rise and a negatively buoyant object will sink.

Caecal sac – The sac-like, thin-walled posterior portion of the caecum in the digestive tract that lacks the internal, ciliated leaflets characteristic of the anterior portion of the caecum.

Caecum – Region of the digestive tract of all cephalopods between the stomach and intestine. It is the primary site of food absorption.

Calcified – Chalky, calcareous material of calcium salts (calcium carbonate), formed by deposition.

Cambrian period – Oldest period of the modern geological timescale.

Carpal cluster (= Carpal pad) – An usually distinct group of suckers and knobs on the carpus of the tentacular club (Fig. 8).

Carpal knobs – Small, rounded, hemispherical, muscular protuberances on the carpus to which carpal suckers from the opposite club adhere during the locking of the clubs (Fig. 8).

Carpal-locking apparatus – Arrangement of suckers and matching knobs on the carpal region of the tentacular club that permits the 2 clubs to be locked together (Fig. 8).

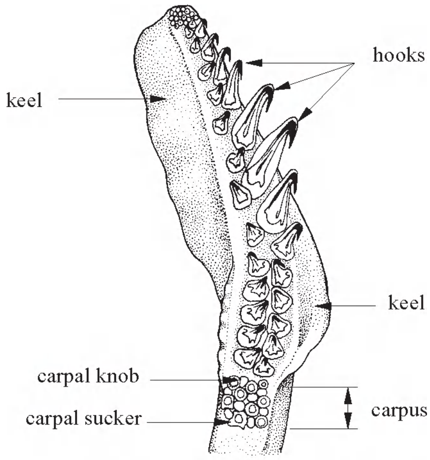


Fig. 8 Tentacular club of squid

Carpal suckers – Small suckers on the carpus of the club that adhere to the carpal knobs on the opposite carpus during the locking of the clubs (Fig. 8).

Carpus – The proximal zone of small suckers and knobs on the base of the tentacular club in some families (Fig. 8).

Cartilaginous structures or "scales" – Cartilage-like structures in the skin of certain squids; may be overlapping and scale-like, or multifaceted platelets, knobs or papillae (Fig. 9).

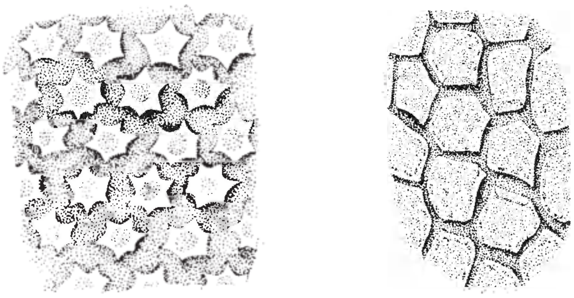


Fig. 9 Two types of cartilagineous structures or "scales"

Cement body – Structure in the spermatophore that allows adhesion of the discharged spermatophore to a female (Fig. 29).

Cephalic cartilage – Cartilage-like tissue that envelops the posterior part of the brain of cephalopods and encompasses the statocysts. Anteriorly the cartilage thins and entwines with muscular tissue, which makes a well-defined limit difficult to distinguish. The cartilage has a large central foramen through which the oesophagus passes and minor foramina for nerves and blood vessels.

Cephalic vein – Large vein that drains blood from the head region; it lies along the ventral surface of the visceral sac, beside or dorsal to the intestine. The cephalic vein terminates by dividing into the 2 vena cavae, each of which passes through the 'kidney' (nephridium), the branchial heart and into the gill.

Cephalopoda – The class within the Mollusca, characterized by bilateral symmetry, internal 'shell' or absence of shell (except nautiluses), anterior head, appendages and funnel, posterior mantle, mantle cavity with organs, and shell and fins when present.

Character state – A particular condition of a taxonomic character. For example, the character 'sucker' may include the 2 states: sucker with a horny ring or sucker without a horny ring.

Chemotactile – Refers to chemical and touch sensitivity.

Chitin(ous) – A horny polysaccharide substance (fingernail-like) that forms the sucker rings, hooks and beaks.

Chorion – A tough secreted membrane that encapsules the egg.

Chromatophores – Pigment-filled muscular sacs in the skin under individual nervous control that collectively provide the background colour, colour patterns and colour dynamics (play) of cephalopods.

Circumoral appendages – The 8 arms plus the 2 tentacles. All arise from the head and encircle the mouth (Fig. 7).

Clade – A monophyletic group. That is, a group whose members share a closer common ancestor with one another than with members of any other group.

Coelom – An internal body cavity of mesodermal orgin that is lined by an epithelium. Cephalopods have 2 coeloms, the viscero-pericardial coelom and the nephridial coelom.

Collar – Muscular, flange-like structure that extends from the nuchal cartilage to the funnel; it forms a one-way valve that allows water to enter the mantle cavity but closes as the mantle contracts, thereby forcing exhalent water out through the funnel.

Cone, conus – The spoon-like, cup-like, spiked or simple conical posterior terminus of the gladius; homologous to the phragmacone of fossil squids (Fig. 10).

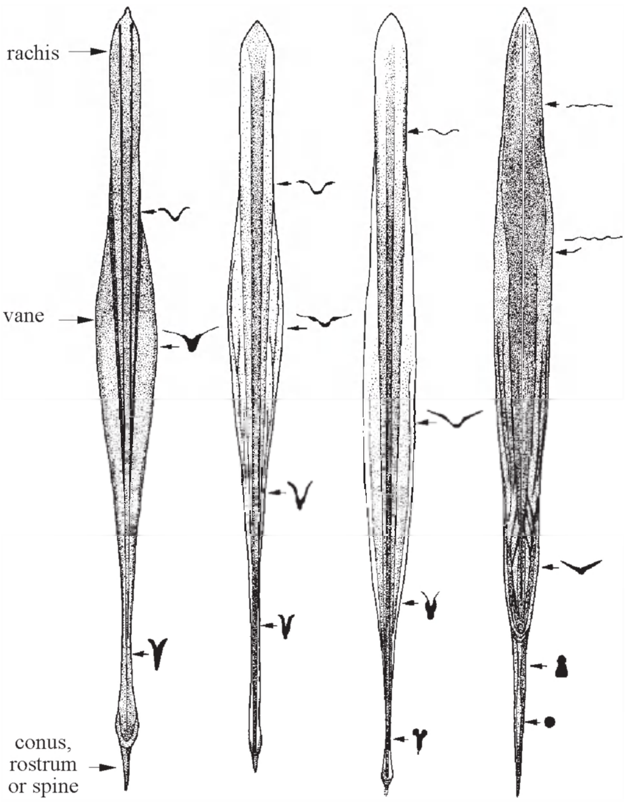


Fig. 10 Gladii of some squids

Conus field – The sides of the conus that continue anteriorly along the vanes of the gladius.

Cornea – Smooth, thin, turgid, transparent skin without muscles that covers the eyes to protect the eye lenses of myopsid squids (Fig. 11).

Counter illumination – The production of bioluminescent light by an animal to conceal its silhouette against a lighted background. The process can allow an animal to become virtually invisible under dim directional light.

Cretaceous – The last period of the Mesozoic Era.

Cusp – A point or projection on a tooth of the radula or on a cartilagenous tubercule in the skin.

Dactylus – The distal, terminal section of the tentacular club, often characterized by suckers of reduced size (Fig. 11).

Decapodiformes – Higher-level taxon that includes all 10-limbed cephalopods (Fig. 2). Within the Decapodiformes, typically, two higher taxa are recognized: the Sepioidea, which includes the Sepiidae, Idiosepiidae, Sepiolidae, Spirulidae and Sepiadariidae and the Teuthoidea, which includes Myopsid and Oegopsid squids. Because of the long history of referring to these cephalopods by the common name **'decapods'**, the latter is maintained as the common name for the **Decapodiformes**.

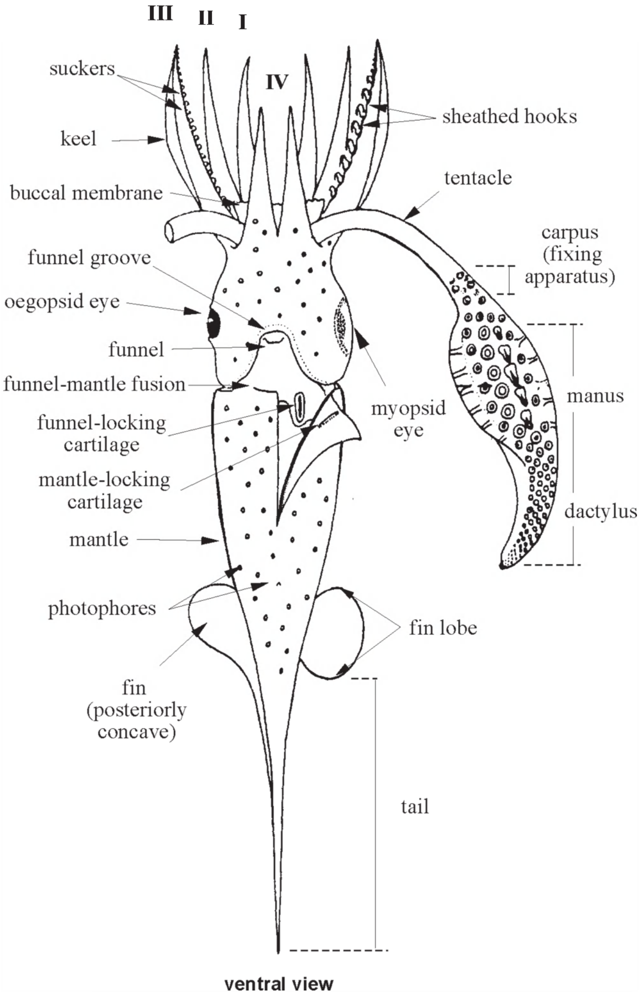


Fig. 11 A composite diagram illustrating basic squid features

Decapods – Common name for the **Decapodiformes**.

Demersal – Organisms that live close to the ocean floor.

Diel vertical migration – Vertical animal migration during twilight periods. Many mesopelagic animals migrate to shallow depths at sunset, where they spend the night feeding; then they descend at sunrise from near-surface waters to spend the day hiding at greater, darker depths. Some animals migrate vertically over 1 000 m, others migrate less than 100 m.

Digestive gland – Primary organ in cephalopods that secretes digestive enzymes. It is also important in absorption and excretion (Fig. 12).

Digestive gland duct appendages – Outpockets of the ducts leading from the digestive gland that are covered with glandular epithelium (Fig. 12).

Distal – Away from the central region of the body or point of origin; toward the peripheral parts (opposite of proximal).

Doratopsis – The peculiar paralarval stage that is characteristic of all members of the oegopsid squid family **Chiroteuthidae**.

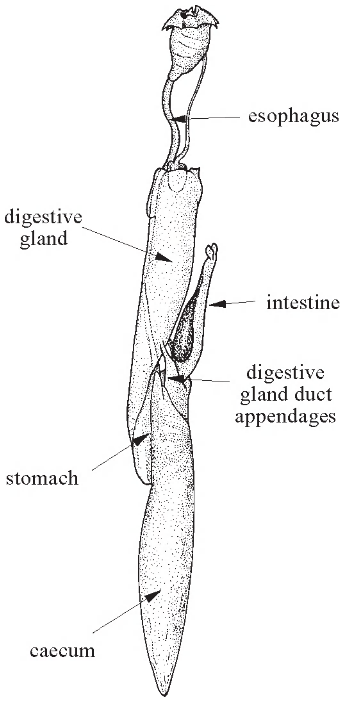


Fig. 12 Digestive system of squids
(after Bidder, 1966)

Dorsal – The uppermost or back surface of a cephalopod, opposite the ventral surface where the funnel is located (Fig. 13).

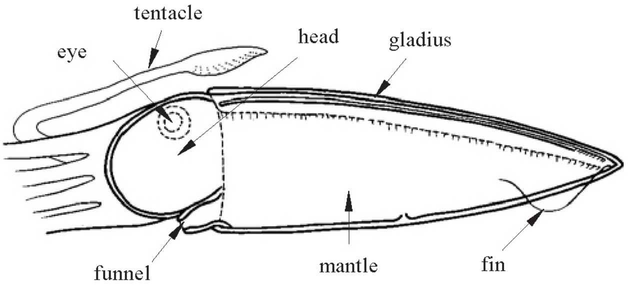


Fig. 13 Schematic lateral view of squid features

Efferent vein – Vein that carries blood away from the heart or an organ.

Efferent nerve – Nerve carrying impulses away from the brain or specific ganglia.

Egg mass – A large number of eggs encapsulated in a gelatinous matrix or a large number of such structures that are attached together. The pelagic egg mass of an oceanic squid can be a large, fragile, gelatinous ball that carries many thousands of eggs. In contrast, the egg mass of a neritic squid (loliginid) can be composed of hundreds of very tough, encapsulated eggs in strings, attached together at their bases and to the substrate.

Ejaculatory apparatus – Portion of the spermatophore involved in the vigorous extrusion of the sperm mass (Fig. 29).

Epipelagic zone – The uppermost pelagic zone of the ocean.

Epithelial pigmentation – The pigmentation contained in epithelial cells that are unable to change their shape in the absence of muscles and nerves. Colour in most cephalopods, however, is created by pigment granules that are contained in specialized organs, the chromatophores, that can change shape rapidly, by muscular action under nervous control (see **Chromatophores**).

Esophagus – See **Oesophagus**.

Exploitation rate (E) – When fishing mortality (F) and natural mortality (M) operate concurrently, the exploitation rate represents the fraction of dead animals due to the fishery (i.e. caught by the fishery), which is, F/Z where Z denotes the total (i.e. M+F) mortality rate.

Eye (position and size) – Eyes are the primary sensory organs of cephalopods; they usually are large and located one on each side of the head. However, some species have small eyes, eyes on stalks or telescopic eyes.

Eye pore (= orbital pore) – Small pore in the anterior edge of the corneal membrane which covers the eyes; present in most myopsid squids. The pore is the remnant of the large eye opening of oegopsids and allows fluid exchange between the lens and the exterior environment (Fig. 66).

Eyelid sinus (= optic sinus, = orbital sinus) – Indentation, often complex, of the anterior margin of the eyelid (Fig. 20).

Family – The taxon above the genus level, comprised of the most closely related genera.

Fin(s) – The pair of muscular flaps that arise along the dorsolateral surface of the mantle of squids; used for locomotion, steering and stabilization (Fig. 11).

Fin angle – The angle between the longitudinal axis of the mantle and the posterior border of one fin (Fig. 14).

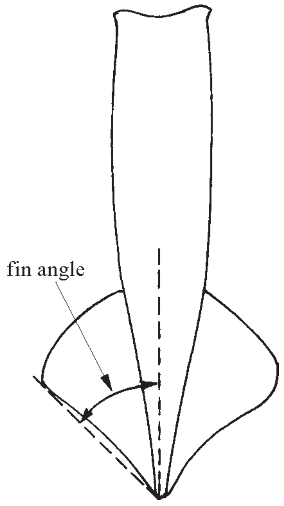


Fig. 14 Fin angle on squid

Fin attachment – A fin attaches to the mantle, to the opposite fin or some combination of these.

Fin cartilage – Cartilage associated with the fins of all fin-bearing cephalopods.

Fin length – Length from anterior lobe or anteriormost attachment of lobe to posteriormost attachment of fin to mantle or tail. Extremely long, spike-like tails usually do not include fin tissue.

Fin lobe – The portion of a fin that extends anteriorly from the fin's anterior point of attachment, or posteriorly from the fin's posterior point of attachment of the fin, to the mantle (Fig. 11). This often is called the 'free' lobe.

Fin position – Fins are located anterior to the termination of the muscular mantle (subterminal position) or mostly posterior to it (terminal position) or in an area of overlap between the two.

Fin shape – Fins are classified, somewhat arbitrarily, by their shape as sagittate, rhomboid, circular/elliptical, lanceolate, ear-shaped, ribbed, lobate or skirt-like.

Fixing apparatus – The mechanism of suckers and knobs on the carpal region of the tentacular club that permits the two clubs to be locked together during capture of prey (Figs 8 and 11) (see **Carpus**).

Foot – See **Molluscan foot**.

Foveola – Transverse, membranous fold of skin that forms a pocket in the anterior end of the funnel groove of some oegopsid squids (Fig. 15) (see **Side pockets**).

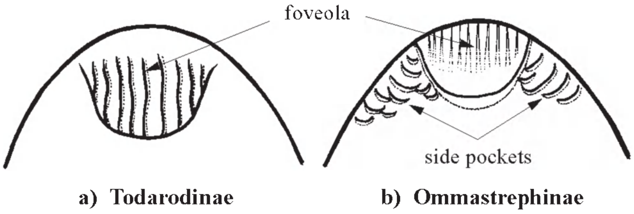


Fig. 15 Funnel groove

Funnel – The ventral, subconical tube through which water is expelled from the mantle cavity during locomotion and respiration (reproductive and waste products and the ink also pass through the funnel) (Figs 11 and 13). Archaic term: **siphon**.

Funnel adductor muscles – Muscles that support the lateral attachment of the funnel to the head.

Funnel groove – The depression in the posteroventral surface of the head in which lies the anterior portion of the funnel (Fig. 11).

Funnel-locking cartilage – The cartilaginous groove, pit, pocket or depression on each ventrolateral side of the posterior part of the funnel that joins with the mantle component to lock the funnel and mantle together during locomotion and respiration, so that water is expelled only through the funnel and not around the mantle opening (Figs 11 and 16) (see **Mantle-locking cartilage**).

Funnel-mantle locking apparatus – The structure composed by the funnel-locking cartilage and the mantle-locking cartilage.

Funnel organ – The glandular structure fused to the internal surface of the funnel, generally a dorsal inverted V-shaped component with opposed ventral oblong components in squids (Fig. 17).

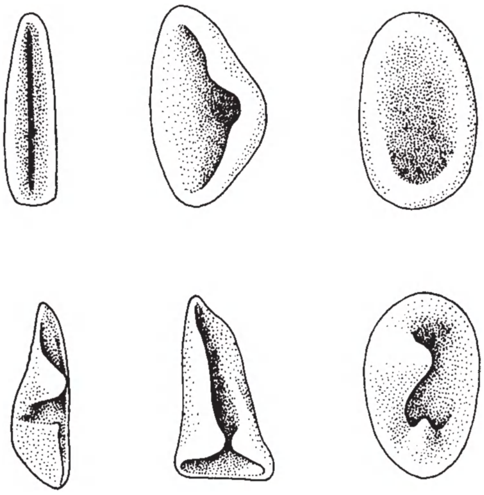


Fig. 16 Funnel-locking cartilage; examples of shapes and structures

Funnel-retractor muscles – Large muscles that attach to the posterior corners of the funnel and extend posteriorly to attach to the sides of the shell sac (generally near the base of the gills) or, in some species, insert on the interior mantle wall.

Funnel valve – The semilunar muscular flap in the dorsal inner surface near the distal opening of the funnel in some species (Fig. 17).

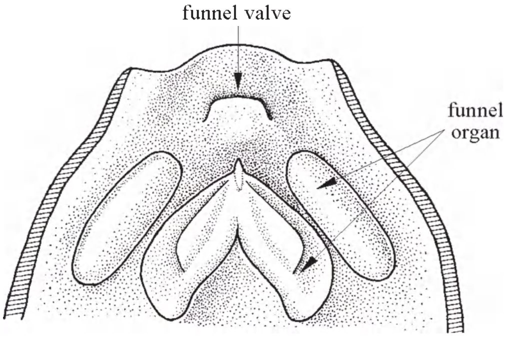


Fig. 17 Funnel organ and funnel valve components on inner surface of funnel of squids

Genus – The taxon below the family level and above the species level.

Gill – Primary organ for the exchange of respiratory gases with seawater (Fig. 22).

Gill lamella(e) – The leaf-like convoluted individual components of the gill through which gas exchange occurs (Figs 18 and 22).

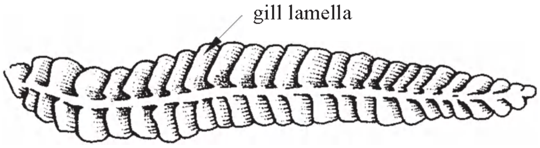


Fig. 18 Gill lamella, a single element from a complex structure

Gladius (= pen) – The feather or rod-shaped chitinous supporting structure in the dorsal midline of squids; the homologue of the shell of ancestral forms (Fig. 10).

Gladius length (GL) – Sometimes used as a measure of the body (= mantle) length when direct measurement of the mantle is unreliable (usually due to damage or deformation).

Gonoduct(s) – Tubular structure(s) of the reproductive system which serve(s) to transport reproductive products from the gonad into the mantle cavity, then to the exterior (see **Oviducts**).

Hatchling – Young cephalopod newly hatched from the egg.

Head length – A standard measurement within species growth stages and for species comparisons; measured from posterior limit to V-notch base of arms I (Fig. 4).

Head-mantle fusion – Zone of fusion of head and mantle; it varies among groups/families; of systematic and biological significance.

Hectocotylus – One (or more) modified arm in male squids used to transfer spermatophores to the female; modifications may involve suckers, sucker stalks, protective membranes, trabeculae (Fig. 19).

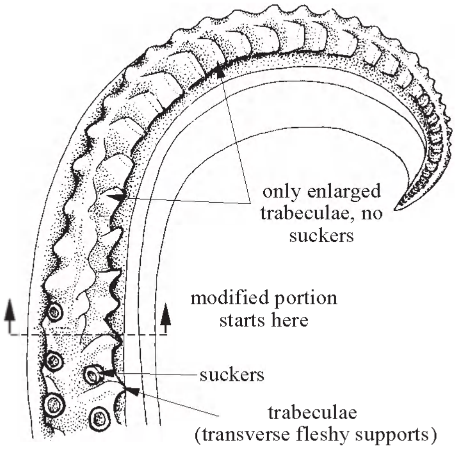


Fig. 19 Hectocotylized arm (*Illex oxygonius*)

Holotype – The single specimen designated by the original author of a species to represent the new species name. It is an international standard of reference that provides objectivity and stability for the species name.

Hooks – Chitinous, claw-like structures ontogenetically derived from the suckers on the arms and/or clubs of some oegopsid squids (Fig. 8).

Horny rings of suckers – Suckers of squids have 2 types of hard, horny rings. One, the inner ring, lies around the inner walls of the acetabulum (cup) and often bears teeth. The other, the outer ring, is composed of numerous minute platelets and lies on the surface of the infundibulum (outer rim) (Fig. 31).

Ink sac – The structure that manufactures and stores the ink of cephalopods; it lies parallel with the intestine and empties via a duct into the rectum (Figs 5 and 22).

Intestine – Distal region of the alimentary canal between the stomach/caecum complex and the anus (Fig. 12).

Juvenile – Life history stage between the hatchling and the nearly-mature subadult stages.

Keel – **(1)** A flattened, muscular extension along the aboral surface of some arms to render them more hydrodynamic (Fig. 11); **(2)** 1 or 2 expanded muscular membranes along the tentacular club of some groups (Fig. 8).

Lateral – Pertaining to the side(s) of an organism or structure, away from the centre or midline.

Lateral funnel-adductor muscles – See **Funnel-adductor muscles**.

Lateral membranes of arms IV – See **Tentacular sheath**.

Lateral-line analogue – Sensory structure analogous to the lateral-line of fishes. The lateral-line analogue, which senses vibrations transmitted by seawater, is located along a series of lines on the dorsal surface of the head, with some sensory cells extending onto the bases of the arms.

Length at 50% maturity – Mantle length at which 50% of specimens examined in a representative sample is sexually mature, according to the maturity scale and the statistical model used.

Lens (eye) – A spheroidal, transparent, polysaccharide structure through which light is transmitted to the retina.

Lens (in photophores) – Structure in a photophore that can focus or disperse bioluminescent light.

Light guides – Structures in photophores that specifically direct light via internal reflection.

Light organ (= photophore) – A simple or complex structure that produces bioluminescence (cool light) by intrinsic (self generated) or extrinsic (bacterial) means (Figs 11 and 20).

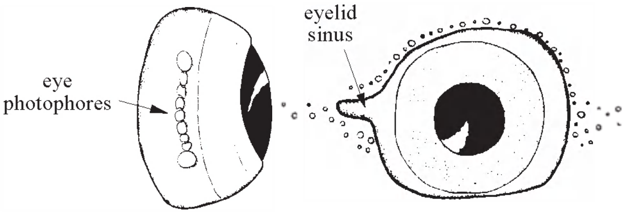


Fig. 20 Light organs (photophores) on ventral surface of squid eyeball, eyelid or orbital sinus

Lips – Two concentric, muscular, glandular rings of skin that surround the mouth and beaks.

Mantle – The fleshy (muscular) tubular or sac-like body of cephalopods; provides propulsion through jet-like expulsion of water; contains the viscera *sensu lato* (Figs 11 and 13).

Mantle cavity – Space enclosed by the mantle. In cephalopods the mantle cavity contains the visceral sac, gills, anus, ink sac, gonads, nephridial pores and various muscles and septa (Fig. 22).

Mantle length (ML) – The standard measure of length in coleoid cephalopods. In **squids** ML is measured along the dorsal midline from the anterior mantle margin to the posterior tip of the body (Fig. 4).

Mantle-locking cartilage – The cartilaginous ridge, knob or swelling on each side of the ventrolateral, internal surface of mantle that locks into the funnel component of the locking apparatus during locomotion (Figs 11 and 16) (see **Funnel-locking cartilage**).

Manus – Central or 'hand' portion of club between the dactylus distally and the carpus proximally (Fig. 11).

Mature – In cephalopods this term refers to sexual maturity which is determined for females by the presence of ova (mature eggs) free in the coelom or oviducts (Fig. 22) and for males by the presence of spermatophores in Needham's sac (see **Adult**).

Medial(n) – Pertaining to a structure located toward, on, or along the dorsal or ventral midline.

Mesopelagic zone – The middle-depth zone of the pelagic realm of the ocean.

Mollusca – One of the major invertebrate phyla. Some of the common molluscs are snails and clams. The **Cephalopoda** is a class within the Phylum Mollusca.

Molluscan foot – A major structure in molluscan morphology. In gastropods the foot is the muscular sole that the animal crawls with. In cephalopods the funnel, and possibly the arms and tentacles are derived from the molluscan foot.

Monophyletic group – A natural group (taxon) that shares a common ancestor.

Myopsida – A high-level taxon (order) within the **Decapodiformes**. In recent classification, the **Myopsida** (including the families Loliginidae and Australiteuthidae) have been considered the sister group of the **Oegopsida** and the 2 groups together compose the **Teuthoidea** (squids).

Neck – The region that separates the posterior end of the cephalic cartilage and head musculature. Only those cephalopods with elongate heads (e.g. the oegopsid squid family Chiroteuthidae) have distinct necks.

Needham's sac (=spermatophore/ spermatophoric sac) – The elongate, membraneous organ of males where completed, functional spermatophores are stored. It opens into the mantle cavity (or externally) through the penis (Fig. 21).

Nephridial coelom – The cavity of the renal (kidney) sac. It connects with the exterior via the renal pore and with the viscero-pericardial coelom via a pair of slender ducts from the latter.

Nephridial papillae – Small raised openings to the renal cavities.

Neritic – The region of the ocean that overlies the continental shelf.

Nidamental glands – Large glandular structures in females that lie in and open directly into the mantle cavity. The glands are composed of numerous lamellae that are involved in secretion of egg cases or the jelly of egg masses (Fig. 22).

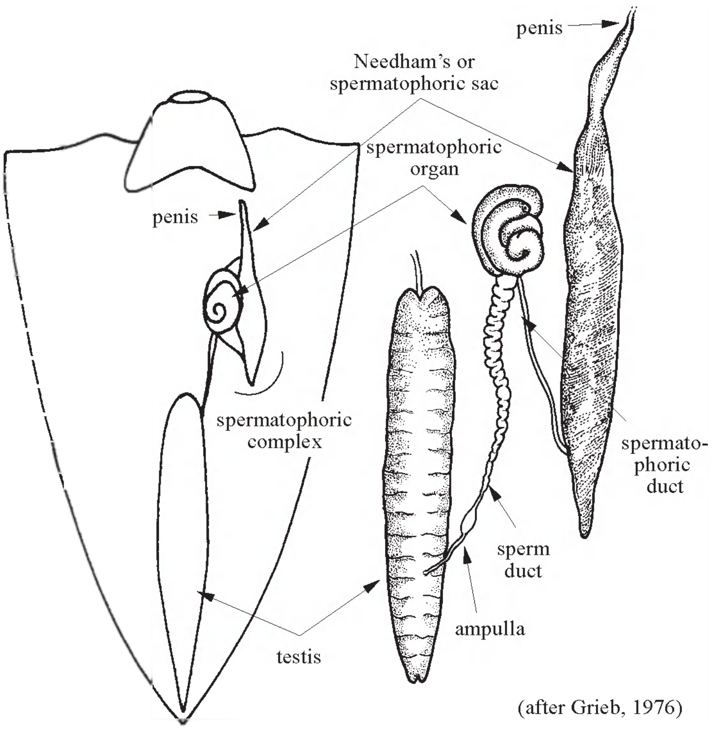
Nominal species – A species that has been formerly described and is based on a morphological type. It is an available name but not necessarily a valid species.

Nuchal cartilage – See **Nuchal-locking apparatus.**

Nuchal crest – Prominent transverse ridge that extends across the dorsal head and down the lateral head surfaces at its posterior end.

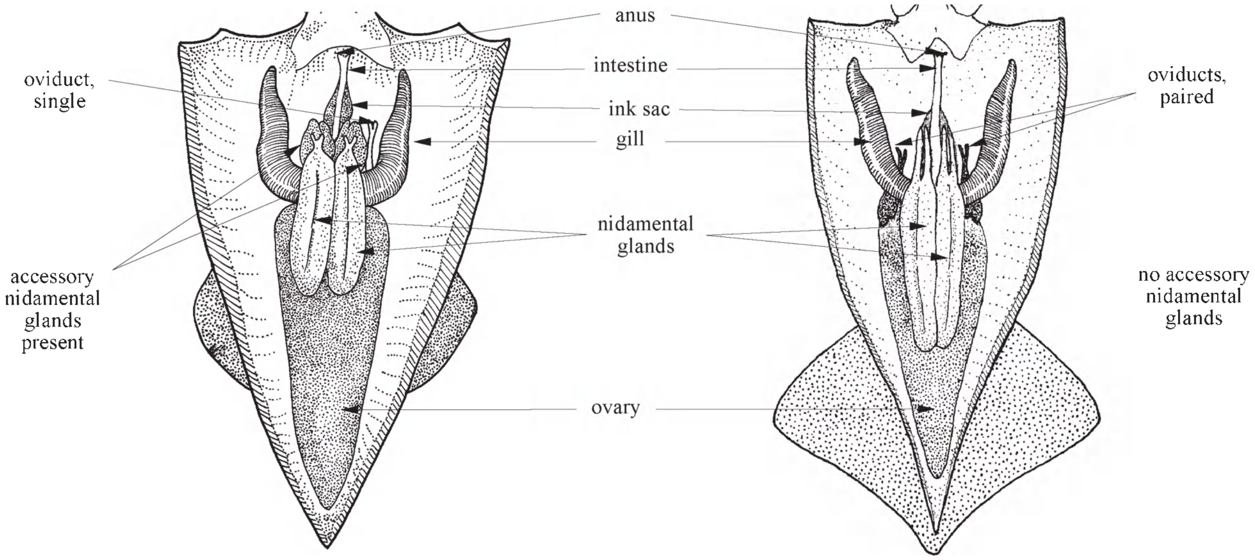
Nuchal folds – Fixed folds or pleats of the head integument that adjoin the nuchal crest posteriorly and are perpendicular to it. The function of the folds is uncertain (Fig. 23).

Nuchal-locking apparatus – An oblong, cartilaginous-locking structure located mid-dorsally just posterior to the head. It is composed of the nuchal cartilage, which also forms an attachment site for collar and head retractor muscles, and an interlocking, complementary cartilage on the mantle that underlies the gladius. The apparatus keeps the head and mantle aligned dorsally during mantle contractions (Fig. 23).



(after Grieb, 1976)

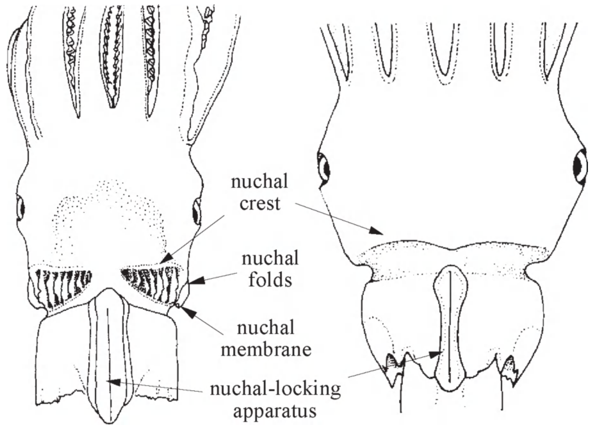
Fig. 21 Male squid reproductive apparatus



a) Loliginidae **b) Ommastrephidae**

Fig. 22 Internal organs of Decapodiformes

Nuchal membrane (= occipital membrane) – A thin membrane that connects the main nuchal folds at their posterior ends (Fig. 23).



a) ***Onychoteuthis*** **b)** ***Onykia***

Fig. 23 Nuchal folds and nuchal crest

Nuchal organ – Small sensory organ with photoreceptor-like sensory cells that is located in the nuchal region of apparently all coleoid cephalopods.

Nuchal region – The dorsolateral area around posterior part of the head and the area immediately posterior to it, normally covered by the anterior mantle wall.

Occipital crest – See **Nuchal crest**.

Occipital folds – See **Nuchal folds**.

Occipital membrane – See **Nuchal membrane**.

Ocular photophore – Photophore that lies on the eyeball (Fig. 20).

Oegopsida – A high-level taxon within the **Decapodiformes**. In recent classification, the **Oegopsida** (oceanic or open-eyed squids) has been considered the sister group of the **Myopsida** (inshore or covered eyed squids) and the 2 groups together compose the **Teuthoidea** (squids). At present the the composition and affinities of the **Oegopsida** are unresolved.

Oesophagus (esophagus) – The portion of the digestive tract between the buccal mass and the stomach (Fig. 12).

Olfactory organ – A chemosensory organ present in all coleoid cephalopods.

Olfactory papilla – A pit, or bump-like to finger-like protuberance on the posterolateral surface of each side of the head; of olfactory function.

Ontogenetic descent – The progressive descent into a deeper-water habitat as a mesopelagic cephalopod grows older and larger. This distribution pattern is particularly common in many pelagic chiroteuthid and cranchiid squids.

Opening/closing trawl – A trawl whose mouth is open during fishing at a known depth but is closed during descent and retrieval.

Optic lobes of brain – Large lobes of the brain associated with the eyes. In some squids the optic lobes may be separated from the rest of the brain by an optic stalk of varying length.

Optic sinus – See **Eyelid sinus**.

Oral – Toward or pertaining to the mouth.

Orbital pore (= eye pore) – Minute pore in the anterior part of the transparent tissue (cornea) that covers the eyes of most myopsid squids; remnant of the primary eyelids (Fig. 66).

Orbital sinus – See **Eyelid sinus**.

Order – The taxonomic catageory above the family level.

Oviduct(s) – Female gonoduct(s). The oviduct conducts eggs from the visceropericardial coelom, that encompasses the ovary, to the mantle cavity and often is used to store eggs (Fig. 22).

Oviducal gland – Glandular structure that surrounds the anterior end of the primary oviduct and secrets some of the external coatings around spawned eggs.

Paralarva – The term that indicates the first free-living life history stage (typically planktonic) for those cephalopods that differ in morphology and ecology from older juveniles.

Pedicel (= sucker stalk) – A short, tubular stalk that supports a sucker in sepioids and teuthoids (Fig. 24).

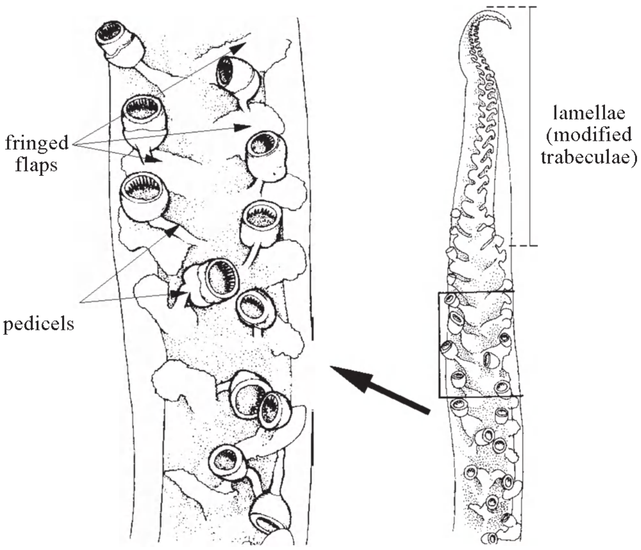


Fig. 24 Hectocotylized arm of males

Pelagic – **(1)** Free swimming in open ocean; **(2)** The region of the ocean away from the ocean floor.

Pen – See **Gladius**.

Penis – The long, muscular terminal section of the male gonoduct that serves to transfer spermatophores to the female (Fig. 21). Apparently, in species with a hectocotylus, the penis transfers spermatophores to the hectocotylus which in turn transfers them to the female. In species without a hectocotylus, the penis often is greatly elongate, capable of extending beyond the mantle opening and apparently can transfer spermatophores directly to the female.

Photocytes – Cells that produce bioluminescence in photophores.

Photophore – An organ that produces and distributes bioluminescence or ‘living light’, either intrinsically through biochemical reaction or extrinsically through luminescent bacteria (Figs 11 and 20) (see **Light organ**).

Phylum – The major, formative, principal taxonomic level, above Class.

Polarity (Evolutionary) – The direction of evolution. That is, one state is ‘primitive’ (plesiomorphic) and another is ‘derived’ (apomorphic).

Polarize (Evolutionary) – To determine the direction of evolution. That is, to determine which state is ‘primitive’ (plesiomorphic) and which is ‘derived’ (apomorphic).

Posterior – Toward the closed, tail-end of the mantle, away from the head and arms.

Primary conus – A solid conus on the gladius that is not formed by the in-folding of the lateral vanes.

Protective membrane – Thin web-like integument along the lateral angles of the oral surface of the arms and clubs lateral to the suckers, supported by muscular rods called trabeculae (Fig. 25) (see **Trabeculae**).

Proximal – Situated nearest or next to the centre of the body or nearest the point of origin or attachment of a muscle, appendage, etc. (opposite of distal).

Pseudomorph – An ejected mass of ink and mucous that approximates the size and shape of the cephalopod that released it; i.e. a false body that fixes the attention of a predator while the cephalopod escapes.

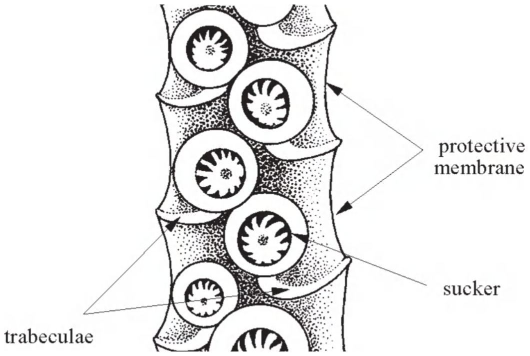


Fig. 25 Trabeculae, protective membranes and suckers on arm of squid

Rachis – The thickened central axis that usually extends the entire length of the gladius. Free rachis is the portion that does not support vanes (Fig. 10) (see **Gladius, Vane**).

Radula – The chitinous, ribbon-like band in the mouth of cephalopods that contains up to 7 transverse rows of teeth that aid in transport of food into the oesophagus (Fig. 26); is a significant higher taxonomic value.

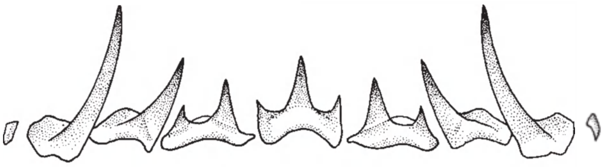


Fig. 26 Radula

Recent – Geological term referring to an organism or species that is living or has lived within the past 10 000 years, or to an object formed or events that have occurred within the past 10 000 years.

Renal appendages – Structures that form the nephridium (= kidney). The renal appendages are out-pockets of the veins within the renal sac (primarily the venae cavae) that are covered with renal epithelium. The renal sac empties into the mantle cavity via the nephridial (or renal) pores.

Renal pore – The opening(s) of the renal cavities into the mantle cavity, through which urine is discharged.

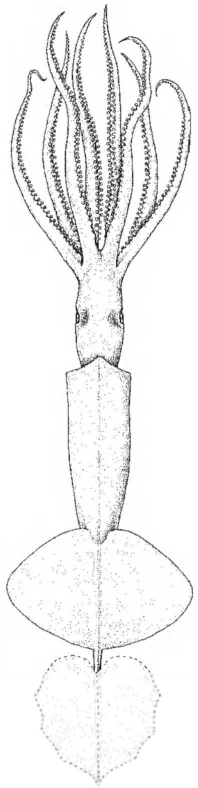
Rhynchoteuthion – Paralarval stage of the Ommastrephidae characterized by the fusion of the tentacles into a trunk-like proboscis (Plate VIII, 49).

Rostrum (= spine) – A spike-like posterior projection of the gladius, exterior to the conus (Fig. 10).

Secondary conus – A conical region at the posterior end of the gladius that is formed by an in-rolling and fusion of the vanes. The ventral line of fusion usually is apparent. The secondary conus may be rather short or exceed half the gladius length (Fig. 27).

Secondary fin – A non-muscular fin-shaped structure found in some oegopsid squids, located posterior to the true or primary fin (Fig. 28) The secondary fin may act as a buoyancy organ.

Fig. 27 Secondary conus



Grimalditeuthis bonplandii

Fig. 28 Secondary fin

Semelparous – A reproductive strategy in which females spawn once then die. Sometimes called terminal or 'big-bang' spawners. Many squids are semelparous but in some species reproduction is prolonged.

Shell sac – The sac that secretes the shell in the **Coleoidea**, composed of ectodermal epithelium that invaginates during embryonic development to form an internal sac.

Side pockets – Small membranous folds of the integument that form small, shallow pockets lateral to the foveola in the funnel groove (Fig. 15) (see **Foveola**).

Species – Populations of animals that interbreed or are potentially capable of interbreeding in nature. Considerable debate exists over the general definition of a species and how the theoretical definition should be applied in practice. With regard to the latter problem, cephalopod species generally are defined by distinct morphological traits not exhibited by any other species. This practice is valid if interbreeding does not occur. However, the amount of interbreeding (i.e. hybridization) that actually occurs in nature and contributes to or diminishes speciation is virtually unknown in cephalopods.

Sperm cord – The coiled rope of sperm that lies within the spermatophore (Fig. 29).

Sperm duct (= seminal duct) – The duct of male reproductive system that joins the testis with the spermatophoric organ (Fig. 21).

Sperm groove – Sulcus along the ventral side of the hectocotylus used to transfer the spermatophores.

Sperm mass – The mass of sperm held within the spermatangia of everted spermatophores.

Sperm receptacle – A bulbous structure in the buccal region or at the openings of the oviducts in females of certain squids for deposition of spermatangia.

Spermatangium (pl. spermatangia) – Extruded, exploded, evaginated spermatophores, often in the form of a round bulb.

Spermatheca(e) – Specialized sperm-storage structure(s) found in the skin of some female squids.

Spermatophore – A tubular structure manufactured by male cephalopods for packaging sperm; capable of holding millions of sperm, it is transferred and attached to the female until fertilization occurs (Fig. 29). It forms a spermatangium after the spermatophoric reaction occurs and the spermatophore has everted.

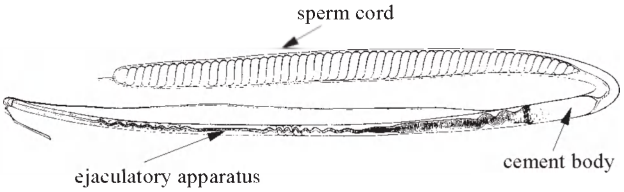


Fig. 29 Spermatophore

Spermatophore pad – A fleshy patch of tissue, usually in the mantle cavity of some female squids (e.g. loliginids), to which spermatangia adhere after mating and remain until fertilization occurs.

Spermatophoric complex – The unit formed by the sperm duct, the spermatophoric organ, the spermatophoric sac, the spermatophoric duct and the penis (Fig. 21).

Spermatophoric duct – The duct of male reproductive system through which the spermatophores, once formed, pass from the spermatophoric organ to the spermatophoric sac (Fig. 21).

Spermatophoric organ – Male organ where the spermatophores are formed (Fig. 21).

Spermatophoric reaction – The evagination of a spermatophore with the extrusion of the sperm mass, caused by the penetration of water inside the spermatophoric cavity, where the osmotic pressure is higher.

Spermatophoric sac – See **Needham's sac** (Fig. 21).

Spine – See **Rostrum**.

Squid – Common name given to members of the Teuthoidea and some members of the Sepiolidae.

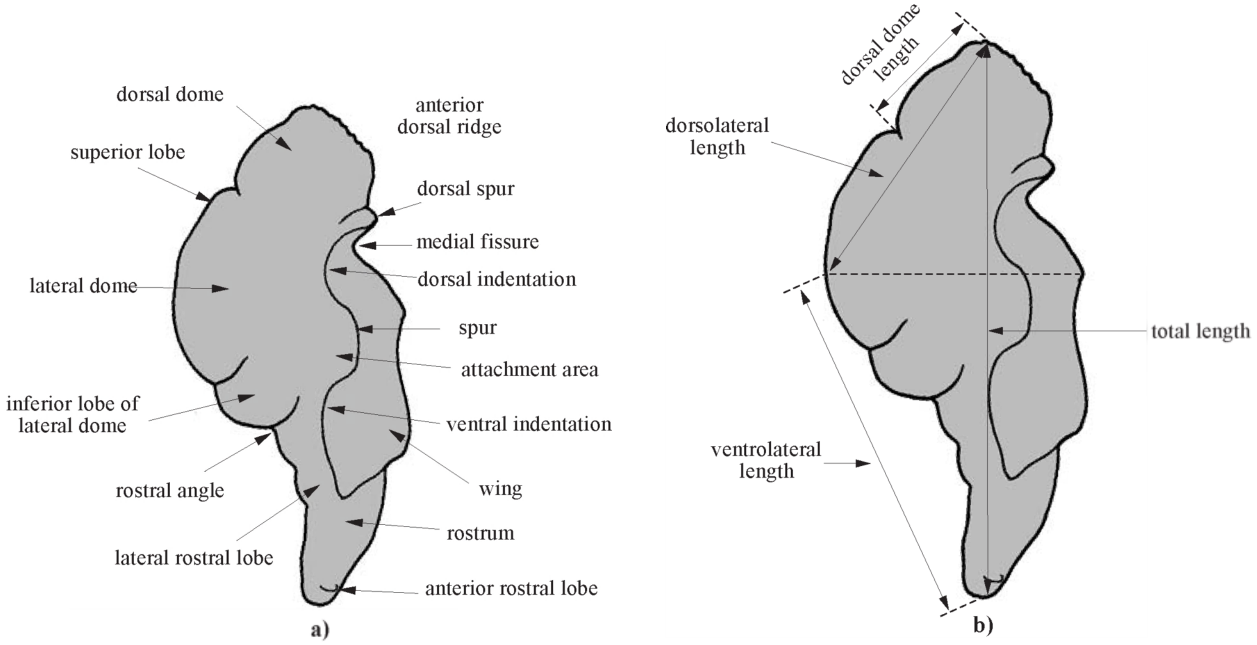


Fig. 30 Diagrams of a generalized teuthoid statolith (anterior view) with a) basic terms and b) basic dimensions labelled
(after Clarke, 1978)

Squid, general terminology – Diagramatic drawing with external features labeled, ventral view (Fig. 11).

Stalk of tentacle – See **Tentacle stalk**.

Stalked eyes – See **Eye, position and size**.

Statocyst – A paired sense-organ that detects gravity, angular acceleration and low-frequency sound. The statocysts are embedded within the cephalic cartilage and contain the statoliths.

Statolith – A calcareous stone in the statocyst that detects linear acceleration, angular acceleration and orientation (Fig. 30). Concentric rings in complex statoliths of many species can be used to estimate age.

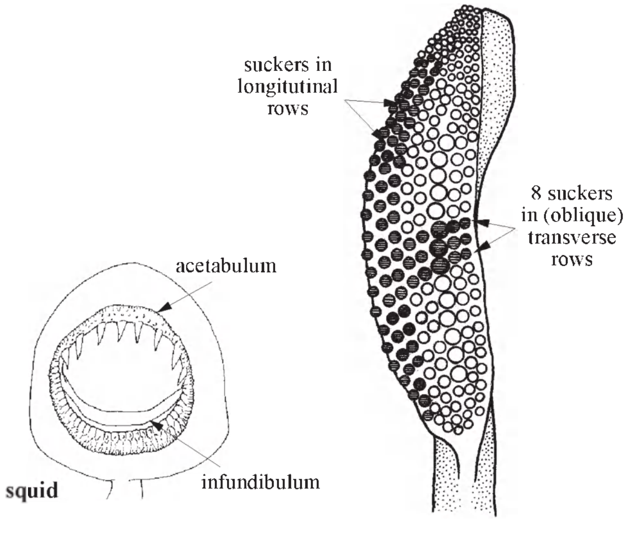
Stellate ganglion – Major ganglion of the peripherial nervous system of neocoleoid cephalopods that controls nerves to the mantle muscles.

Stomach – The muscular organ of the digestive system where primary digestion occurs (Fig. 12). The stomach generally is lined with cuticular ridges to aid in grinding food and is supplied with digestive enzymes from the digestive gland. The stomach may be greatly expandable in size and serve as a storage area until food can be fully processed.

Subadult – Stage at which all of the characters that typically define the species are present, but the reproductive system is not mature and functional. It follows the juvenile stage and precedes the adult stage. A subadult stage is defined in cephalopods since the adult phase frequently is abbreviated.

Subequal – Nearly equal. Generally refers to the length of the arms when these appear to be approximately the same length. Arm lengths cannot be measured very accurately due to variation in their states of contraction.

Sucker/s – Muscular, suction-cup structure/s on the arms and tentacles (occasionally on the buccal membrane) of squids; they are stalked, placed on muscular rods that contract (Fig. 31a). They usually are counted either in longitudinal or in transverse (oblique) rows (Fig. 31 b).



a) sucker b) club

Fig. 31 Squid sucker and squid suckers orientation

Sucker ring – Chitinous, often serrated or toothed, ring that encircles the opening of suckers of squids (Fig. 32).

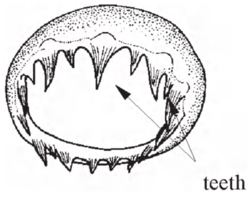


Fig. 32 Sucker ring

Sucker series – The longitudinal rows of suckers on the arms or tentacles. Series (= longitudinal rows) contrasts with rows (= transverse rows) in describing sucker arrangement.

Sucker stalk – The muscular support and connective structure between the sucker and the arm. It is constricted into a conical pillar.

Sucker teeth – Sharp, blunt or rounded teeth on the inner horny sucker rings of some squids.

Superior buccal lobes – Lobes of the central nervous system that occur dorsal to the oesophagus where the latter enters the buccal mass.

Swimming membrane (= keel) – An elongate, flat muscular vane along the aboral surface of arms of squids that functions to streamline and support the arms during swimming (Fig. 8).

Synonym – One of 2 or more names applied to the same taxon/species.

Systematics – The classification of organisms into hierarchial groups based on phylogenetic relationships.

Tail – Posterior narrow extension of the body posterior to the fins. The end of the fins and the beginning of the tail often overlap. An operational definition for point of demarcation for the purposes of measurement is: the point where a hypothetical line, continuous with the broad posterior edge of the fin, crosses the midline of the body (Fig. 11).

Taxa, taxon – A taxonomic group of any rank. A taxonomic unit.

Tentacles – Modified fourth pair of appendages in squids, used for prey capture. The distal ends contain clubs with suckers and/or hooks; stalks frequently devoid of suckers (Fig. 11). Tentacles are capable of considerable extension and contraction, but they are not retractile into tentacular pockets in squids. Although the tentacles are derived evolutionarily from the fourth pair of appendages, the term ‘arms IV’ is reserved for the ventralmost pair of appendages, the ventral arms, which are evolutionarily the fifth pair of arms.

Tentacle absence – Tentacles can be absent because the species lacks tentacles, they are accidentally lost during capture, or they are naturally lost at a particular stage of development.

Tentacle pads – Poorly understood and complex pad-like photophores that are found on the tentacular stalks of some squids of the family **Chiroteuthidae**.

Tentacle stalk – Region of the tentacle proximal to the club.

Tentacle terminology – See Fig. 11.

Tentacular club – The distal, terminal, usually expanded, part of the tentacle that bears suckers and/or hooks. Used for capturing prey (Figs 8 and 11).

Tentacular pocket – A pocket that encompasses the base of each tentacle at its fusion with the head and provides space for complete retraction of the tentacle into the pocket (as in members of the Sepioidea and “sepioid squids”), or contraction of the tentacular stalk without retraction into the pocket (as in the true squids). It is present in members of the families Australiteuthidae and Loliginidae (Myopsida), Bathyteuthidae and Chtenopterygidae (Oegopsida).

Tentacular retractor muscles – Muscles that serve to coil the tentacle when retracted, in contrast with those muscles that serve to shorten (contract) the tentacle.

Tentacular sheath –The keels of arms IV are off-set laterally and often enlarged to fully or partially conceal, protect or encase the adjacent tentacles. The latter function is most fully developed in the chiroteuthids and mastigoteuthids.

Terminal fins – Fins with more than 50% of their length posterior to the muscular mantle. These fins, therefore, are at the ‘terminal’ or posterior end of the body and generally are supported by an elongate secondary conus of the gladius.

Terminal organ – Alternative name for penis, as true definition of a penis is ‘organ of insertion’. In most cephalopods, the hectocotylized arm is used for spermatophore insertion, or placement, in the females.

Terminal pad (of tentacular club) – A small, distinct pad or circlet of small terminate suckers at the tip of the club.

Teuthoidea – The higher taxon that includes all squid-like **decapods**; now archaic. The monophyly of this taxon is questionable.

Total Length (TL) – Length measured from the posterior tip of the mantle to the anterior tip of the outstretched appendages (Fig. 4)

Trabeculae – Muscular rods that support the protective membranes on the arms and clubs of squids (Fig. 25). Occasionally membranes are reduced and/or trabeculae are elongated, so they extend beyond the edge of the membrane, papilla-like.

Tragus – Particular inward-projecting knob in the funnel-locking apparatus of some squids. It is the knob found on the medial surface of the central depression.

Truncate teeth – Teeth on the inner chitinous rings of decapod suckers that do not terminate in a point but rather a broad, flat tip.

Vane – Thin, lateral expansion of the gladius that arises from the rachis (Fig. 10) (see **Rachis**).

Ventral – The lowermost or belly surface of a cephalopod, the surface on which the funnel is located. Opposite the dorsal surface (Figs 11 and 13).

Visceral sac – The body region posterior to the head surrounded by the mantle. The body wall in this region that encases the viscera usually is rather thin-walled, hence the name ‘visceral sac’. The visceral sac also is called the ‘visceral dome’.

Visceropericardial coelom – The largest coelom in squids. It encloses the gonads, and partially encapsulates the stomach, caecum and ventricle, among other structures. The viscero-percardial coelom also communicates with the other squid coelom, the nephridial coelom, and the mantle cavity via a pair of ducts that open at the base of the nephridial papillae.

Web – A membranous sheet of greater or lesser extent that extends between the arms of many **octopods**, giving an umbrella-like appearance when the arms are spread out, e.g. on cirroteuthids. It is reduced or absent in most **decapods**.

1.6 Key to Recent Myopsid and Oegopsid Squids

1. Eight or 10 circumoral appendages; suckers (and/or hooks) present; no external shell . . . . . . **Coleoidea → 2**

2. Suckers stalked with chitinous rings; 10 circumoral appendages, 8 arms and 2 ventrolateral tentacles (tentacles may be lost in some species); mantle cavity communicates with the exterior via 3 openings . . . . **Cuttlefishes, Bobtail squids, Bottletail squids, Pigmy squids, Ram's Horn squid, Myopsid squids, Oegopsid squids → 3**

3. Internal shell straight, feather- or rod-shaped, chitinous; tentacles contractile, not retractile, into tentacular pockets; fins usually joined posteriorly; mantle edge near mantle cartilages with small projections or 'angles' . . . . **Myopsid Squids, Oegopsid Squids → 4**

4a. Eye covered by transparent membrane (cornea) (Fig. 33a) . . . . . . **Myopsid squids → 5**

4b. Eye without cornea and len in open contact with seawater (Fig. 33b) . . . . **Oegopsids squids → 6**

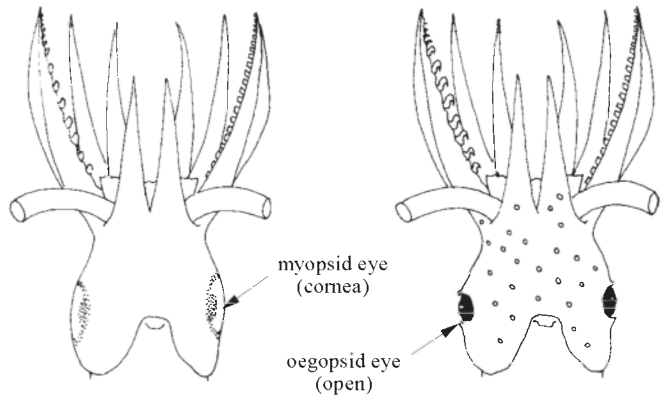


Fig. 33

5a. Four longitudinal rows (series) of suckers on manus of tentacular clubs; fins united at posterior end of mantle; medial posterior border of fins concave (Fig. 34) . . . . . . **Family Loliginidae**

5b. Two longitudinal rows (series) of suckers on manus of tentacular clubs; fins not united at posterior end of mantle; medial posterior borders of fins convex (Fig. 35) . . . . . **Pickfordiateuthis**[1/]

5c. Fins not united at posterior end of mantle; a sepiolid-like, dumb-bell shaped photophore on the ventral surface of ink sac. . . **Family Australiteuthidae**[2/]

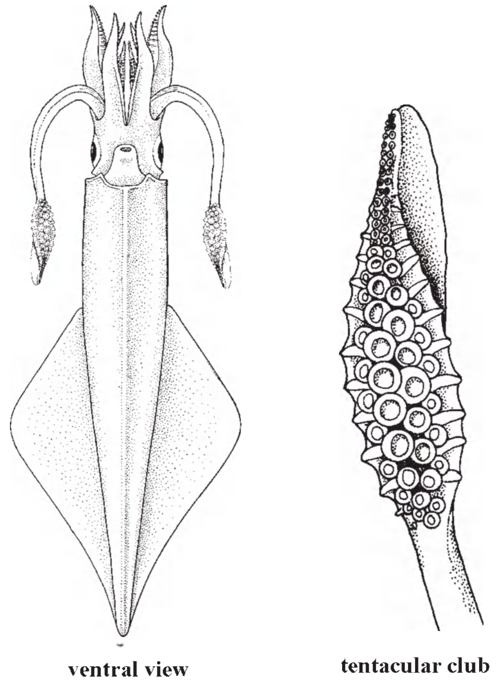


Fig. 34 Loliginidae (*Loligo*)

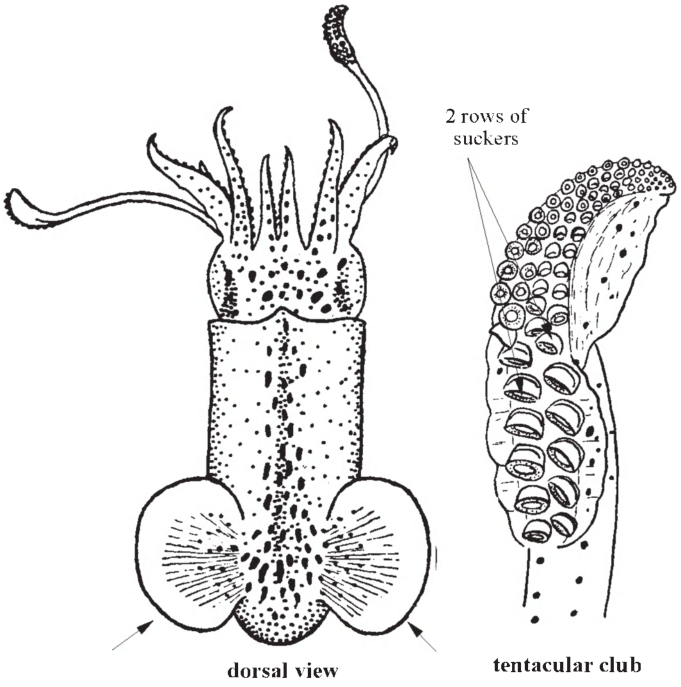


Fig. 35 Loliginidae (*Pickfordiateuthis*)

[1/] *Pickfordiateuthis*, the sole genus in a formerly recognized family, recently has been placed in the family Loliginidae; it is included in the Key to indicate its unique characters within the loliginids.

[2/] This new family of myopsid squid has been described from Australian waters by C.C. Lu, 2005.

6a. Funnel free from mantle; funnel-mantle locking apparatus present . . . . → **7**
6b. Funnel fused to mantle on each side[3]; no funnel-mantle locking apparatus present. . . . . → **32**

7a. Funnel-locking cartilage a simple, straight groove and ridge[4] (Fig. 36a) . . . . → **8**
7b. Funnel-locking cartilage not a simple, straight groove and ridge (Fig. 36b, c, d, e, f) . . . . → **25**

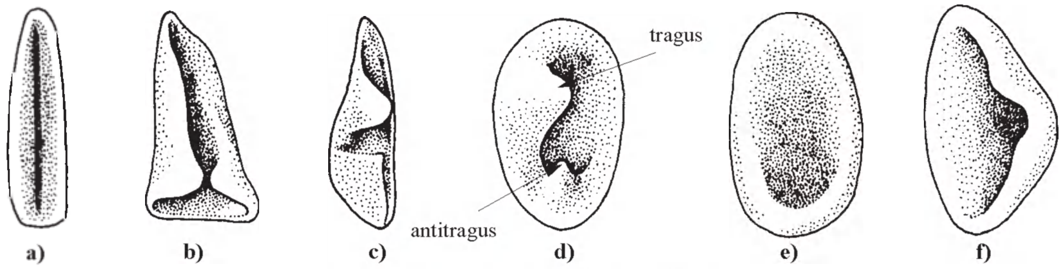


Fig. 36 Funnel-locking cartilage

8a. Arms with hooks or with suckers in 4 longitudinal rows on proximal half of ventral arms . . . . → **9**
8b. Arms without hooks and with suckers in 2 longitudinal rows on proximal half of ventral arms . . . . → **13**

9a. Armature (suckers, hooks) of arms in 2 rows . . . . → **10**
9b. Armature (suckers, hooks) of arms in 4 rows (Fig. 37). . . . . **Family Gonatidae**

10a. Tentacles and clubs absent in adults although present in larvae or occasionally in juveniles (*Taningia*) but, when present, always with rudimentary clubs armed with few suckers (Fig. 38). . . . . **Family Octopoteuthidae**
10b. Tentacles present; fully developed clubs present (Fig. 39) . . . . → **11**

11a. Photophores on viscera but not on mantle or surface of head and/or arms . . . . **Family Pyroteuthidae** (Fig. 39)
11b. Photophores on mantle and surface of head and arms but not on viscera . . . . → **12**

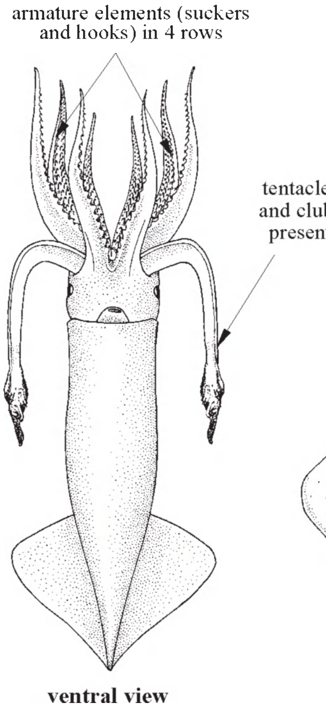


Fig. 37 Gonatidae (*Gonatus*)

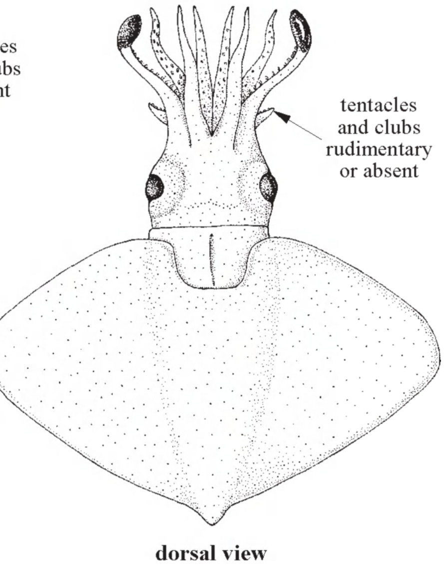


Fig. 38 Octopoteuthidae (*Taningia*)

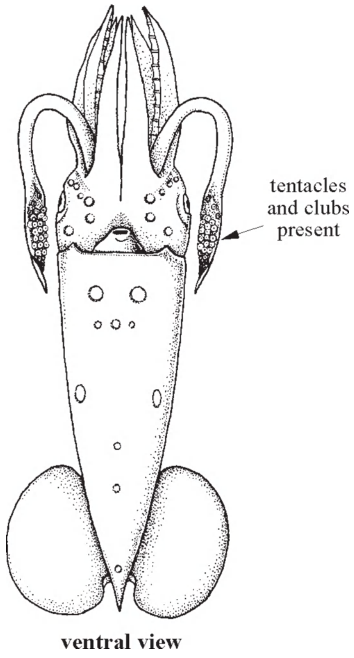


Fig. 39 Pyroteuthidae (*Pterygioteuthis*)

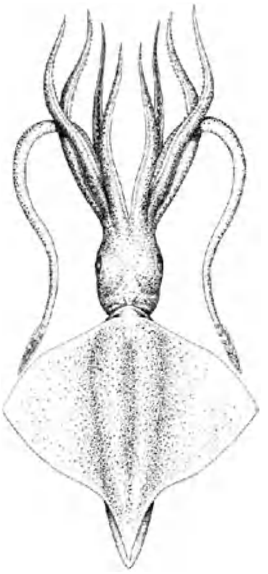
---

[3] Fusion of the mantle component of locking apparatus to the funnel component also occurs in adults of one ommastrephid genus, *Sthenoteuthis*. However, the ommastrephid inverted T-shape (⊥) is retained.

[4] The classification "simple and straight" includes some locking apparatuses that show considerable variation. For example, in the Octopoteuthidae and the Histioteuthidae the central groove is fairly broad and may curve slightly. The homogeneity of this classification becomes apparent when this type of locking cartilage is contrasted in the more highly specialized types, e.g. oval, ⊥-shaped.

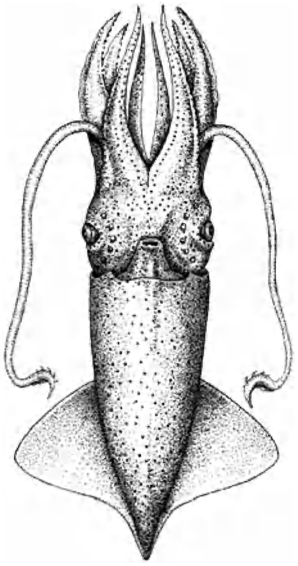
12a. Photophores on tentacles but not on eyeballs . . . . **Family Ancistrocheiridae** (Fig. 40)
12b. Photophores on ventral eyeballs but not on tentacles . . . . **Family Enoploteuthidae** (Fig. 41)

13a. Buccal membrane connectives attach to ventral sides of arms IV (Fig. 42b) . . . . → **14**
13b. Buccal membrane connectives attach to dorsal sides of arms IV[5/] (Fig. 42a) . . . . → **20**



dorsal view

Fig. 40 Ancistrocheiridae (*Ancistrocheirus*)



ventral view

Fig. 41 Enoploteuthidae (*Abralia*)

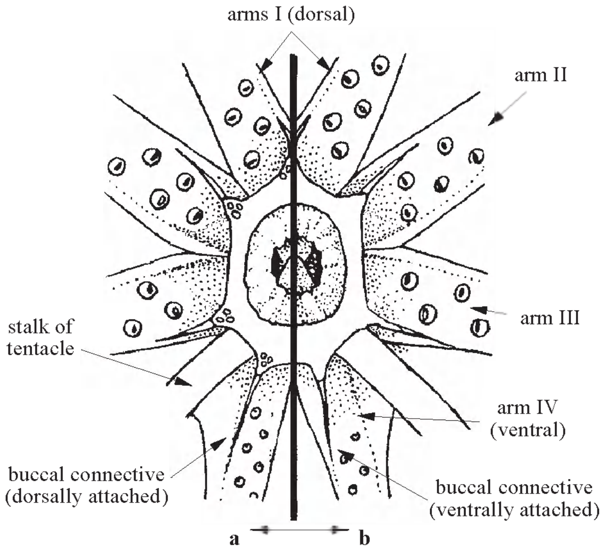
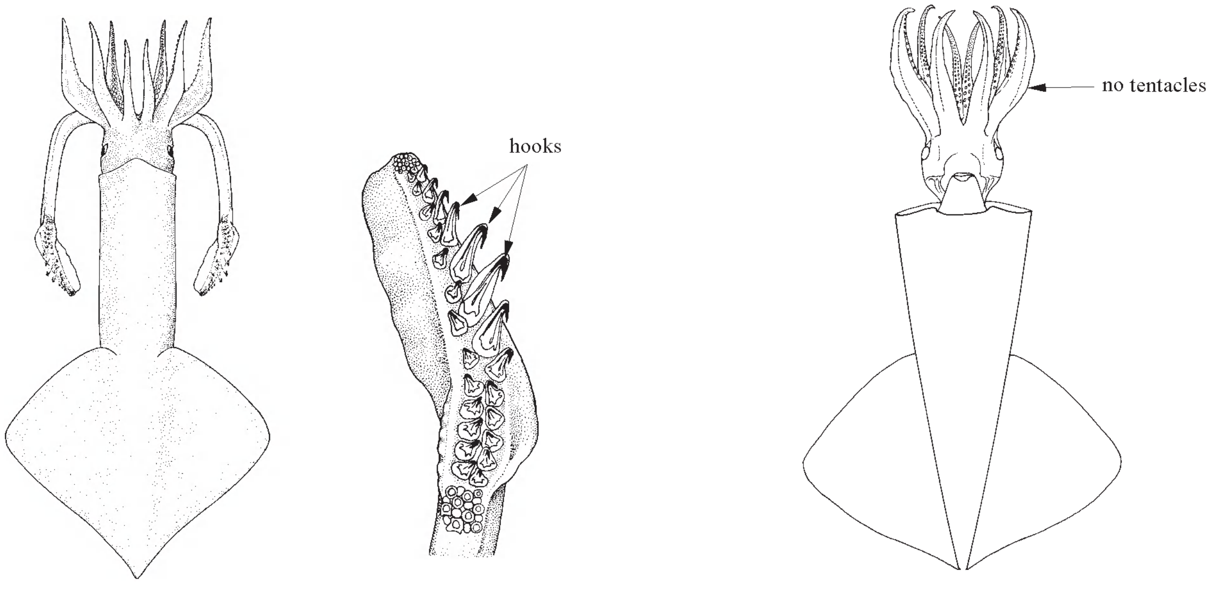


Fig. 42 Oral view

14a. Hooks present on tentacular clubs (Fig. 43a and b); tentacles and clubs are lost in mature animals (Fig. 43c) . . . . **Family Onychoteuthidae**
14b. Hooks lacking on tentacular clubs . . . . → **15**

15a. Cartilaginous scales present on mantle (may be minute); tentacular clubs with 4 longitudinal rows (series) of suckers . . . . → **16**
15b. Cartilaginous scales lacking; tentacular clubs with more than 4 longitudinal rows (series) of suckers on some areas . . . . → **17**



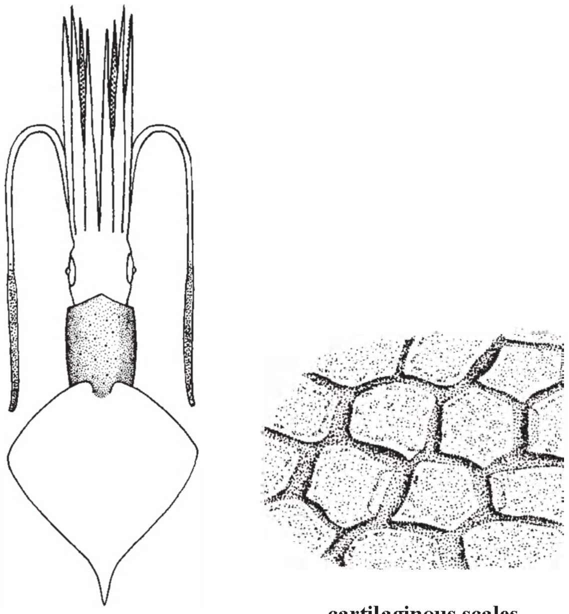
a) dorsal view **b) tentacular club** **c) ventral view (mature female)**

Fig. 43 Onychoteuthidae (*Onychoteuthis*)

[5/] This character is difficult to detect in some histioteuthids that have secondary modifications to the buccal membrane connectives.

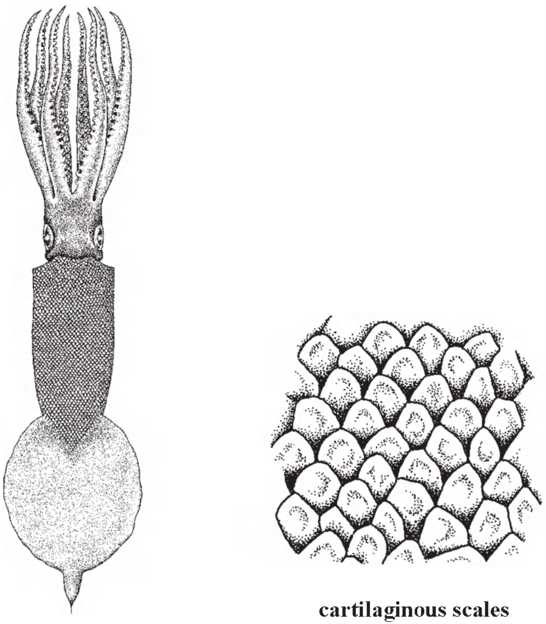
16a. Tentacles present with numerous, laterally compressed club suckers . . . . . **Family Pholidoteuthidae** (Fig. 44)

16b. Tentacles lost in adults; tentacles in juveniles small and weak, with a few (about 6) poorly differentiated suckers . . . . **Family Lepidoteuthidae** (Fig. 45)


dorsal view

cartilaginous scales on mantle

Fig. 44 Pholidoteuthidae (*Pholidoteuthis*)


dorsal view

cartilaginous scales on mantle

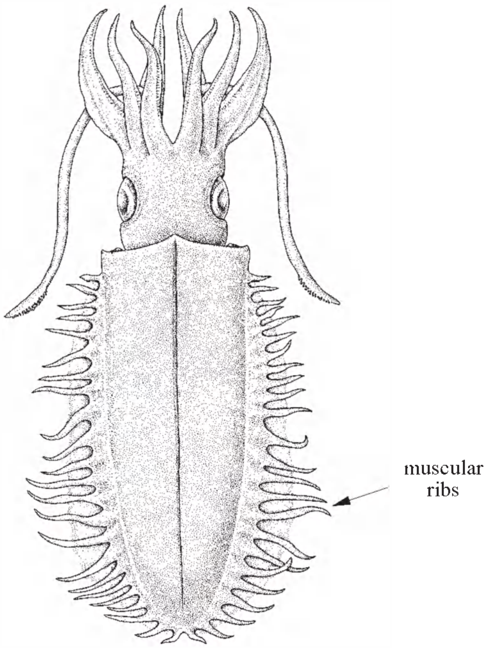
Fig. 45 Lepidoteuthidae (*Lepidoteuthis*)

17a. Fins nearly as long as mantle, supported by strong, transverse, muscular ribs; minute suckers present on oral surface of buccal lappets (Fig. 46) . . . . **Family Chtenopterygidae**

17b. Fins less than half the body length and without supporting ribs; no suckers on buccal lappets . . . . → **18**

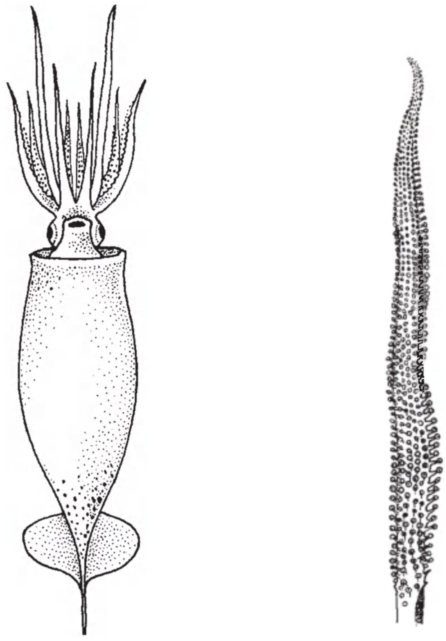
18a. Tentacular clubs with 6 uniform longitudinal rows (series) of suckers; a long, spike-like tail present, greater than fin length (Fig. 47) . . . . **Family Batoteuthidae**

18b. Tentacular clubs with 2 or 4 longitudinal rows (series) of suckers . . . . → **19**



dorsal view

Fig. 46 Chtenopterygidae (*Chtenopteryx*)


ventral view

tentacular club

Fig. 47 Batoteuthidae (*Batoteuthis*)

19a. Tentacular clubs with 4 longitudinal rows (series) of suckers on distal portion, numerous rows on proximal portion; no long, spike-like tail (Fig. 48) . . . . **Family Brachioteuthidae**

19b. Tentacular clubs with 2 longitudinal rows (series) of very widely spaced, tiny suckers; mantle broad, bluntly rounded posteriorly; fin short, wide, transversely oval (Fig. 49). . . . . ***Walvisteuthids***[6/]

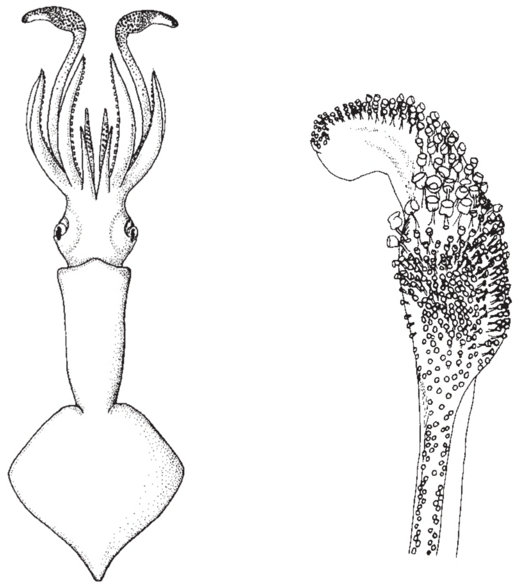

dorsal view tentacular club

Fig. 48 Brachioteuthidae (*Brachioteuthis*)

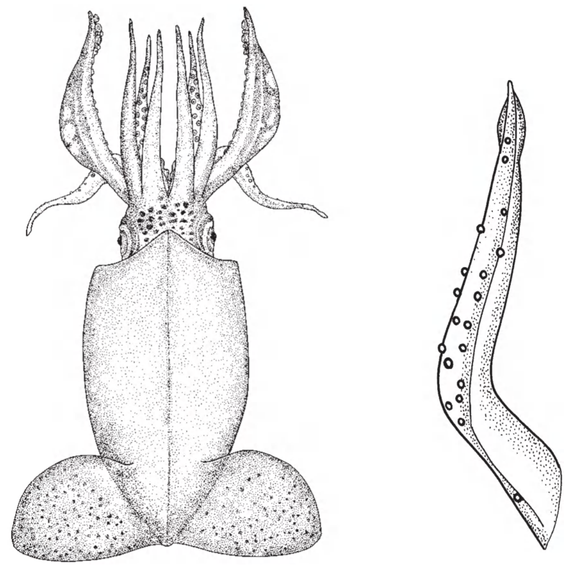

dorsal view tentacular club

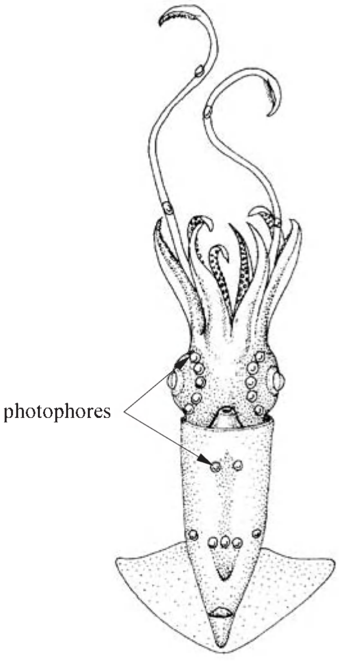
Fig. 49 Onychoteuthidae (*Walvisteuthis)*

20a. Ventral surface of eye with a single row of photophores; buccal membrane with 8 separate lappets (Fig. 50) . . . . **Family Lycoteuthidae**

20b. No photophores on eyes; buccal membrane with 7 lappets or less . . . . → **21**

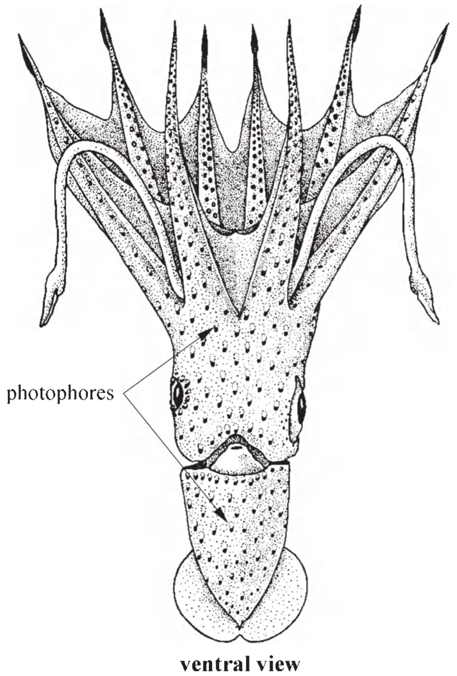
21a. Surface of mantle, head and arms covered with numerous photophores (usually large and distinct) (Fig. 51) . . . . **Family Histioteuthidae**

21b. Surface of mantle and head without photophores (base of arms may have a few photophores) . . . . → **22**



ventral view

Fig. 50 Lycoteuthidae (*Lycoteuthis*)

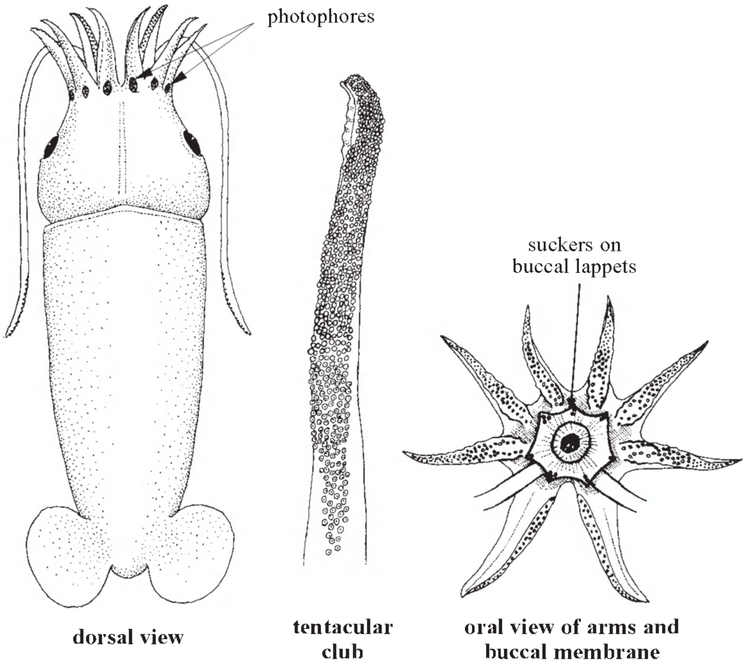


ventral view

Fig. 51 Histioteuthidae (*Histioteuthis*)

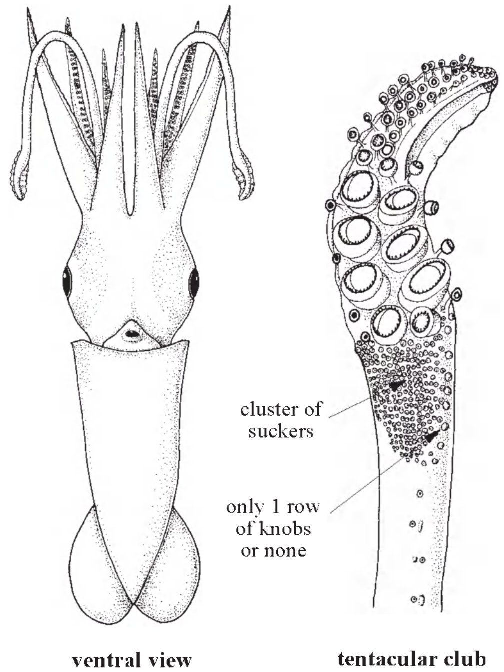
[6/] *Walvisteuthis*, the sole genus in a formerly recognized family, Walvisteuthidae, now considered to belong to the family Onychoteuthidae by an authoritative fraction of the scientific community (i.e. Young *et al.*, 2003). It is placed in the Key to indicate its unique characters within Onychoteuthidae.

22a. Minute suckers present on oral surface of buccal membrane/lappets (Fig. 52) . . . . . . **Family Bathyteuthidae**
22b. No suckers on oral surface of buccal membrane/lappets . . . . → **23**



dorsal view tentacular club oral view of arms and buccal membrane

Fig. 52 Bathyteuthidae (*Bathyteuthis*)

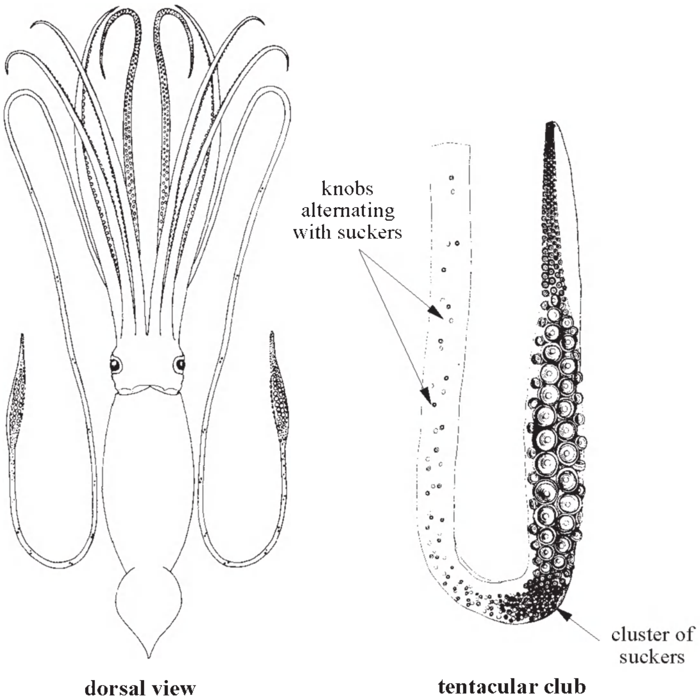


ventral view tentacular club

Fig. 53 Neoteuthidae (*Alluroteuthis*)

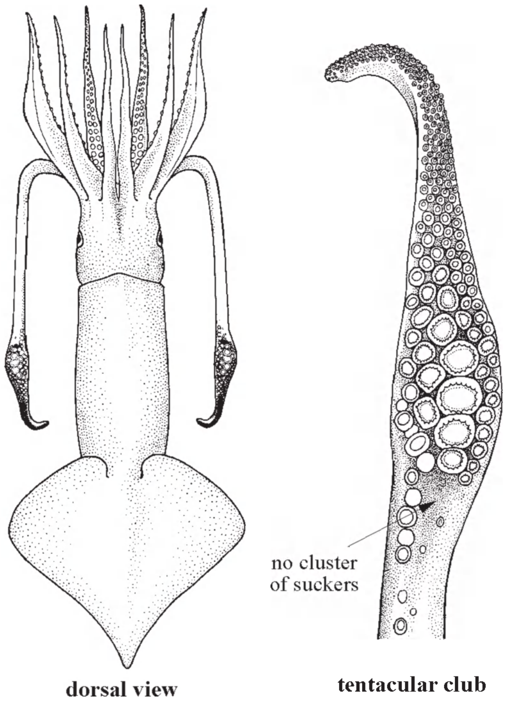
23a. Many small to minute suckers (or suckers and knobs) at proximal (carpal) end of manus (Figs 53 and 54) . . . . . . → **24**
23b. No cluster of small suckers at proximal (carpal) end of manus (Fig. 55) . . . . **Family Psychroteuthidae**

24a. Posterior borders of fins slightly convex; carpal knobs in a single dorsal row or absent; adults attain small size (Fig. 53) . . . . **Family Neoteuthidae**
24b. Posterior borders of fins concave; carpal knobs in a cluster alternating with carpal suckers; adults attain gigantic size (Fig. 54) . . . . **Family Architeuthidae**



dorsal view tentacular club

Fig. 54 Architeuthidae (*Architeuthis*)



dorsal view tentacular club

Fig. 55 Psychroteuthidae (*Psychroteuthis*)

25a. Funnel-locking cartilage with a longitudinal and a transverse groove: ⊥-shaped or ⊣-shaped (Fig. 36b and c) . . . . → **26**

25b. Funnel-locking cartilage (sub)triangular or oval with or without inward projecting knobs (Fig. 36d, e and f) . . . . → **27**

26a. Funnel-locking cartilage with a longitudinal groove crossed by a transverse groove at its posterior end, ⊥-shaped (Fig. 36b); fins less than 60% of mantle length (Fig. 56) . . . . **Family Ommastrephidae**

26b. Funnel-locking cartilage with a longitudinal groove from which a shorter groove branches medially, ⊣-shaped (Fig. 36c); fins more than 80% of mantle length (Fig. 57) . . . . **Family Thysanoteuthidae**

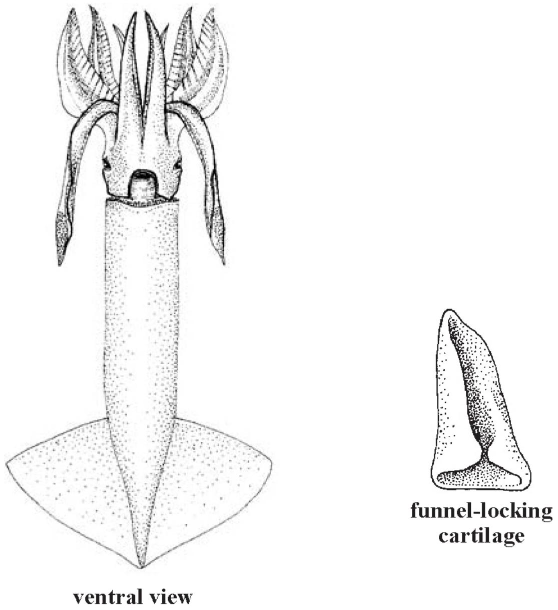


Fig. 56 Ommastrephidae (*Ommastrephes*)

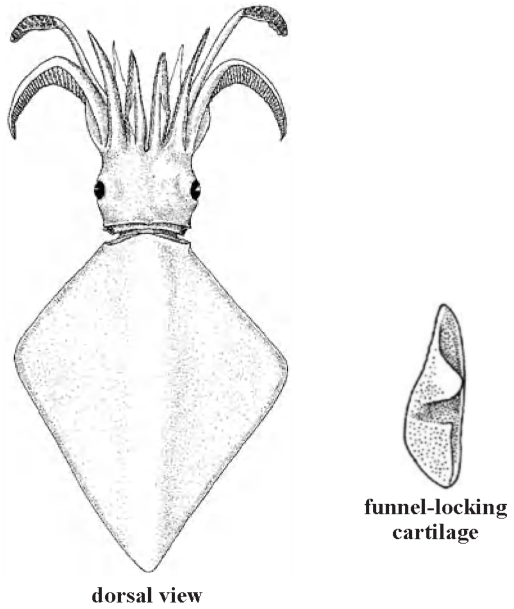


Fig. 57 Thysanoteuthidae (*Thysanoteuthis*)

27a. Funnel-locking cartilage oval with 1 or 2 knobs directed toward the centre of the concavity (Fig. 36d) . . . . . . → **28**

27b. Funnel-locking cartilage oval or subtriangular, without knobs (Fig. 36e and f) . . . . → **29**

28a. Club with only 4 longitudinal rows (series) of suckers (Fig. 58) . . . . **Family Chiroteuthidae**

28b. Club with many (more than 15) longitudinal rows (series) of minute suckers (Fig. 59) . . . **Family Mastigoteuthidae**

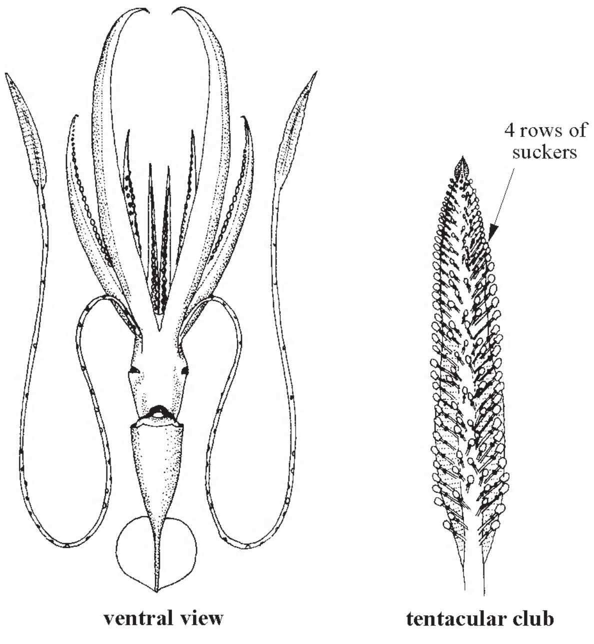


Fig. 58 Chiroteuthidae (*Chiroteuthis*)

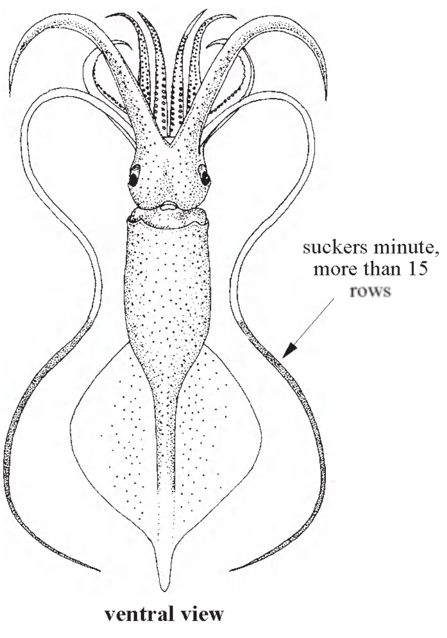


Fig. 59 Mastigoteuthidae (*Mastigoteuthis*)

29a. Suckers on arms in 4 to 6 longitudinal rows (series) . . . . → **30**

29b. Suckers on arms in 2 longitudinal rows (series); tail short (less than half of mantle length) or absent . . . . → **31**

30a. Six longitudinal rows (series) of suckers on arms I to III, 4 longitudinal rows of suckers on arms IV; tail extremely long (greater than mantle length), as a spike-like extension of the gladius; no fins on tail (Fig. 60) . . . . **Family Joubiniteuthidae**

30b. Three or 4 longitudinal rows (series) of suckers proximally on all arms; fins terminal, extremely long and broad, extend far posterior to mantle; gladius incorporated in fins to posterior tip (Fig. 61) . . . . **Family Magnapinnidae**

31a. Suckers on tentacular club in 4 longitudinal rows (series); mantle free dorsally (Fig. 62). . . . . **Family Cycloteuthidae**

31b. Suckers on tentacular club in 8 or more longitudinal rows (series); mantle fused dorsally to head (Fig. 63) . . . . **Family Promachoteuthidae**

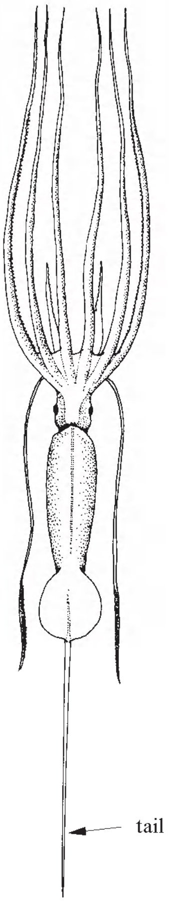


Fig. 60 Joubiniteuthidae (*Joubiniteuthis*)

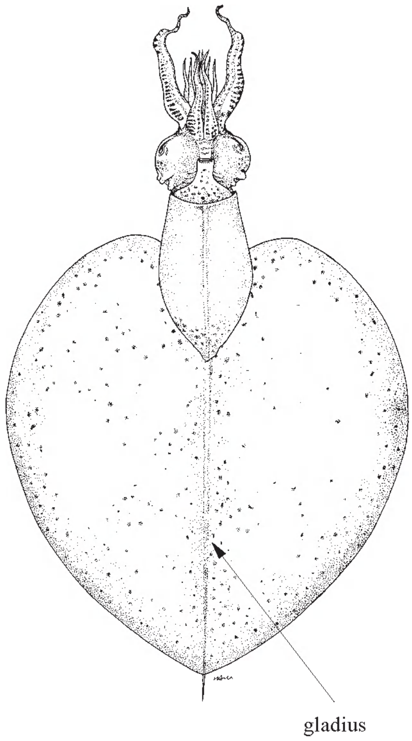


Fig. 61 Magnapinnidae (*Magnapinna*)

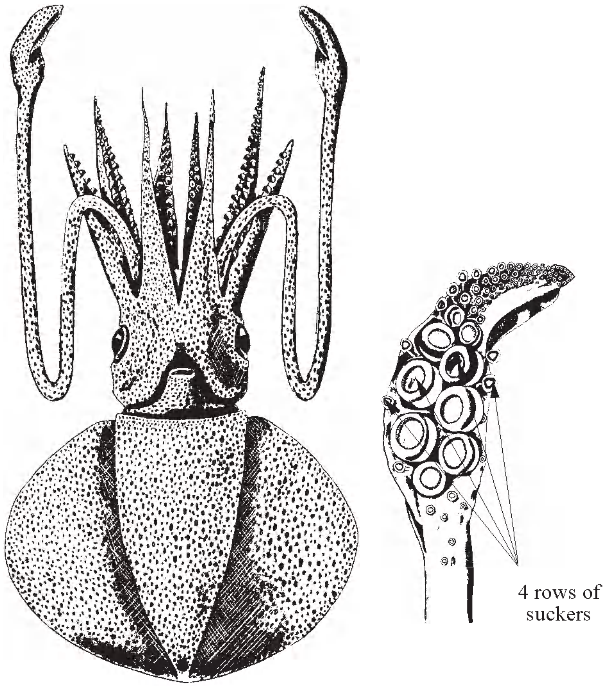


Fig. 62 Cycloteuthidae (*Discoteuthis*)

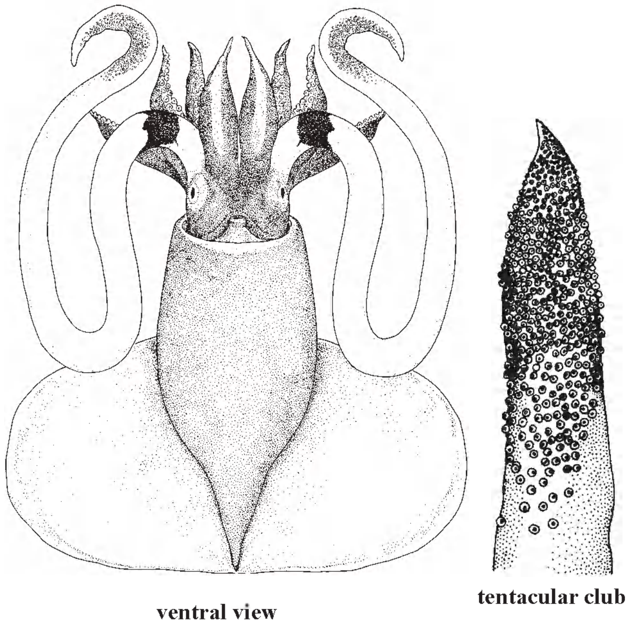


Fig. 63 Promachoteuthidae (*Promachoteuthis*)

32a. Mantle free dorsally, articulates with head by ridge and groove (Fig. 64). . . . . **Family Grimalditeuthidae**

32b. Mantle fused dorsally with head (Fig. 65) . . . . **Family Cranchiidae**

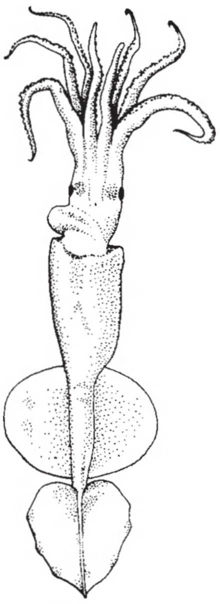


Fig. 64 Grimalditeuthidae (*Grimalditeuthis*)

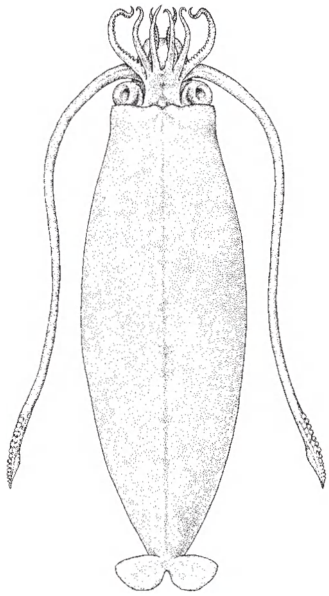


Fig. 65 Cranchiidae (*Helicocranchia*)

2. SQUIDS

by Patrizia Jereb and Clyde F.E. Roper

The origin of "true" squids can be traced to the early Mesozoic (Permian/Triassic) with steady proliferation from the Jurassic through the Recent. The two main groups[1/], Myopsid squids, "covered-eyed", near-shore (neritic) squids, and Oegopsid squids, "open-eyed" oceanic (pelagic) squids, occur in the oceans and seas of the world and together form the basis of the major cephalopod fisheries production. Some species are demersal or epibenthic at some period of their life cycle, but most occur in the water column.

Diagnostic Features: Ten circumoral appendages, the fourth pair, the tentacles, contractile, **but not retractile** into pockets (occasionally tentacles secondarily lost); sucker ornamentation with chitinous rings and/or hooks. Radula teeth commonly with primary (large) projection and a secondary (smaller) cusp(s), especially on the median (rachidian) and the first lateral teeth; buccal membrane present. Olfactory organ consists of 2 projecting papillae; eyes without lids either (1) covered with a transparent membrane, with a minute pore (Myopsid squids) or (2) not covered with a membrane, but completely open to the sea (Oegopsid squids). Gills with branchial canal between afferent and efferent branchial blood vessels. Digestive gland (liver) consists of a single structure. Shell (pen or gladius) internal, simple, rod- or feather-like, chitinous.

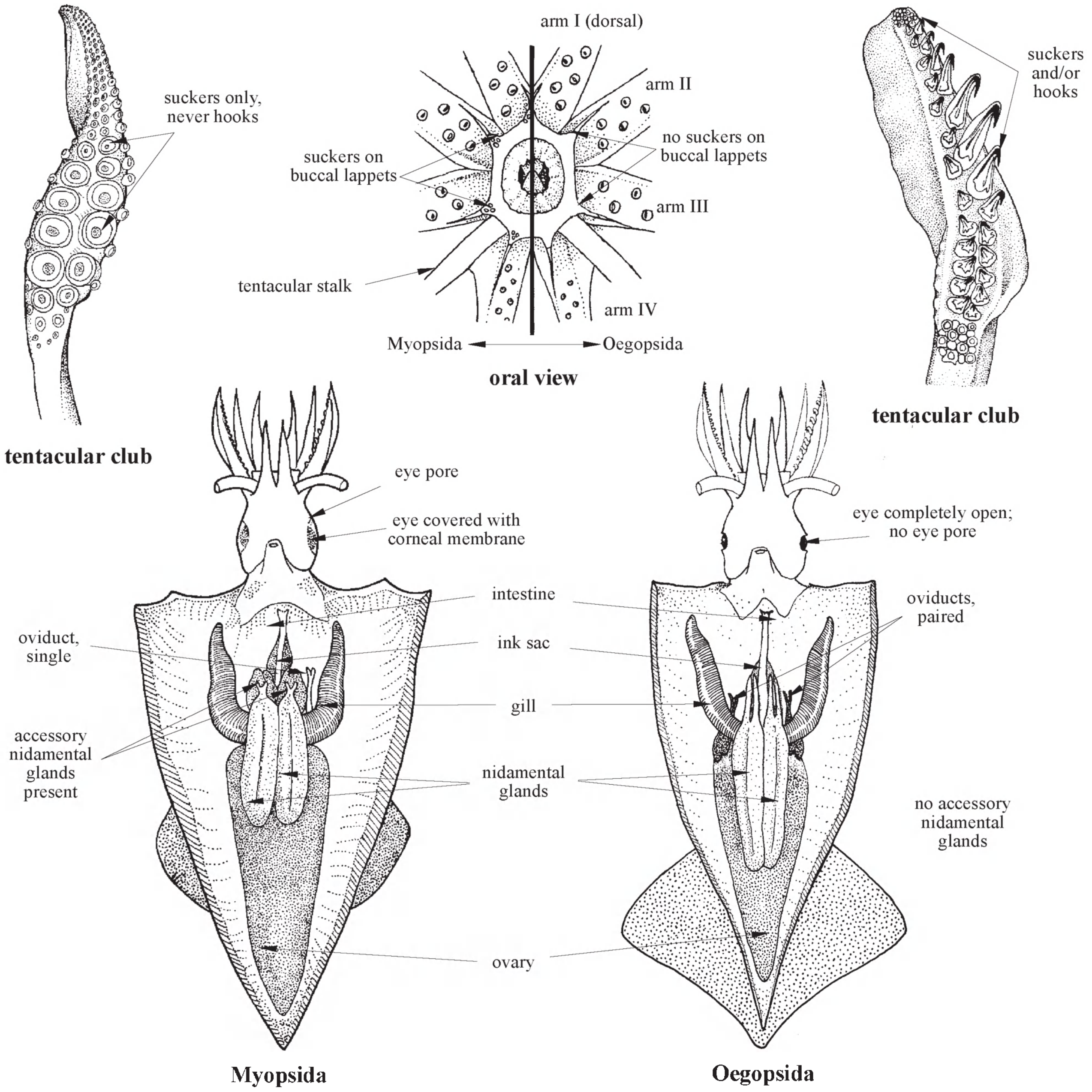


Fig. 66

[1/] As referred to in this Catalogue because of the unsettled nomenclatureal situation at the time of publication.

Myopsid Squids

Diagnostic Features: Corneal membrane covers the eye, with a minute pore, anteriorly, in most species. Eyes without secondary (= ventral) eyelid. Head **with tentacle pocket**. Suckers usually present on the buccal lappets. Funnel without lateral adductor muscles. Arms and clubs with suckers, **never with hooks**. Club **without carpal-locking apparatus**. Shell a gladius, that extends the full length of the mantle. **Right** oviduct **absent**. **Accessory** nidamental glands **present**.

Size: From very small, dwarf-sized species (maximum recorded ML 20 to 22 mm) to rather large squids (over 900 mm ML).

Geographical Distribution: Myopsid squids are widely distributed near shore in all oceans and seas of the world.

Habitat and Biology: All myopsid squids are demersal, predominantly near-shore or shelf species, that frequently feed near or on the bottom. Squids of the Australiteuthidae have not been observed alive. The Loliginidae contains species which can reach a rather large size (at least 900 mm ML in ***Loligo forbesii***), along with dwarf species, like those of ***Pickfordiateuthis***, where males may mature at less than 14 mm mantle length. Some species tolerate reduced salinities and estuarine situations, like, for example, ***Lolliguncula brevis*** in the western North Atlantic. Many species show characteristic onshore-offshore migrations in spring and late autumn respectively, overwintering in deeper waters. The spawning season often is extended with peaks in early summer and autumn. Mating and spawning normally occur near the bottom, where the egg masses are attached to shells and other substrates.

Normally, many small eggs are encapsulated in gelatinous strings (strands of fingers) attached to the substrate, where they develop and hatch without parental care.

Interest to Fisheries: While the small-sized Austaliteuthidae squids are of no commercial interest, many squids of the family Loliginidae represent an important resource for many industrial and small-scale fisheries world-wide. FAO’s fishery yearbook (FAO, 2009) reports about 365 000 tonnes of Loliginid squids caught in 2007, i.e. about 11.3% of the total squid catch for that year. Of this, about 98% is reported to belong to the genus ***Loligo***, a designation that includes species at present placed in other genera/subgenera, following the consensus determined by international experts of the Cephalopod International Advisory Council in Phuket, Thailand, in 2003 (Vecchione *et al*., 2005).

Remarks: Myopsid squids comprise only 2 families: the monotypic Australiteuthidae (described from the inshore waters of Northern Australia), with 1 genus and 1 very small-sized species, and the very speciose Loliginidae that currently is recognized to include 10 genera, with 9 described subgenera and 47 species.

Literature: Naef (1916, 1923), Roper *et al*. (1984), Nesis (1982, 1987), Sweeney and Vecchione (1998), Okutani (2005), Vecchione *et al*. (2005), Vecchione and Young (2008c).

2.1 Family AUSTRALITEUTHIDAE Lu, 2005

by Patrizia Jereb, Clyde F.E. Roper and Michael Vecchione

Australiteuthidae Lu, 2005, *Phuket Marine Biological Center Research Bulletin*, No. 66: 72 -82, figs 1-9. [72].

Type Genus: *Australiteuthis* Lu, 2005: 72.

FAO Names: En – Australasian inshore squid; **Fr** – Petite calmars Australiennes; **Sp** – Calamaretos Australianos.

Diagnostic Features: Myopsid squid with subcircular funnel-locking cartilage, bisected by a boomerang-shaped groove that extends anteroposteriorly. **A dumb-bell-shaped photophore** of sepiolid type occurs **on ventral surface of ink sac. Fins separated**, not united at posterior ends.

Size: Very small-sized squid; maximum mantle length to about 30 mm.

Geographical Distribution: North and Western Australia, Papua New Guinea, Indo-West Pacific.

Remarks: The family Australiteuthidae has some sepiolid characters, such as the deep “tentacular” pockets into which tentacles are retracted, the presence of a sepiolid-type photophore on the ink sac and the lack of acquiferous pores in the cornea. However, it also has some primarily teuthid-type characters, such as tricuspid rachidian teeth, buccal membrane connectives attached to the arm and the absence of eyelids. Within the suborder Myopsida, only one other family is known, the Loliginidae. Australiteuthidae joins the Myopsida because of the shared character of a corneal membrane. It differs from Loliginidae, however, by the shape of the funnel-mantle locking-apparatus and the absence of an aquiferous pore in the cornea. The family is monotypic.

Literature: Lu (2005), Vecchione and Young (2008b).

Australiteuthis Lu, 2005

Australiteuthis, Lu, 2005, *Phuket Marine Biological Center Research Bulletin*, No. 66:72 -82, figs 1-9[72].

Type Species: *Australiteuthis aldrichi* Lu, 2005: 72.

Diagnostic Features: As given for the family.

Geographical Distribution: As given for the family.

Remarks: The genus ***Pickfordiateuthis***, formerly placed in its monotypic family, was incorporated into the Family Loliginidae by Brackoniecki (1996). ***Australiteuthis*** shares similarities with ***Pickfordiateuthis*** in the "sepiolid-like" separated fins, though not so distinct; the radular teeth and the gladius also are similar. However, the two genera differ significantly in the funnel-locking apparatus configuration, and ***Pickfordiateuthis*** lacks the photophore on the ventral surface of the ink sac that is very prominent in ***Australiteuthis***. The genus is monotypic.

Literature: As given for the family.

Australiteuthis aldrichi Lu, 2005

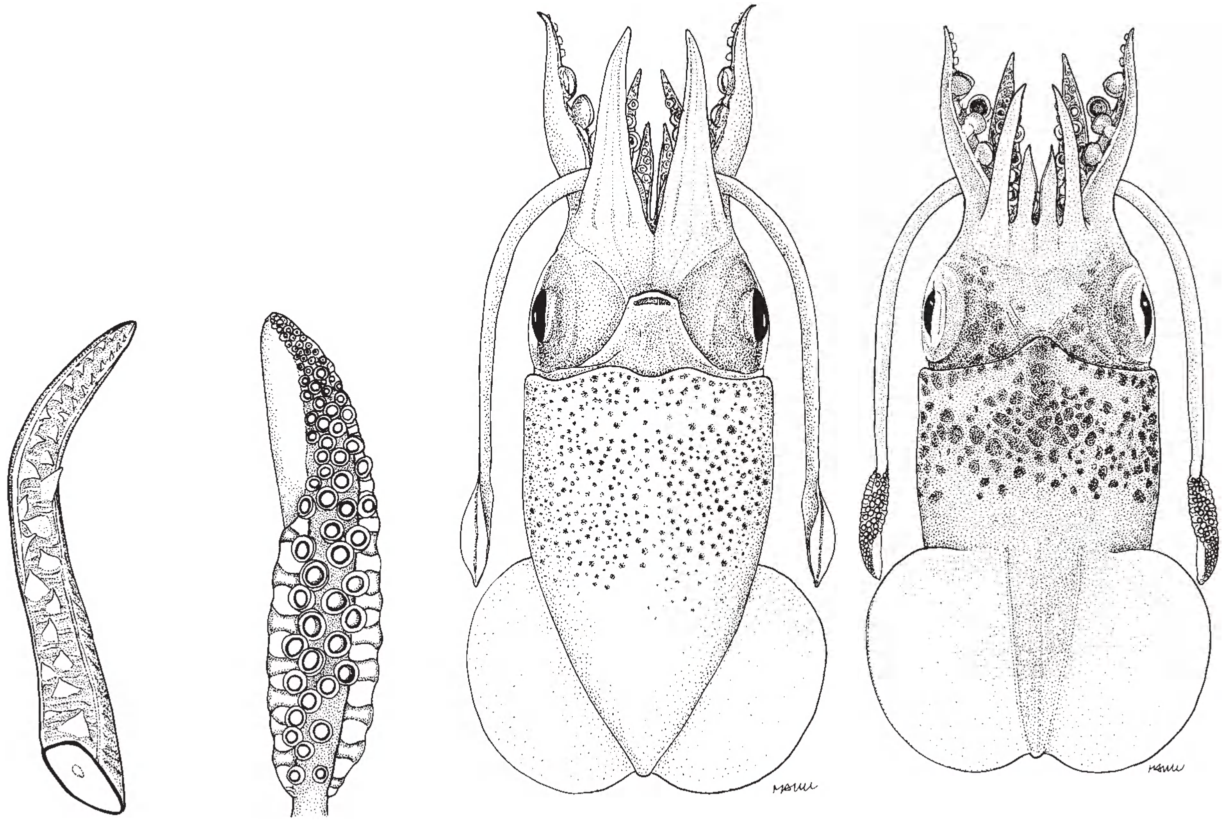
Fig. 67

Australiteuthis, Lu, 2005, *Phuket Marine Biological Center Research Bulletin*, No. 66:72–82, figs 1-9. [72]. [Type locality: 14°07.30'S 28°02.00' E, Joseph Bonaparte Gulf, Western Australia].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Aldrich's Australasian inshore squid; **Fr** – Petite calmar Australien de Aldrich; **Sp** – Calamareto Australiano de Aldrich.



hectocotylus **tentacular club** **ventral view** **dorsal view**

Fig. 67 *Australiteuthis aldrichi*

Diagnostic Features: Eyes covered with transparent cornea, but without aquiferous pores. Funnel-locking cartilage large, subcircular, bisected by a boomerang-shaped groove that runs anteroposteriorly; anterior wing of groove with wide anterior end; groove deepens and becomes slightly narrower posteriorly to form a deep, broad pit, that in turn becomes a narrow, shallow groove posteriorly and curves medially to form posterior wing or "boomerang". Left ventral arm hectocotylized by the reduction in size of suckers of the whole arm to a tiny swelling on top of enlarged conical-shaped sucker stalks. **A sepiolid-like, dumb-bell- shaped photophore is present on the ventral surface of the ink sac**. **Fins separated at posterior ends**.

Size: Very small species; 15 mm to 28 mm mantle length.

Geographical Distribution: Currently known from the Joseph Bonaparte Gulf of Western Australia, the inshore waters of the Northern Territory, Australia, and the Gulf of Papua, Papua New Guinea (PNG). Probably broadly distributed along coastal regions of northern Australia and southern PNG (Fig. 68).

Habitat and Biology: The species was known from about 3 dozen specimens at the time of the original description. They were captured in near-shore waters from 9 to 61 m deep with beam trawls (when gear type was listed). This species probably is a benthic to epibenthic form on soft substrates. Males are reported to mature around 17 mm mantle length and females at a larger size, over 22 mm mantle length.

Interest to Fisheries: None.

Local Names: None reported.

Remarks: The very small size and the apparently sparce abundance of this species make it an unlikely candidate for a fishery.

Literature: Lu (2005), Lu and Young (2005).

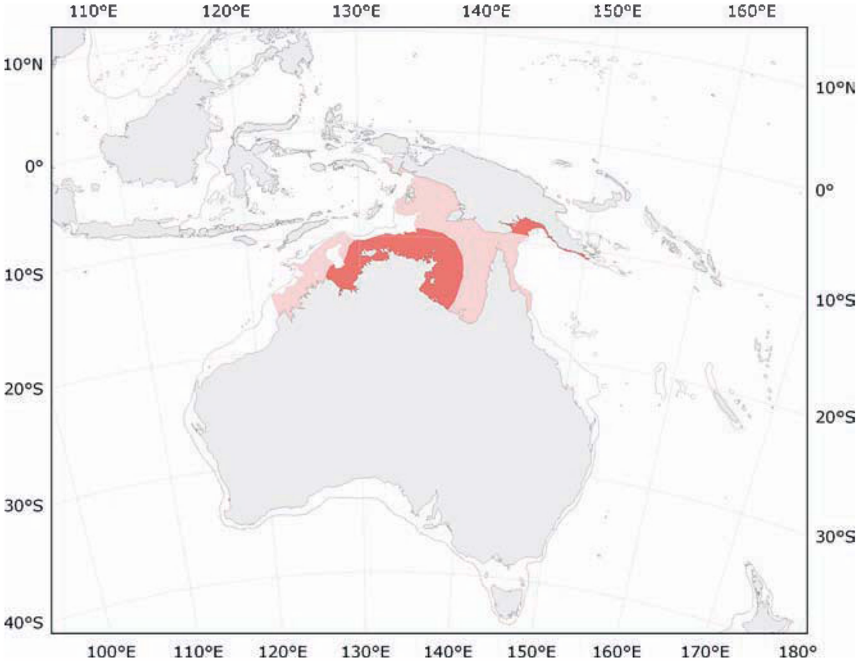


Fig. 68 ***Australiteuthis aldrichi***

🟥 Known distribution ▨ Probable presence

2.2 Family LOLIGINIDAE Lesueur, 1821

by Patrizia Jereb, Michael Vecchione and Clyde Roper

Loligoidea Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101, 7 pls [89].

Type Genus: *Loligo* Lamarck, 1798: 130.

FAO Names: En – Inshore squids; **Fr** – Calmars; **Sp** – Calamares.

Diagnostic Features: Transparent skin (corneal membrane) covers eye lens; with aquiferous pore. Funnel-locking apparatus a simple, straight groove and ridge. Fins attach to lateral regions of mantle. Arms with suckers in 2 series. Tentacular club with suckers usually in 4 series (2 series in at least manal region of ***Pickfordiateuthis*** clubs). **Hooks never present**. Buccal connectives attach to ventral margins of ventral arms (arms IV). **Seven buccal lappets possess small suckers in many species**. Usually the left arm of the ventral pair is hectocotylized in males; structure of the modified portion of the hectocotylus is useful as a species diagnostic character. **Females with a single oviduct and with accessory nidamental glands**. Eggs spawned in finger-like egg masses attached to substrate. Paralarvae are not radically different in appearance from adults. **Colour**: usually reddish brown, darker dorsally, but quite variable depending on behaviour.

Size: Small- to medium- and large-sized squid; maximum mantle length 937 mm (i.e. ***Loligo forbesii*** male from the Azores).

Geographical Distribution: Worldwide, in tropical, temperate and subpolar coastal waters.

Habitat and Biology: Loliginids are demersal, near-shore or shelf species. Various species occur from very shallow water in bays and estuaries, over grass flats and coral reefs, to water over 700 m depth (e.g. during seasonal offshore migrations). Loliginids are important prey for numerous groups of fishes, sharks, marine mammals, seabirds and squids.

Interest to Fisheries: Loliginids are mostly small to medium-sized squids that occur along coastal margins and continental shelves, primarily in warm to temperate waters world-wide. They form one of the major groups of commercially utilized cephalopods. Some species support extensive fisheries in several parts of the world, as the flesh is of excellent quality. As finfish populations have become overfished and exhausted, cephalopod landings have increased dramatically in some regions. For example, in the Gulf of Thailand, the finfish landings in the 1970s and 1980s declined, while landings of loliginids increased annually, to become consistently the most abundant landings.

Remarks: Other squid families that include commercial-sized species of present potential interest to fisheries (e.g. Ommastrephidae, Thysanoteuthidae, Onychoteuthidae) all lack suckers on the buccal lappets and have eye lenses open to the sea, not covered by a transparent corneal membrane. Variation in loliginids can be prominent and is a natural phenomenon. Nesis (1998) addressed the situation of several partly or wholly sympatric intraspecific groupings of squids that differ "only" in size at maturity (early- or late-maturing populations) and/or spawning season. Some groupings seem to maintain these spatial-temporal units that may represent a separate stock of a population or supra-population rank. However, such a stability and consistency in differences is not the case with the groupings of ***Doryteuthis (Amerigo) gahi*** from the same region (Carvalho and Nigmatullin 1998). Also, it is not the case with the Japanese species groups of warm-season spawning and cold-season spawning ***Uroteuthis (Photololigo) edulis*** (Natsukari and Tashiro 1991). This phenomenon is an example of incipient speciation, and such species complexes are well recognized in other loliginids, e.g. ***Loligo vulgaris*** and ***Loligo forbesii***, each of which is represented by distinct entities.

The systematics of this family has long been problematic (Vecchione *et al*., 1998b). A workshop on loliginid systematics was convened during the 2003 meeting of the Cephalopod International Advisory Council held in Phuket, Thailand (Vecchione *et al*., 2005). One goal of the workshop was to resolve conflicting generic-level classifications of the family in light of recent observations and cladistic analyses on morphological (e.g. Alexeyev, 1989; 1992 [1991]; Anderson, 1996; 2000b) and molecular (e.g. Anderson, 2000a; 2000b) characters. Among other conclusions, the workshop participants decided that the genus ***Loligo*** sensu Vecchione *et al*. (1998b) is paraphyletic and must be reorganized into geographic groups in order to be consistent with molecular inferences; currently, no morphological characters are known to distinguish these genera consistently. The assembled taxonomic experts reached consensus on the following classification:

Table 1

Taxonomic classification

Genus	Subgenus	species included
Loligo		*forbesii, reynaudii, vulgaris*
Afrololigo		*mercatoris*
Alloteuthis		*africana, media, subulata*
Doryteuthis	*Doryteuthis*	*plei, roperi*
	Amerigo	*gahi, ocula, opalescens, pealeii, surinamensis*
	subgenus undescribed	*sanpaulensis*
Heterololigo		*bleekeri*
Loliolus	*Loliolus*	*affinis, hardwickei*
	Nipponololigo	*beka, japonica, sumatrensis, uyii*
Lolliguncula	*Lolliguncula*	*argus, brevis, panamensis*
	Loliolopsis	*diomedeae*
Pickfordiateuthis		*bayeri, pulchella, vossi*
Sepioteuthis		*australis, lessoniana, sepioidea*
Uroteuthis	*Uroteuthis*	*bartschi*
	Aestuariolus	*noctiluca*
	Photololigo	*abulati, arabica, bengalensis, chinensis, duvaucelii, edulis, machelae, robsoni, sibogae, singhalensis, vossi*
	subgenus undetermined	*pickfordi, reesi*

Literature: Naef (1912a, b), Adam (1954), Roper *et al*. (1984), Alexeyev (1989, 1991, 1992), Brakoniecki (1986), Okutani *et al*. (1987), Nesis (1998), Vecchione *et al*. (1998b), Dunning (1998d), Sweeney and Young (2003o),Vecchione *et al*. (2005), Jereb and Roper (2006), Hastie *et al*. (2009).

Key to the genera of Lologinidae

1a. Suckers in 2 series on proximal tentacular clubs; fins with rounded posterior lobes, not joined posteriorly . . . . ***Pickfordiateuthis***

1b. Suckers in 4 series on proximal tentacular clubs; fins extend to posterior end of mantle, without rounded posterior lobes . . . . ***→ 2***

2a. Fins in adults occupy >85% of mantle length, combined shape broadly elliptical . . . . ***Sepioteuthis***

2b. Fins in adults occupy <70% of mantle length, round or rhomboidal . . . . ***→ 3***

3a. Fins in adults wider than long, round or auriform, not rhomboidal; mantle short, stout, broadly rounded posteriorly . . . . ***→ 4***

3b. Fins in adults rhomboidal, longer than broad, not round; mantle elongate, pointed posteriorly . . . . ***→ 6***

4a. Hectocotylus with ventral crest formed by fusion of the protective membrane with the ventral row of papillae . . . . ***Loliolus***

4b. Hectocotylus without ventral crest . . . . ***→ 5***

5a. American distribution; suckers on midsections of lateral arms of males not greatly enlarged . . . . . ***Lolliguncula***

5b. West African distribution; suckers on midsections of lateral arms of males greatly enlarged . . . . ***Afroloigo***

6a. A pair of photophores on ventral surface of ink sac . . . . ***Uroteuthis***

6b. No photophores on ventral surface of ink sac . . . . ***→ 7***

7a. Northwestern Pacific distribution; dorsal series of papillae and trabeculae at distal tip of modified hectocotylus form bicuspid lamelliform flaps separated from ventral series of suckers by serrated membrane . . . . ***Heterololigo***
7b. Not northwestern Pacific; hectocotylus tip not as above . . . . ***→ 8***

8a. American distribution . . . . ***Doryteuthis***
8b. Eastern Atlantic distribution. . . . . ***→ 9***

9a. Gladius with a small rostrum, posterior mantle elongated as a tail-like structure . . . . ***Alloteuthis***
9b. No rostrum on gladius, elongation of posterior mantle not extreme and tail-like . . . . ***Loligo***

Loligo Lamarck, 1798

Plate III, 12 & 13

Loligo Lamarck, 1798, *Bulletin des Sciences par la Société Philomatique*, 2(5):129–131 [130].

Type Species: *Loligo vulgaris* Lamarck, 1798: 130.

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Hectocotylus with proximal suckers unmodified; ventral crest absent; suckers in modified portion of reduced size; sucker stalks elongated to form papillae in either dorsal or both dorsal and ventral series. **Fins posterior**. **Eggs small to moderate sized – less than 4 mm**. Spermatophore cement body short. Photophores absent.

Size: Small- to medium- and large-sized squids; maximum recorded mantle length 937 mm.

Geographical Distribution: Eastern Atlantic Ocean and Mediterranean Sea.

Habitat and Biology: As given for the family.

Literature: As given for the family.

Loligo vulgaris Lamarck, 1798

Fig. 69

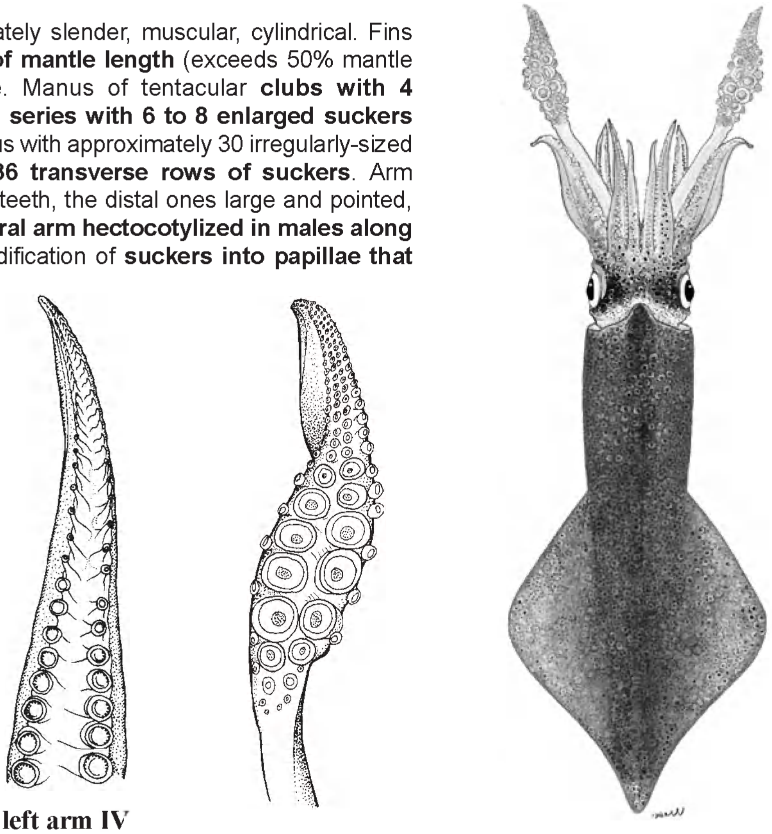
Loligo vulgaris Lamarck, 1798, *Bulletin des Sciences par la Société Philomatique*, 2(5):129–131 [130]. [Type locality: Not designated].

Frequent Synonyms: *Loligo pulchra* Blainville, 1823, *Loligo rangii* Ferussac, 1835, *Loligo berthelotii* Verany, 1839a, *Loligo neglecta* Gray, 1849, *Loligo breviceps* Steenstrup, 1862, *Loligo mediterranea* Targioni-Tozzetti, 1869, *Loligo affinis* Lafont, 1871, *Loligo microcephala* Lafont, 1871.

Misidentifications: *Loligo forbesii* (formerly, multiple authors).

FAO Names: En – European squid; **Fr** – Encornet européenne; **Sp** – Calamar europeo.

Diagnostic Features: Mantle long, moderately slender, muscular, cylindrical. Fins rhomboidal, their length **up to two-thirds of mantle length** (exceeds 50% mantle length), posterior border slightly concave. Manus of tentacular **clubs with 4 longitudinal series of suckers; 2 median series with 6 to 8 enlarged suckers each**; sucker rings of median series on manus with approximately 30 irregularly-sized and distributed teeth; **clubs with about 36 transverse rows of suckers**. Arm suckers biserial; sucker rings with about 20 teeth, the distal ones large and pointed, the proximal ones small or absent. **Left ventral arm hectocotylized in males along its distal one-third to one-quarter** by modification of **suckers into papillae that decrease in size distally**.



left arm IV hectocotylized

tentacular club

dorsal view

Fig. 69 *Loligo vulgaris*

Size: Maximum mantle length 640 mm in males, 485 mm in females (West African coast); maximum body weight, 2.3 kg for the same males, 1.32 kg for a slightly smaller female from the English Channel.

Geographical Distribution: Eastern Atlantic Ocean: from approximately 55°N, around the British Isles, the North Sea (including the Skagerrak, the Kattegat and the western Baltic Sea), to 20°S, off the southwestern coast of Africa, including Madeiran waters. Mediterranean Sea: from the western to the eastern basins, including the Adriatic Sea (Fig. 70).

Habitat and Biology: A neritic species that inhabits the circumlittoral region in temperate waters, the European squid ranges in depth from the surface down to the upper slope (200 to 500 m), mainly near coasts with abruptly sloping bottoms, but it is more abundant in waters shallower than 100 m in most of its range. It occurs mainly over coarse sand bottoms, but it also is reported over silt and other different mixtures of sediments and terrain, including sea grass beds. It lives in water temperatures that range from 12.5° to 20°C, with salinity ranges of between 30 psu (North Atlantic) and 38 psu (western Mediterranean), but it can tolerate lower salinity waters, e.g. Sea of Marmara. *Loligo vulgaris* generally has a pelagic habitus, but it becomes more dependent on the bottom during spawning seasons. Animals, especially young individuals, perform daily vertical migrations mainly related to feeding; they remain close to the bottom during the day, then disperse into the water column at night. Vertical as well as horizontal migrations in response to changes in environmental conditions also are known. The northeastern Atlantic population overwinters in deeper waters off the French coasts then migrates farther north from May through June-July, into the North Sea to spawn. A similar migration from the Bay of Biscay and more southern waters to the English Channel probably also occurs. Southward migrations take place in the autumn. Offshore and onshore migrations related to reproduction also occur. In the western Mediterranean, European squid migrate into deeper water in late autumn; the largest individuals begin their onshore migration as early as January and February, followed in summer by the smaller ones. Sex ratios slightly different from the usual 1:1 value may occur along the distributional range of the species. In

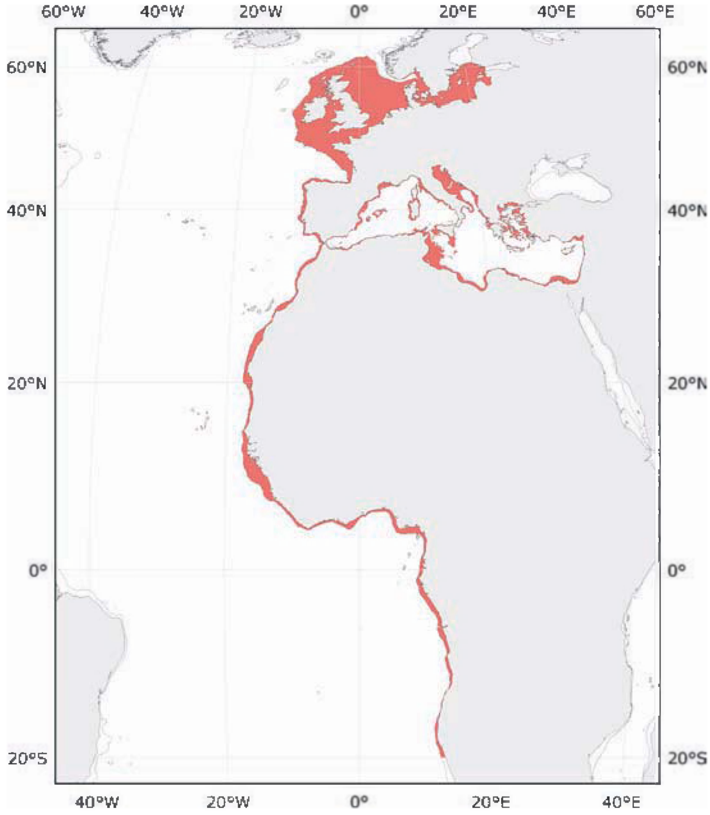


Fig. 70 *Loligo vulgaris*

🟥 Known distribution

Atlantic waters, females were found to slightly outnumber males during some parts of the year, while the opposite occurs in some Mediterranean areas. No segregation between sexes has been reported for the Atlantic populations, whereas observations from landings in the western Mediterranean suggest that males and females may congregate in different schools.

No dramatic changes in the general morphology occur with sexual maturity; males attain larger sizes and weights than females, but females generally exhibit higher weights than males at a given length. A north–south (in the Atlantic) and west–east (from the Atlantic towards the eastern Mediterranean) decreasing gradient occurs in the weight to length growth ratio. Size at maturity is variable, depending on the geographic location, but generally males mature at a smaller size than females. The minimum reported size at maturity is 80 mm mantle length for males and 119 mm mantle length for females, with size at 50% mature (ML50) 168 mm and 188 mm mantle length for males and females, respectively, based on samples collected from different areas from the Atlantic Ocean and the Mediterranean Sea. The smaller-maturing males are reported from the Greek seas, the smaller females from the waters off France, while the larger animals for both sexes come from the Saharan Bank region, eastern Atlantic Ocean. Two modes in size at maturity are reported for males from most areas in the Atlantic.

Spawning extends throughout the year in most of the distributional range of the species, usually with 2 seasonal peaks that occur earlier in the south than in the north in Atlantic waters and earlier in the Atlantic than in the Mediterranean. A more restricted spawning period is reported for the North Sea and for the Greek Seas. A potential fecundity of more than 70 000 eggs is estimated for this species; fecundity usually varies with the size of females, as do spermatophore number and size in males, but sometimes small mature females may have a larger number of oocytes than larger-sized mature females. The maximum number of spermatophores reported is slightly over 1 000, and spermatophore length varies between 7.5 and 18 mm. Males reproducing for the second time usually carry more spermatophores than those reproducing for the first time. Eggs are small (diameter about 2 mm), although variability exists in egg size in relation to geographical area; they are deposited in gelatinous capsules (“fingers”) 60 to 160 mm long. Each capsule contains tens of eggs. Capsules are attached in clusters to rocks, debris and other hard objects on sandy to muddy bottoms. Females tend to lay eggs close to or on top other egg masses, so that large clusters of up to 40 000 eggs occur in nature. The individual contribution by a single female is limited to a thousand, up to 6 000, eggs. Apparently certain strains of *Roseobacter* bacteria associated with the accessory nidamental glands function to aid in the production of carotenoids and in the protection of eggs by production of antibiotics and toxins.

Embryonic development lasts from a few weeks to a few months, depending mainly on the ambient water temperature, e.g. 25 to 27 days at 22°C; 30 days at 17°C and 40 to 45 days at 12ºC to 14°C. A longer incubation time increases mortality risks for egg masses attached to the sea bottom; however, slow development at a lower temperature can improve yolk conversion and produce larger hatchlings, likely with increased hatching competence. Consequently, a compromise between longer-versus-shorter incubation time and related characteristics seems to exist. Paralarvae have a planktonic life style that lasts about 2 months. Although specific identification of ***L. vulgaris*** paralarvae is known in samples from the Galician and Portuguese waters, in general, little knowledge exists on this phase of the life cycle of the European squid in the wild, due mainly to the close resemblance with the juveniles of the co-occurring species, ***L. forbesii*** and ***Alloteuthis*** spp. Paralarvae in captivity feed on crustacean and fish larvae and small mysids; occasionally they attack conspecifics, but cannibalism seems not to occur in the wild. Hatchling growth rates are highly variable and strongly dependent on the water temperature. Experimental rearing under very different temperature regimes, i.e. summer-like and winter-like, resulted in sizes twice as large in the summer-like regime. As a consequence, sizes of juveniles and adults are strongly related to the environmental conditions close to hatching times, and growth rates are dependent on the hatching season. Early paralarval growth in ***L. vulgaris*** is exponential. Several mathematical models have been used to describe growth in juveniles and adults, namely, power, exponential, double exponential and logistic models. Differences in the growth rates between sexes also occur; males show higher growth rates than females. In both sexes, however, growth is not isometric and weight increases more slowly than length.

Life span duration based on statolith analysis is estimated to range between 9 and 10 months (southern Portuguese and West Saharan shelf waters) and 1.5 years (north Portuguese waters), considerably shorter than the 2 to 4 years previously estimated on the basis of length frequency analyses. Spawning represents the terminal phase of the life cycle. It progresses with active feeding in between periods of egg releases, as has been noted for other loliginid species. This behaviour is defined as “intermittent terminal spawning”, a strategy that combines with continuous oocyte maturation in the ovary to better utilize the high potential fecundity during the long periods of intermittent spawning.

The European squid feeds mainly on fishes and crustaceans. Cannibalism seldom occurs and no differences in the feeding habits exist between sexes. Young squids feed mainly on planktonic crustaceans and fish larvae, while fish dominate in the diet of adult animals. Diet and food intake vary with season, probably in relation to seasonal changes in the foraging grounds. ***Loligo vulgaris*** is preyed upon by a variety of whales and fishes, including comnmon dolphin, pilot whale, bottlenose dolphin, swordfish, greater amberjack and many other fishes and marine mammals. ***Loligo vulgaris*** is an important intermediate host for the parasitic nematode *Anisakis simplex*, to top-level predators such as marine mammals.

Interest to Fisheries: ***Loligo vulgaris*** is taken throughout its distributional range all the year round, mainly as a by catch of the multi-species bottom and pelagic trawl fisheries. Major fishing grounds are located off Portugal, on the West African Banks and in the western Mediterranean, where the species is caught in the international fisheries with otter trawls and purse seines in daytime and occasionally at night with light attraction. Usually it is landed mixed with ***L. forbesii***, and specific catch statistics are not recorded. In the western Mediterranean, however, it is one of the most important commercial species of cephalopod, and it has the highest market value. Also, it is a secondary target species in the Saharan Bank cephalopod trawl fishery. Throughout its distributional range, the European squid is the object of local artisanal fisheries that deploy a variety of gears, particularly jigs. Some directed small-scale hand-jig artisanal fisheries exist in Spain, Portugal and southern Italy. The species is marketed fresh and frozen. Catches by commercial beach seines in the Thracian Sea (eastern Mediterranean) are affected to a varying degree by meteorological conditions, e.g. temperature, rainfall and local wind conditions, all negatively correlated. Also, in other areas, occurrence and abundance are related to oceanographic conditions, especially to sea temperature and salinity, and seasonal and annual abundance can be markedly variable (e.g. as recently is the case for the Catalan coast, northwestern Mediterranean).

Remarks: Male specimens occasionally may display stripes similar to those typical of ***Loligo forbesii***, on the ventral sides of the mantle; however, these stripes are much smaller, less numerous and less intensely coloured than in ***L. forbesii***. ***Loligo reynaudii*** was proposed to be subspecies of ***L. vulgaris*** (Augustyn and Grant, 1988). However, Vecchione *et al*. (2005) reinstated ***Loligo vulgaris*** and ***Loligo reynaudii*** as distinct species, a decision with which we concur.

Local Names: ALGERIA, BULGARIA, TURKEY, RUSSIA: Kalmar; CYPRUS, GREECE: Kalamari; FRANCE: Encornet; ITALY: Calamaro, Calamaro comune; EGYPT: Sobbeit Totanu; LIBYA: Habbar; MALTA: Kalamar; MOROCCO, SPAIN: Calamar; TUNISIA: Mettik; YUGOSLAVIA: Lignja.

Literature: Naef (1923), Mangold Wirz (1963), Worms (1983a, b), Roper *et al*. (1984), Nesis (1982, 1987), Augustyn and Grant (1988), Guerra (1992), Guerra and Rocha (1994), Boyle and Pierce (1994), Belcari (1999e), Moreno *et al*. (2002), Vecchione (2008e), Hastie *et al*. (2009).

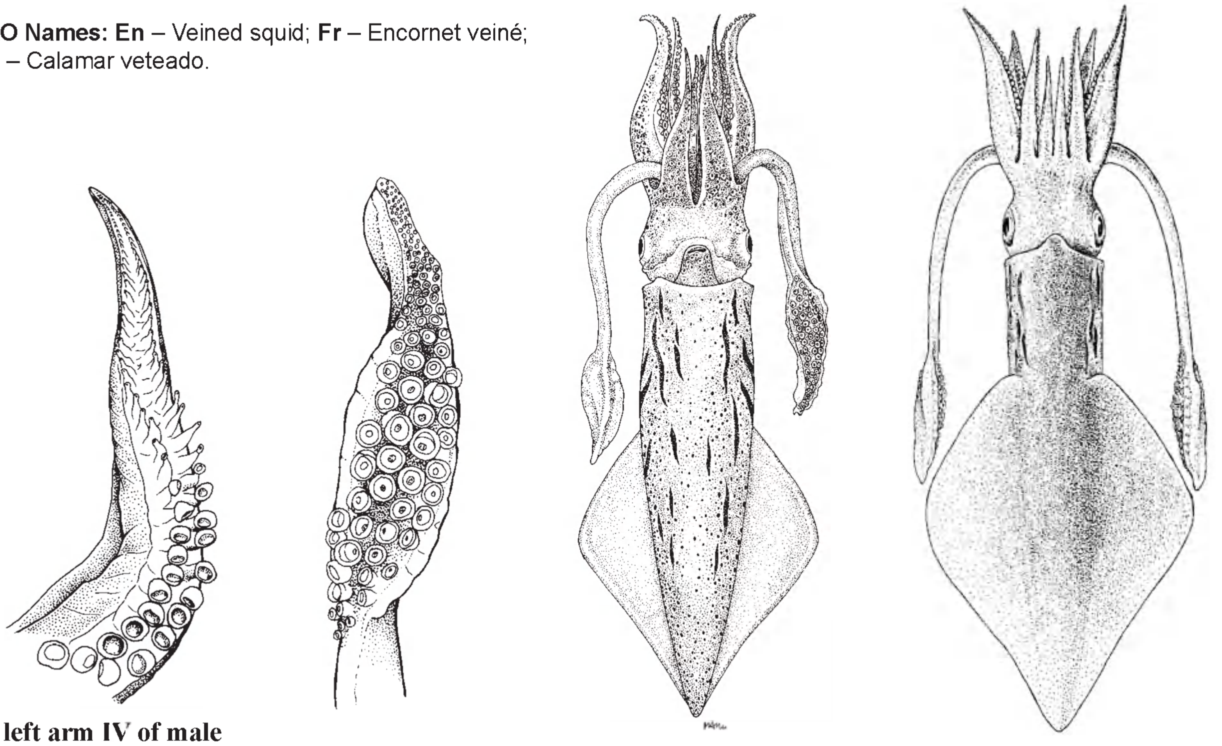
Loligo forbesii Steenstrup, 1856 **Fig. 71; Plate III, 14**

Loligo forbesii Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 4:185-216, 2 pls [189]. [Type locality: Atlantic Ocean].

Frequent Synonyms: *Loligo fusus* Risso, 1854, *Loligo moulinsi* Lafont, 1871.

Misidentifications: *Loligo vulgaris* (formerly, multiple authors).

FAO Names: En – Veined squid; **Fr** – Encornet veiné; **Sp** – Calamar veteado.



left arm IV of male hectocotylized **tentacular club** **ventral view** **dorsal view**

Fig. 71 *Loligo forbesii*

Diagnostic Features: Mantle long, moderately slender, cylindrical; fins rhomboidal, **their length three quarters that of mantle**, their posterior borders slightly concave. **Suckers on manus of tentacular club subequal in size**; sucker rings **regularly toothed** all around, with 13 to 18 larger sharp, conical teeth; largest arm sucker rings with 7 or 8 teeth; **left ventral arm hectocotylized in its distal third** by modification of **sucker stalks into long papillae which gradually decrease in size** distally; **accessory nidamental** glad present **in males**. **Colour**: prominent longitudinal **flame-like stripes** of purplish dark chromatophores on the anterior and ventrolateral surfaces of the mantle.

Size: Maximum mantle length 937 mm in males (8.3 kg weight) and 462 mm in females (2.2 kg weight), for animals from the Azores. Common at smaller sizes (200 to 300 mm mantle length) in the Mediterranean and on the eastern North Atlantic continental shelf.

Geographical Distribution: Eastern North Atlantic: 20°N to 60°N, including the North Sea; absent in the Baltic Sea. It ranges from the Faeroe Islands, along the western European coasts, west to the Azore Islands and south to the Canary Islands, along the West African coast. Its southern boundary is unknown. Occurs throughout the Mediterranean Sea, but early records of the species farther east and south, in the Red Sea and along the east coast of Africa are not confirmed (Fig. 72).

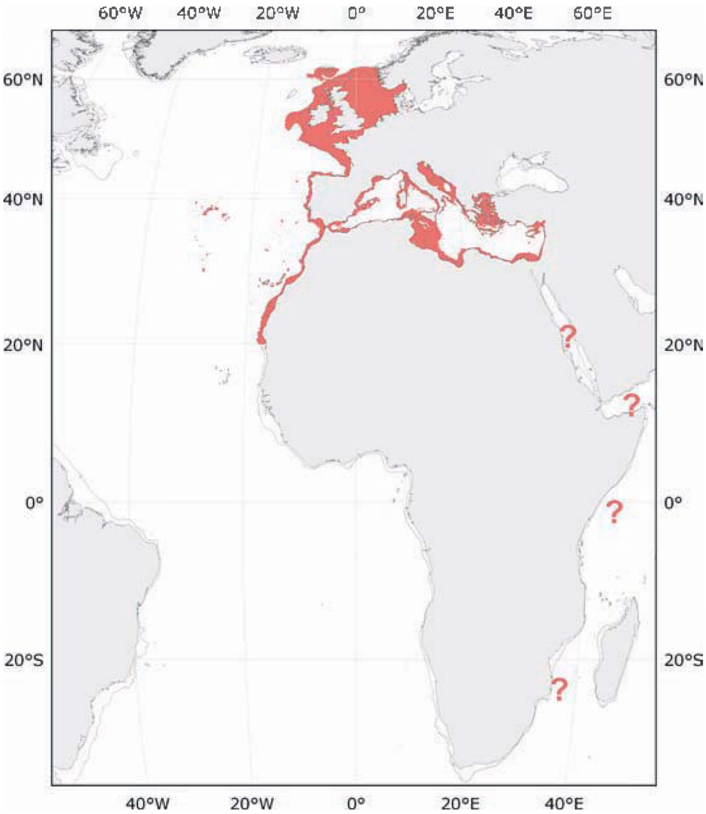


Fig. 72 ***Loligo forbesii***

🟥 Known distribution ◻ Doubtful record

Habitat and Biology: ***Loligo forbesii*** is a species of subtropical and temperate waters; it avoids temperatures below 8.5°C. It occurs over the continental shelf in the temperate part of its distributional range, but it is found in deeper waters in subtropical areas. Its entire vertical range extends from depths shallower than 50 to over 700 m, while the Azores population occurs deeper than 1 000 m. In the Mediterranean Sea, it very seldom occurs in waters less that 80 to100 m depth, and its bathymetric range overlaps only slightly with that of its congener ***Loligo vulgaris***. In Atlantic waters depth distribution varies by season, with squid remaining mostly in waters along the shelf edge (100 to 200 m), then gathering in waters of less than 50 m during the spawning peaks. In the North Sea and in the eastern North Atlantic, squid move inshore during winter, whereas they are more abundant in offshore waters during summer. Seasonal migrations also occur in the southern North Sea area, where the squid spend the summer in the eastern part of the English Channel and southern North Sea, then return to the deeper southwestern part of the Channel in winter. Sea surface temperature (SST), bottom water temperature (BWT) and the North Atlantic Oscillation (NAO) all are critical factors to ***L. forbesii*** abundance. Peak squid abundance in the English Channel coincides with bottom water temperatures of 13°C and squid abundance in the Northeast Atlantic, as well as in the Portuguese and Greek waters, is positively correlated with local SST.

No clear seasonal trend occurs in sex ratio in populations of the eastern North Atlantic waters, although in the Scottish population more young animals are males but adults are mostly females. Sexual dimorphism is striking: males attain much larger sizes and weights than females, but, as in ***L. vulgaris***, females generally exhibit higher weights than males at a given length. Size at maturity is very variable, as is the rule in many loliginids. The smallest mature male measured 80 mm mantle length, and the smallest mature female 103 mm mantle length, both recorded in Portuguese waters; considering the whole northeastern Atlantic range of the species, however, males start to mature at a minimum size around 150 mm mantle length and females around 170 mm mantle length. The Azores population exhibits the largest minimum mature sizes, 240 mm mantle length and 200 mm mantle length for males and females respectively. Two or 3 different size modes of maturity exist in both sexes, but they are more pronounced in males; this makes it less convenient to compute standard parameters like mean size at maturity (i.e. 50% maturity; ML 50).

Spawning occurs nearly throughout the year, with different seasonal peaks that depend on the geographical area, and multiple peaks may occur. For example, most of the Atlantic populations have winter breeding peaks, but secondary peaks may occur in other seasons, including summer. Little information is available on spermatophores. The maximum reported number of spermatophores is slightly over 1 000. Males show a positive relationship between spermatophore length and body length, but a weak relationship between total number of spermatophores and body size; males that mature at a larger size produce fewer but larger spermatophores than those that mature at a small size.

Potential fecundity is low compared with that of ***L. vulgaris***; it varies between 1 000 and 23 000 eggs and it is slightly positively related to the size of the female, but small mature females may have a larger number of oocytes than larger-sized mature females. Permanent oocyte maturation occurs, as it does in ***L. vulgaris***. Eggs are large compared to those of ***L. vulgaris*** and ***L. reynaudii***, about 3 mm x 2 to 2.8 mm, and they are more elongate in shape; they are embedded in the gelatinous substance produced by the oviducal and nidamental glands and then deposited in finger-like strings that usually contain 50 to 130 eggs each. Strings are attached in clusters to hard objects on various kinds of substrate (rocky, sandy or muddy bottoms). The number of egg strings in each cluster is variable and clusters may be formed by strings spawned by more than one female. Because mated females may carry spermatophores of more than one male, each string may be multi-paternal (i.e. fertilized by more than one male). Most egg mass records from the eastern North Atlantic are from shallow waters in inshore areas; only three records exist of deposition in offshore waters, 2 from off the west coasts of Ireland and France at 135 and 507 m depths, and another caught by deep trawlers in the Aegean Sea from 720 to 740 m depth. Since most of the commercial samples that contain spawning animals are obtained from offshore waters, these findings support the hypothesis that ***L. forbesii*** may spawn at those sites, as suggested for this species in the Scottish waters. The scarcity of data may be due to unreported records of trawled egg masses and/or to the squids' preference for rocky substrates inaccessible to the bottom trawl fisheries. Embryonic development duration is closely related to water temperature; it increases as temperature decreases and varies between a few weeks (36 days at 16°C) and a few months (60 to 75 days at 12°C, 140 days at 8°C). Variation of the incubation period of eggs from strings in the same mass range between 45 to 64 days at 12°C; within-string variation in development time occurs in the majority of egg strings, with about 20 days between the first and last hatchling emergence. Such a wide variability in development may assure a spread of paralarval survival and recruitment. Newly hatched animals have mantle lengths between 3.0 and 4.6 mm, and they are already strong swimmers. An optimum temperature range of around 13°C is necessary for normal hatchling development. Growth is rapid, and males grow faster and attain a much larger size than females. As is the case observed in most loliginids, growth rates are higly variable, and growth itself is usually best described by an exponential phase in juveniles, followed by a secondary, slower, logarithmic stage. Several studies on ***L. forbesii*** growth patterns and characteristics in an aquarium include length-frequency, statolith and gladius increment analyses. Much variation in growth rates by sex, maturity stage, season and reproductive strategies exists. Despite the differences in age estimations by different techniques, a life span between 1 and 2 years generally is acknowledged. Sexual differences in the length-weight relationships indicate that females are always heavier than males at a given length.

Spawning represents the terminal phase of the life cycle. As with its congenerics, ***L. forbesii*** is an intermittent terminal spawner, wherein females lay several batches of eggs before they die.

Loligo forbesii feeds on small fishes and to a minor extent on other cephalopod species, crustaceans and polychaetes; cannibalism also occurs, but it seems limited to large squids feeding on much smaller ones. Primary prey items vary among geographical areas and seasons. The main food sources are as follows: in Scottish waters whiting (*Merlangius merlangius*), poor-cod (*Trisopterus* spp.) and sandeels (Ammodytidae) comprise the most abundant fish species in the diet, whereas in Irish waters sprat (*Sprattus sprattus*) and poor-cod *Trisopterus* spp., and off the Azores blue jack mackerel (*Trachurus picturatus*) dominate. Ontogenetic shifts in feeding habits occur. Crustaceans dominate in the diet of juveniles, but no sex-related nor maturation-related differences occur. Biochemical studies indicate than the veined squid is an important part of the benthic food-web. Several marine mammals like pygmy sperm whales, orca (killer) whales, common, striped and bottle-nosed dolphins, large demersal fishes (e.g. cod and scabbardfish), seals and seabirds feed on this species.

Interest to Fisheries: ***Loligo forbesii*** is one of the loliginid species of commercial importance in the eastern North Atlantic, especially in Scottish and Irish waters and the English Channel. It is taken mainly as bycatch in deeper water trawl fisheries throughout its range, and it rarely is abundant in the Mediterranean Sea, although some exceptions are known. A long-term, directed, strongly seasonal, fishery exists in the Moray Firth (North Sea, Scotland), and this has increased dramatically in recent years. Also, a directed jigging fishery is carried out off Madeira and the Azores, where the veined squid is the only squid species of economic importance. It is fished in the English Channel and marketed along with ***L. vulgaris*** which also occurs in Portuguese waters, where local artisanal hand-jig fisheries occur. Specific statistics do not exist, but this squid is highly appreciated for human consumption and as bait. It is marketed fresh, frozen and canned (small quantities in the Azores).

Remarks: Confusion about the name of the species exists (i.e. ***forbesi*** versus ***forbesii***). According to the International Code of Zooogical Nomenclature, both forms, in principle, are admissible (see Art. 31.1 and 3.1.2; ICNZ, 1999). However, Steenstrup's original description ended in "ii". According to Art. 32 (ICZN, 1999) original spelling is correct unless it is in one of the categories listed in Art. 32.5 as "spellings that must be corrected". In our opinion, this is not the case and the change in ending is an unjustified emendation (see also Sweeney and Vecchione, 1998).

Long placed in the genus ***Loligo***, the species was discussed as one of those with "unresolved generic affinities" in Vecchione *et al.* (1998). This was due to reports on potential bioluminescence and photophores presence (i.e. Alexeyev, 1992 [1991], Lum-Kong and Hastings, 1992), which were not confirmed subsequently. General consensus was reached in the 2003 CIAC meeting in Phuket to place the species back in the genus ***Loligo*** (Vecchione *et al.*, 2005).

Various studies of morphometric variability throughout the species range in the Atlantic, along with molecular observations, suggest that no significant stock separations exist among mainland coastal populations (Pierce *et al.*, 1994d, Brierley *et al.*, 1995, Collins *et al.*, 1999, Shaw *et al.*, 1999). However, evidence indicates that animals from the offshore population around the Rockall Bank are different from coastal populations and that the Azores population is highly isolated. ***Loligo forbesii*** experienced a strong population decline in the southern end of its range in Atlantic waters in the 1990s, while its abundance increased in the northern areas (Chen *et al.*, 2006); these trends seemed to be related to variations in the North Atlantic Oscillation (NAO). Also, changes in some Mediterranean areas occurred in the species distribution in recent decades, with an abrupt decrease in the Sicilian Channel, while the population in the Ionian Sea increased. Studies suggest that the changes in the deep water layers of the eastern Mediterranean influence these distributional shifts (Chen *et al.*, 2006). *Roseobacter* bacteria in the accessory nidamental glands may aid in carotenoid production and in production of antibiotics and toxins for egg protection (Pichon *et al.*, 2005b).

Local Names: FRANCE: Calmar, Encornet de Forbes, Encornet veiné; GERMANY: Langflossenkalmar; ITALY: Calamaro venato, Occhione; NETHERLANDS: Noordse pijlinktvis; PORTUGAL and AZORES: Lula, Lula riscada; SPAIN: Calamar veteado, Calamar de Forbes; RUSSIA: Dlinnoperiy Kalmar; UNITED KINGDOM: Common squid, Forbe's squid, Veined squid.

Literature: Naef (1923), Holme (1974), Martins (1982), Roper *et al.* (1984), Mangold and Boletzky (1987), Segawa *et al.* (1988), Guerra (1992), Boyle and Pierce (1994), Guerra and Rocha (1994), Boyle *et al.* (1995b), Belcari (1999d), Chen *et al.* (2006), Vecchione (2008e), Hastie *et al.* (2009).

Loligo reynaudii Orbigny, 1839–1841

Fig. 73; Plate III, 15–16

Loligo reynaudii Orbigny, 1839-1841, *in* Ferussac and D'Orbigny, 1834–1848, *Histoire Naturelle Générale et Particuliere Céphalopodes Acétabulifères Vivants et Fossiles*. 96 pages + lvi pages + 361 pages, Atlas with 144 plates. Paris. [315, Calamar pl 24]. [fide Tillier and Boucher-Rodoni (1994:102); taxon dated from plate]. [Type locality: Cape of Good Hope, Atlantic Ocean].

Frequent Synonyms: *Loligo vulgaris reynaudii*, Augustyn and Grant, 1988.

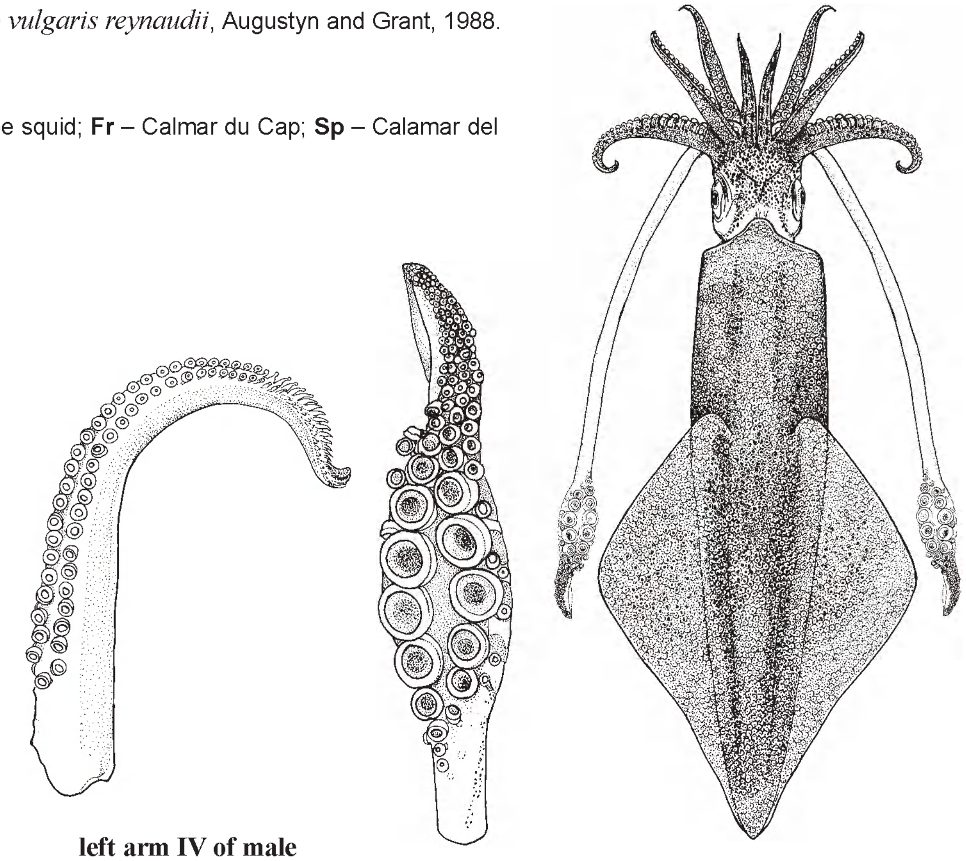
Misidentifications: None.

FAO Names: En – Cape Hope squid; **Fr** – Calmar du Cap; **Sp** – Calamar del Cabo.

Diagnostic Features: Mantle narrow, elongate. Fins long, 65% or more of mantle length. Tentacles long; **clubs expanded, with more than 36 transverse rows of suckers**; **club suckers on the manus** (medial series) **greatly enlarged**, club sucker rings smooth (medial manal sucker), or with 16 to 20 teeth.

Size: Maximum mantle length 400 mm; weight more than 1 kg.

Geographical Distribution: Southern African waters: eastern South Atlantic and southwestern Indian Ocean, from Namibia (28°S) on the west coast of Africa, to Cape Agulhas (35°S) and north on the east coast to at least 34°S, Port Alfred. Its eastern limits are unknown (Fig. 74).



left arm IV of male hectocotylized

tentacular club

dorsal view

Fig. 73 *Loligo reynaudii*

Habitat and Biology: *Loligo reynaudii* occurs mainly along the continental shelf, down to depths of about 200 m. Offshore distribution reaches depths of 300 to 350 m. A migratory pattern exists for a large fraction of the population. Hatching occurs on the south and the east coasts of South Africa, between Plettenberg Bay, Cape St Francis and Port Alfred, where the major spawning areas are located. Paralarvae and juveniles are transported westward to the main nursery area on the Central Agulhas Bank, where feeding grounds for the adults also are located. The young squid migrate farther north along the southwestern African coast where they take advantage of the Benguela Current system to feed and grow; then they return to the eastern inshore waters to spawn. Size at maturity is highly variable, depending on geographic location and time of year. Males may be mature at 90 mm mantle length or immature at 250 mm mantle length and females at 100 mm mantle length and

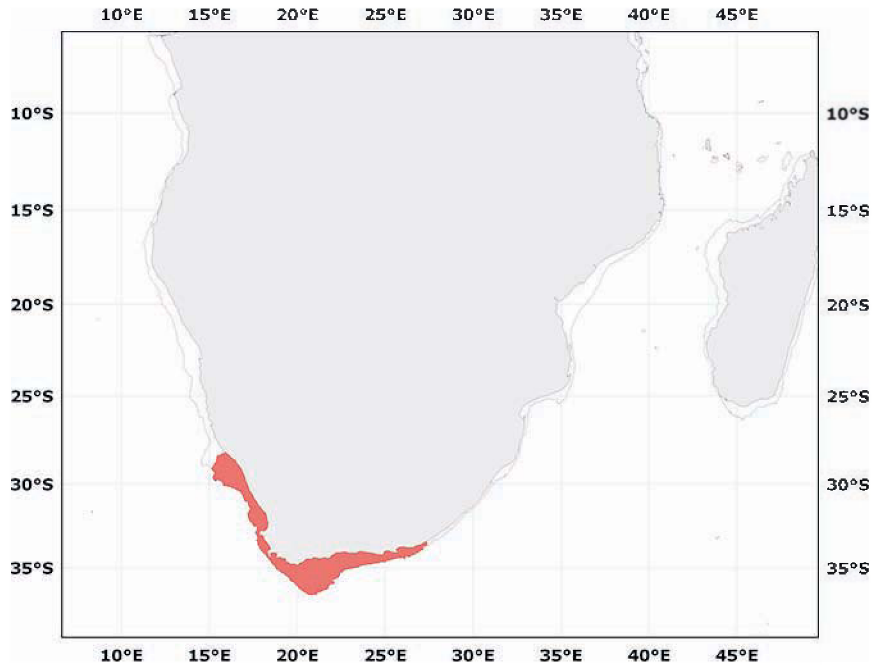


Fig. 74 *Loligo reynaudii*

🟥 Known distribution

180 mm mantle length respectively. Modal length at spawning varies between 265 and 305 mm mantle length in males and between 175 and 195 mm mantle length in females. Spawning occurs mainly in shallow inshore waters (<60 m) of the bays off the Eastern Cape, with peaks in spring and summer (September to February), when the water temperature exhibits considerable variability (9° to 25°C), due mainly to wind-induced coastal upwellings. This may affect survival and development in the eggs and embryos. However, a small fraction of the spawning population occurs in deeper, cooler waters offshore to 120 m depth at 9° to 12°C, where the temperature regime remains relatively stable. Spawning concentrations are greater in association with westerly winds, zero turbidity conditions and sea surface temperature between 15° and 17°C.

Mature squid arrive on the spawning grounds in sexually segregated schools. Sandy areas or low-profile rocky reefs are favoured by spawning squid, and upwelling events, coincident with the formation of spawning aggregations, support the hypothesis that changes in temperature trigger spawning. Complex reproductive nuptial rituals occur on the spawning grounds. These rituals involve fighting, guarding, sneaking, mating and egg-laying behaviour. Mating occurs after the formation of squid “pairs”, where large males mate with ripe females. Smaller, “sneaker” males frequently are excluded by the coupled pairs, but eventually are successful in mating with paired females.

Tagging studies, histological examination of the ovaries and aquarium observations confirm that the chokka squid is a serial spawner, and the term “uniseasonal iteroparity” has been proposed to define this spawning pattern, in which batch spawning occurs over an extended period of time and at different sites.

Ovulation in this species appears to be a rapid process, seen by the occurrence of both mature oocytes and post-ovulatory follicles in partially spent ovaries. Squid exhibit a diel pattern of spawning, with egg accumulation at night and active spawning during the day. During the spawning phase, ovaries go through ripe, partially spent and recovering stages by undergoing a process of maturation, ovulation and redeveloping, where a new batch of advanced oocytes is recruited. The cycle typically appears to last between 24 and 36 hours, and may depend on a number of factors such as environmental conditions and the presence of predators. Potential fecundity is about 17 000 eggs, and egg strands that contain an average of about 150 eggs are concentrated into distinct, aggregated spawning beds. Eggs are ovate, heavily yolked, about 2.8 mm long and 2.0 mm wide, and they are arranged in a spiral of about 100 eggs each in the gelatinous capsule (“finger”). Early-stage egg capsules are smooth, elongate, bright orange-coloured and transparent, with the eggs clearly visible. The capsules are attached to each other by interwined stalks that form large clusters embedded into the substrate. The eggs require about 35 days to hatch at 14°C and 16 days at 21° to 22 °C; they do not develop normally at temperatures below 10°C or above 24°C. The optimum temperature range for normal embryonic development is between 12° and 17°C, at which the development takes between 50 and 27 days, respectively.

Newly hatched chokka squid range between 2.3 and 2.5 mm mantle length; they are not strong swimmers and live a planktonic life for a short period. Abundant food for paralarvae exists in all regions of the Agulhas Bank. While paralarvae feed mainly on copepods, fishes constitute the main prey of adult squids, followed by crustaceans, polychaetes and cephalopods; maximum cannibalism occurs on the spawning grounds during the day. Chokka squid are preyed upon by several fishes, sharks and marine mammals when they congregate on their spawning beds. They also constitute the main prey for the groundfish community in the southern Benguela system. The duration of the life cycle is less than 2 years, and it ends after the last spawning event takes place; however, immediate post-spawning mortality seems not to occur on the spawning grounds investigated to date.

Interest to Fisheries: ***Loligo reynaudii***, commonly known as “chokka”, it is the only cephalopod of major commercial importance in the South African fishing industry. The erratic fluctuations in catches have been the object of intensive research focused on the species distribution and spawning biology and the relationship of population composition with environmental constraints. Prior to 1980, the South African catch of squid was limited to bycatch from demersal trawlers that targeted fish species. Since then, however, increased demand has led to the establishment of a directed squid fishery that includes jig fishing. Commercial catches of chokka squid varied between a maximum of about 10 000 tonnes in 1989 to 2 500 tonnes in 1992. Catch values have risen dramatically, and chokka squid has become the most valuable South African fishery at USD 23 million in 1997. However, the high variability in squid catches can have devastating economic consequences to the fishing industry during years of reduced production. In an effort to forecast these fluctuations, quantitative models have been developed for prediction of spawning aggregations and spawning success in relation to environmental factors. Geographical Information Systems (GIS) are used to help understand the spatial and temporal biology of the chokka squid. Management measures are in place that control effort and designate a specified season for the directed jig fishery.

Remarks: Male specimens may display stripes similar to those typical of ***Loligo forbesii*** on the ventral sides of the mantle; however, these stripes are much smaller, less numerous and less intensely coloured than in ***L. forbesii***. ***Loligo reynaudii*** originally was differentiated from the closely related ***Loligo vulgaris*** by d’Orbigny (1839-1845) on the basis of morphological characters. Subsequently, Adam (1952) found the differences between the 2 species not to be significant, and additional studies based on the combination of morphological characters, meristic data on selected characters and electrophoresis lead to the conclusion that ***Loligo reynaudii*** was a subspecies of ***Loligo vulgaris*** (Augustyn and Grant, 1988). General consensus was reached in the 2003 CIAC meeting in Phuket that ***Loligo vulgaris*** and ***Loligo reynaudii*** are 2 distinct and separate species (Vecchione *et al*., 2005).

Literature: Adam (1952), Roper *et al*. (1984), Nesis (1982, 1987), Augustyn (1991a,b), Augustyn *et al*. (1994), Augustyn and Grant (1988), Lipinski *et al*. (1998a), Roeleveld (1998), Vecchione (2008e).

Afrololigo Brakoniecki, 1986

Afrololigo Brakoniecki, 1986, *Ph.D. Dissertation, University of Miami, Coral Gables, FL*, 163 pp. [92].

Type Species: *Afrololigo mercatoris* (Adam, 1941).

Diagnostic Features: Tentacular **clubs narrow**, small; suckers arranged in 4 series, 4 or 5 pairs of medial suckers on manus much larger than the lateral sukers; club sucker rings with 15 to 25 teeth. **Arms I extremely short** in comparison to the others. Arm sucker rings with square, plate-like teeth around entire margin. Left ventral arm of males hectocotylized, its proximal half with 6 to 12 pairs of normal suckers, its distal half with elongate papillae replacing the suckers, those of the dorsal row more strongly developed. Suckers on midsections of dorsolateral and ventrolateral arms (arms II, III) of males greatly enlarged. Head short; **buccal lappets without suckers**. **Mantle without posterior tail-like elongation**. **Fins rounded, short, broad with convex posterior margins**. Photophores absent.

Size: Very small-sized squid; maximum mantle length 50 mm.

Geographical Distribution: Atlantic coast of Africa.

Remarks: Brakoniecki established the genus ***Afrololigo*** in his Ph.D. Dissertation. Normally Dissertations do not have standing for systematic/nomenclatural purposes. However, Sweeney and Vecchione (1998:224) included a paragraph stating essentially that in F.M. Bayer's opinion, as a commissioner of ICZN, the way that Bakoniecki distributed his dissertation made the names available. Currently the genus is monotypic.

Afrololigo mercatoris (Adam, 1941)

Fig. 75

Lolliguncula mercatoris Adam, 1941, *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, series 2, 21: 83–162. [125]. [Type locality: Luderitz Bay, southwestern Africa, South Atlantic Ocean].

Frequent Synonyms: *Lolliguncula mercatoris* Adam, 1941, Roper *et al.* (1984).

FAO Names: En – Guinean thumbstall squid; **Fr** – Calmar doigtier de Guinée; **Sp** – Calamar dedal de Guinea.

Diagnostic Features: Mantle broad (width about 35% of mantle length), and bluntly rounded posteriorly. **Fins rounded, short** (length 40 to 45% of mantle length), **broad** (width of both fins about 55 to 65% of mantle length) with convex posterior margins. Head short; buccal lappets without suckers. Tentacular **clubs narrow, small, with suckers arranged in 4 longitudinal series, 4 or 5 pairs of medial suckers on manus much larger than the lateral suckers**; club sucker rings with 15 to 25 more or less sharp teeth, larger and more pointed distally. Dorsal arms extremely short in comparison with the others; left ventral arm of males hectocotylized, its proximal half with 6 to 12 pairs of normal suckers, its distal half with elongate papillae that replace the suckers; the papillae of the dorsal row are more strongly developed.

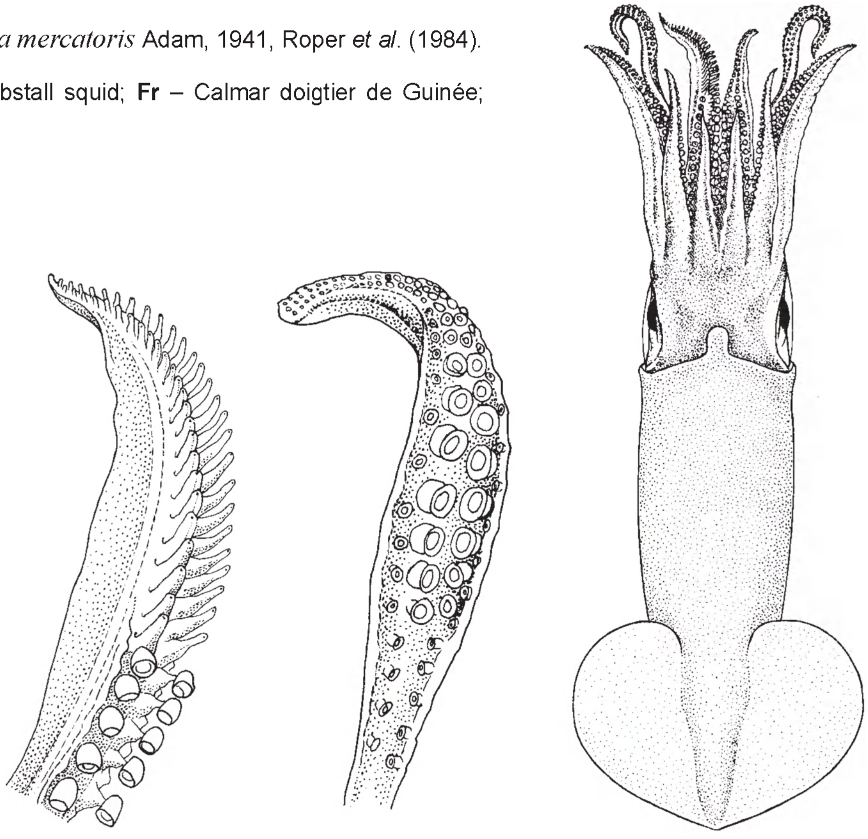


Fig. 75 *Afrololigo mercatoris*

Size: Maximum mantle length 50 mm in females, 35 mm in males.

Geographical Distribution: Eastern central Atlantic Ocean: limited to the west coast of Africa from Rio de Oro (Mauritania) to Lüderitz Bay (Namibia) (Fig. 76).

Habitat and Biology: ***Afrololigo mercatoris*** is collected at depths of less than 50 m on mud and sandy-mud bottoms. Little information is available on its life cycle and biology. Eggs are small. Spermatophores have long cement bodies. Paralarvae are difficult to distinguish from early growth stages of ***Loligo reynaudii***.

Interest to Fisheries: This small species currently is not exploited.

Remarks: ***Afrololigo mercatoris*** shares many morphological characters with species of ***Lolliguncula***, the genus in which it was originally described by Adam (1941). However, based primarily on gladius characters (Alexeyev, 1989, 1991), DNA sequence data (Anderson, 2000a,b) and biogeography considerations, ***Afrololigo*** is recognized as a valid genus for this species (Vecchione *et al*., 2005). ***"Loligo" abulati*** Adam, 1955 in the Red Sea was thought to be related to ***A. mercatoris***, but currently it is placed in ***Uroteuthis (Photololigo)***.

Literature: Adam (1941), Roper *et al*. (1984), Brakoniecki (1986), Roeleveld (1998), Vecchione (2008a).

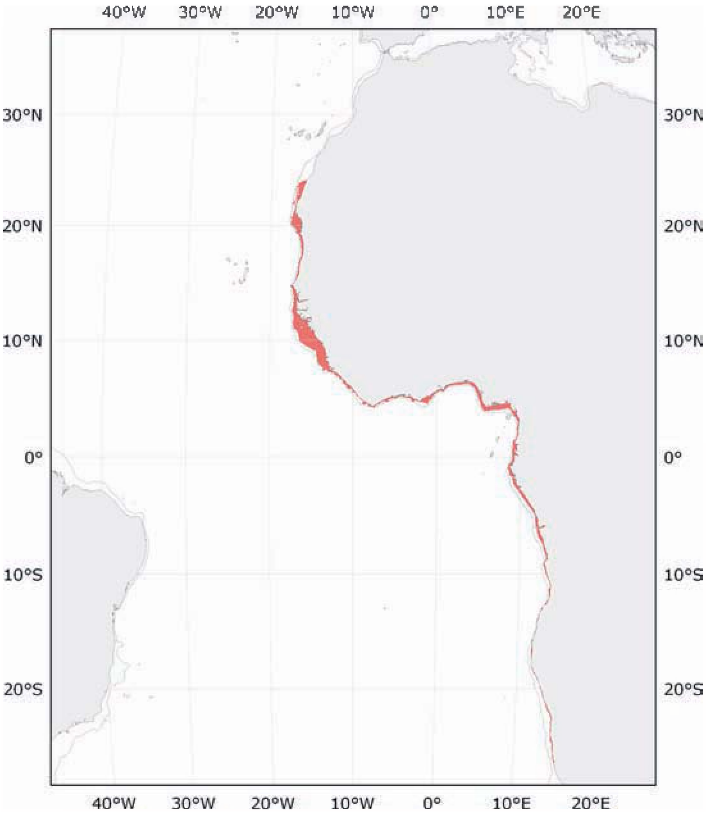


Fig. 76 ***Afrololigo mercatoris***

🟥 Known distribution

Alloteuthis Wülker, 1920

Alloteuthis Wülker, 1920, Senckenbergiana, 2(1): 48-58 [56].

Type Species: *Alloteuthis media* (Linnaeus, 1758).

Diagnostic Features: Tentacles long, robust; **clubs large, expanded**, with large suckers in the 2 median manal series. Hectocotylus without crest; proximal suckers unmodified, 10 to 12 (usually 11) normal suckers in ventral row followed distally by papillae. **Buccal suckers absent**. Mantle long, relatively narrow, **its posterior end drawn out into a narrow, pointed tail**, up to 60 mm long in adults. **Fins posterior, heart-shaped**, their lateral angles rounded, posterior borders concave, **extend posteriorly along tail**. Photophores absent.

Size: Small to medium-sized, maximum mantle length up to 205 mm.

Geographical Distribution: Eastern Atlantic Ocean and Mediterranean Sea.

Remarks: The close similarity between ***Alloteuthis*** and ***Loligo***, lead Vecchione *et al*. (1998b) to consider the former a subgenus of the latter. Subsequent molecular analyses, however (Anderson, 2000a,b), supported early morphological-anatomical considerations by Naef (1921b–1923) and Alexeyev (1989), that ***Alloteuthis*** should be a separate genus (Vecchione *et al*., 2005). The genus comprises 3 nominal species. Two species, ***A. media*** Linnaeus, 1758 and ***A. subulata*** Lamarck, 1798, occur in the eastern Atlantic Ocean, north of 20°N, and in the Mediterranean Sea. The third species, ***A. africana***, lives in the waters off West Africa, from southern Morocco to Namibia. In spite of the low level of species diversity, however, ***Alloteuthis*** taxonomy and systematics are confused and assignment of specimens to species may be difficult (e.g. Laptikhovsky *et al*., 2002b, 2005, Anderson *et al*., 2006, Anderson *et al*., 2008). Recent analyses of populations of

A. media and ***A. subulata*** from the eastern Mediterranean and the northwestern African waters indicate that a species complex probably exists that requires realignment of previous concepts of these 2 nominal species (Laptikhovsky *et al*., 2002b, 2005). Subsequent molecular phylogenetic studies (Anderson *et al*., 2006) reveal clades that do not correspond to the traditionally recognized ***Alloteuthis*** species; these clades include an Angolian/Mauritanian group (referable to ***A. africana***), a large eastern Atlantic/Mediterranean group (referable to ***A. media*** + ***A. subulata***) and a small group represented by specimens from the southwestern Adriatic Sea, morphologically indistinguishable from other specimens of ***A. media*** collected in the same area. It was suggested that this clade may represent a cryptic species. More recent data provide evidence that the character often used to distinguish ***Alloteuthis*** species (relative fin length) can be misleading (Anderson *et al*., 2008). Clearly, further studies are required to help define the whole species complex. Until the taxonomic situation with ***A. media*** and ***A. subulata*** is resolved, we retain them here as separate entities.

Literature: Naef (1921b, 1923), Roper *et al*. (1984), Vecchione *et al*. (1998b), Anderson (2000a,b), Anderson *et al*. (2006, 2008), Laptikhovsky *et al*. (2002b, 2005), Vecchione *et al*. (2005), Vecchione (2008b).

Alloteuthis media (Linnaeus, 1758)

Fig. 77

Sepia media Linnaeus, 1758, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*, 10(1): 824 p. [659]. [Type locality: “Pelago”].

Frequent Synonyms: *Sepia media* Linnaeus, 1758, *Loligo parva* Leach, 1817, *Loligo marmorae* Verany, 1839, *Loligo urceolatus* Risso, 1854.

Misidentifications: *Loligo vulgaris*, *Alloteuthis subulata* (formerly, multiple authors).

FAO Names: En – Midsize squid; **Fr** – Casseron bambou; **Sp** – Calamarín menor.

Diagnostic Features: Mantle long, relatively narrow, its posterior end drawn out into a short, narrow, pointed tail, less than 10 mm long in adults. Fins heart-shaped, their lateral angles rounded, posterior borders concave, extend posteriorly along tail. Buccal suckers absent. Tentacles long, robust; **clubs large, expanded, median manal suckers large (9 to 14% of head width)**. Left ventral arm hectocotylized: 10 to 12 (usually 11) normal suckers in ventral row, followed distally by papillae.

Size: Small-sized squid; maximum mantle length 132 mm.

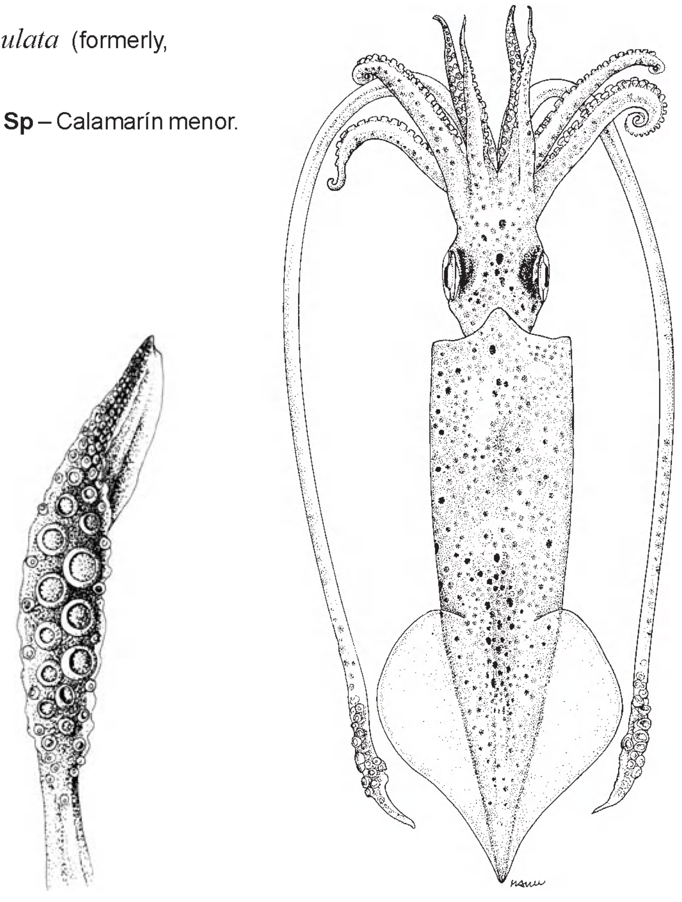

tentacular club
dorsal view

Fig. 77 *Alloteuthis media*

Geographical Distribution: Eastern North Atlantic Ocean and Mediterranean Sea: reported from about 20°N to 60°N in the eastern Atlantic. ***Alloteuthis media*** was considered very rare in the North Sea and, although old records from the Irish Sea and the English Channel do exist (late 1800s, early 1900s), recent reports on the presence of the species north of the Gibraltar Strait are limited to the northwestern Spanish coast. The species is widely distributed throughout the Mediterranean Sea, including the Sea of Marmara (Fig. 78).

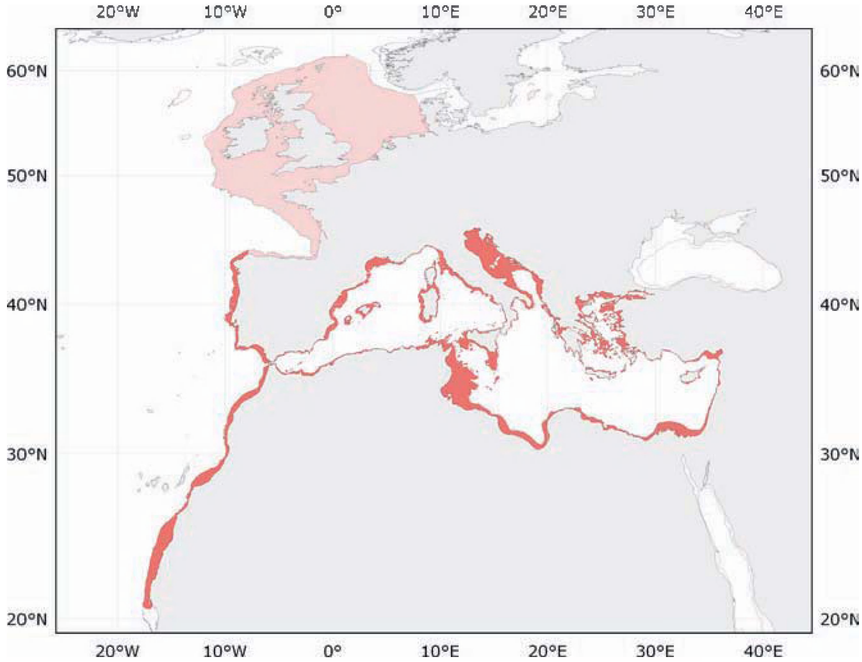


Fig. 78 ***Alloteuthis media***

🟥 Known distribution ▭ Probable presence

Habitat and Biology: ***Alloteuthis media*** occurs on sandy and muddy grounds and preferentially inhabits coastal and shelf waters (from the surface to 200 m), even though it has been recorded down to about 500 m depth. Like other neritic squids, it performs seasonal migrations between offshore and inshore areas. In the western Mediterranean, spawning extends throughout the year, but 2 groups of spawners usually can be distinguished by size and time of peak spawning. Large individuals are encountered in February at depths between 150 and 200 m; from March to April, they start to migrate into shallower waters, where spawning takes place on sandy grounds and to a minor extent on Posidonia grass beds. The second group, composed of smaller individuals, migrates onshore in June and July and spawns later in the year. By late autumn, depending on environmental temperatures, they start returning to deeper waters. Also, 2 main reproductive peaks occur in the Northern Tyrrhenian Sea, in May and in September. Maturation occurs at a wide size range, both in the western and eastern Mediterranean, and a gradient of decreasing values in minimum mantle length at maturity from the western to the eastern basins, probably exists in the ***A. media*** populations, as seen in other Mediterranean cephalopods. The smallest mature females measure 80 mm mantle length, smallest mature males 50 mm mantle length in the western basin, and 37 mm mantle length and 32 mm mantle length in the eastern basin, respectively. The bulk of females mature at about 70 and 90 mm mantle length in the eastern and western Mediterranean, respectively and mantle length 50% was estimated to be about 60 mm mantle length in females and 50 mm mantle length in males in the Tyrrhenian Sea (Central Mediterranean). Females mature at 70 mm mantle length and males at 50 mm mantle length in the Adriatic Sea Central Mediterranean. Maximum length of ripe eggs varies between 1.4 and 1.6 mm in females from the western Mediterranean and from 1.5 to 2.3 mm in females from the eastern Mediterranean; also, fecundity is higher in females from the eastern basin compared to those from the western basin, i.e. 1 500 to 2 500 eggs versus 1 400 eggs. This suggests a higher reproductive potential in the eastern basin. Spermatophore length varies between 2.3 and 3.4 mm and the maximum number of spermatophores per male is 170. The eggs are laid in several batches and are encapsulated in short gelatinous capsules, like those of ***Loligo vulgaris***, but more fragile and transparent. The eggs are attached in batches or clusters to hard objects on the substrate (shells, corals, stones). ***Alloteuthis media*** feeds on crustaceans, molluscs and small fishes. The life cycle is estimated to be about one year in males and 1.5 years in females; females grow larger than males.

Interest to Fisheries: Generally ***A. media*** is captured as bycatch in the bottom trawl fishery throughout its distributional range. It is sold at most Mediterranean markets along with its congeneric species. An active, directed trawl fishery exists for this species in the western Mediterranean, where it is taken between 150 and 200 m depth in winter and in shallower waters of 50 to 150 m in spring, summer and autumn. Abundance of ***A. media*** along the Catalan coast, northwestern Mediterranean, varies significantly seasonally, but annual variations in abundance are minor. It is marketed fresh and frozen, and its commercial interest varies depending on the geographic location.

Local Names: FRANCE: Petit encornet; ITALY: Calamaretto comune; MONACO: Totanitu; SPAIN: Luria; UNITED KINGDOM: Little squid.

Remarks: Studies on the eastern Mediterranean ***Alloteuthis*** species populations suggested that those squids represent a single taxonomic unit and were considered to be ***A. media*** (Laptikovsky *et al*., 2002b). Subsequent morphological analyses indicated that ***A. media*** and ***A. subulata*** may represent extremes of a morphological gradient in a single species (Laptikhovsky, *et al*., 2005). More recent molecular data analysis support a sister-species relationship between ***A. media*** and ***A. subulata*** and reveal significant genetic differentiation between Atlantic and Mediterranean ***A. media*** (Anderson *et al*., 2008). Morphometric analyses by the same authors confirm that central club sucker size is a reliable character to separate ***A. media*** from ***A. subulata*** (Anderson *et al*., 2008).

Literature: Mangold Wirz (1963), Roper *et al*. (1984) Auteri *et al*. (1987), Nesis (1982, 1987), Guerra (1992), Belcari (1999a), Laptikovsky *et al*. (2002b, 2005), Anderson *et al*. (2006, 2008), Vecchione (2008b).

Alloteuthis africana Adam 1950

Alloteuthis africana Adam 1950a, *Bulletin du Institut Royal des Sciences naturelles de Belgique*, 26(45): 1–9. [1]. [Type locality: 0°03'S, 9°07'E, eastern South Atlantic].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – African squid; **Fr** – Casseron africain; **Sp** – Calamarin africano.

Diagnostic Features: Mantle long and narrow; mantle width 20 to 25% mantle length in juveniles, 15% in adult females, 5% in adult males; anterior ventral mantle margin squarish in outline. Tail (fins and posterior mantle projection) very long and pointed in females (37% of dorsal mantle length in juveniles 58% in adults) and extremely long and spike-like in males (35% in juveniles, 73% in adults). Fins oval in outline, fin width index (width of both fins as a percentage of dorsal mantle length) 23% in adult females and 10% in adult males; posterior border of fins concave; arms very short; buccal lappets without suckers. **Diameter of club suckers of median 2 series 3 times greater than lateral suckers**. Club sucker rings with 20 to 30 blunt teeth. Left ventral arm hectocotylized by modification of distal 40% of length; 8 to 11 pairs of normal suckers proximally followed by 2 longitudinal series of elongate papillae that gradually decrease in size distally; arm suckers with 6 to 10 square teeth on distal half, smooth on proximal half.

Size: Medium-sized squid; maximum mantle length 205 mm in males, 175 mm in females.

Geographical Distribution: Eastern Atlantic: from 20°S to 25°N (Fig. 80).

Habitat and Biology: *Alloteuthis africana* is found on the continental shelf off the western African coasts, at depths of 20 to 100 m and temperatures of 16° to 26°C. It feeds on small fishes and reproduction apparently occurs year-round. Studies on age and growth of the species based on statolith analysis indicate a life span of less than 1 year, with males not older than 8 months and females about 6 months old. Growth is faster than that of the congener *A. subulata* in the same area.

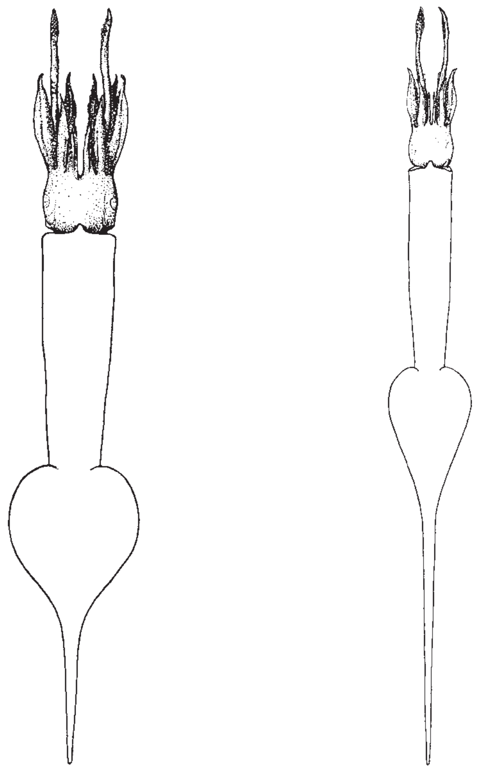
Interest to Fisheries: Captured only as bycatch in local trawl fisheries. Separate statistics are not reported for this species.

Local Names: None available.

Remarks: Analyses of morphometric data suggest that head width can be used to separate *A. africana* from the other 2 species (Anderson *et al*., 2008).

Literature: Adam (1950a), Roper *et al*. (1984), Arkhipkin and Nekludova (1993), Anderson (2000a), Anderson *et al*. (2008), Vecchione (2008b).

Fig. 79



dorsal view of female

dorsal view of male

Fig. 79 ***Alloteuthis africana***

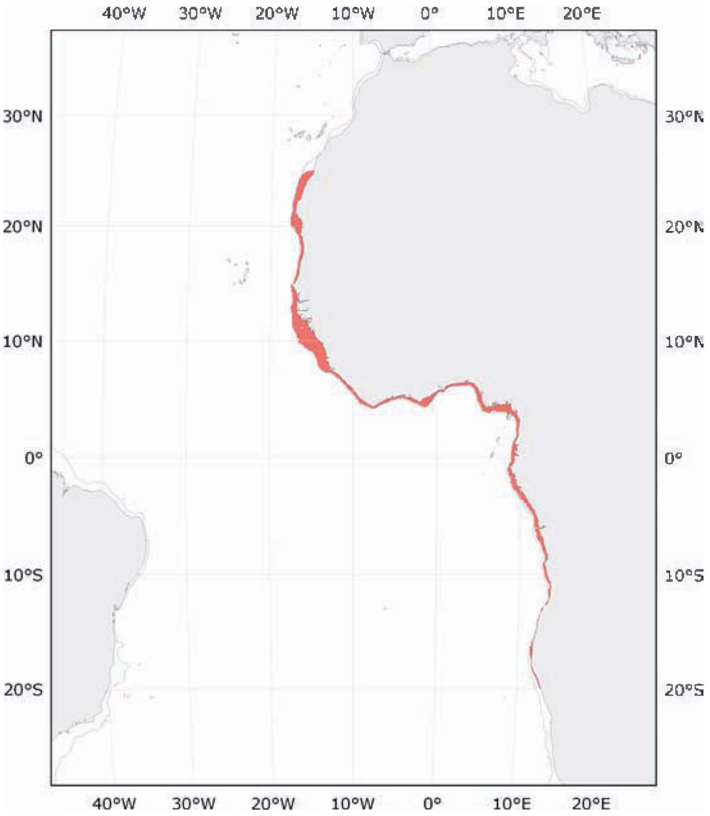


Fig. 80 ***Alloteuthis africana***

🟥 Known distribution

Alloteuthis subulata (Lamarck, 1798)

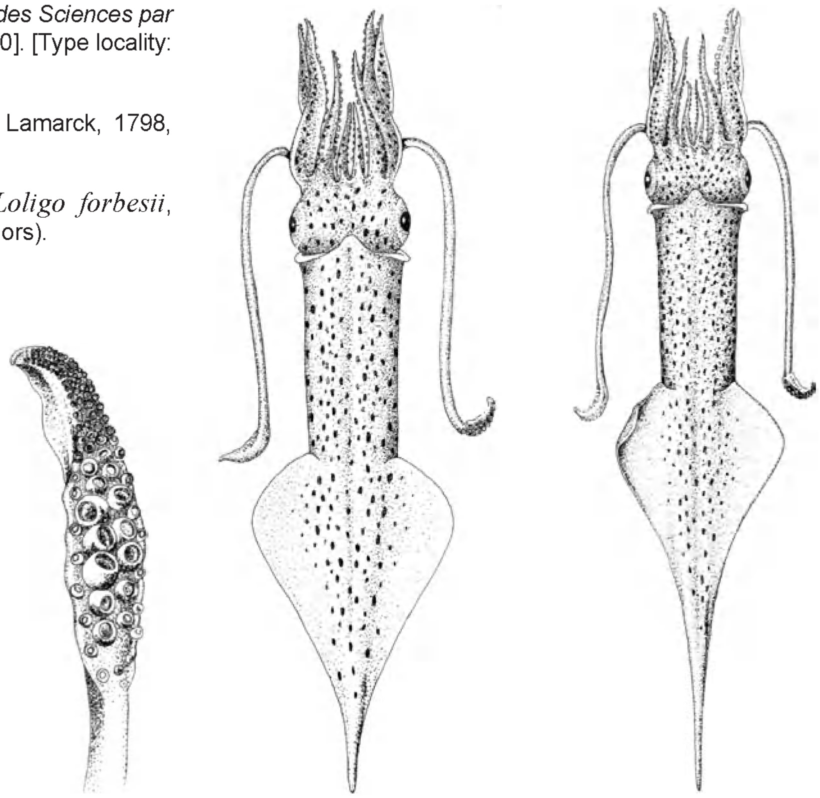
Fig. 81; Plate III, 17

Loligo subulata Lamarck, 1798, *Bulletin des Sciences par la Societe Philomatique*, 2(5):129–131 [130]. [Type locality: Mediterranean Sea].

Frequent Synonyms: *Loligo subulata* Lamarck, 1798, *Sepia subulata* Bosc, 1802.

Misidentifications: *Loligo vulgaris*, *Loligo forbesii*, *Alloteuthis media* (formerly, multiple authors).

FAO Names: En – European common squid; **Fr** – Casseron commun; **Sp** – Calamarín picudo.



tentacular club dorsal view of female dorsal view of male

Fig. 81 *Alloteuthis subulata*

Diagnostic Features: Mantle long and narrow; anterior ventral mantle margin slightly curved; tail long (up to 20 mm) and pointed in adult females (length of posterior extension plus fins equals 66% of mantle length); tail very long (up to 50 to 60 mm) and spike-like in adult males (72% of mantle length). Fins rhombic, with pointed lateral angles, their posterior borders concave and they extend along the tail; fin length exceeds 50% of mantle length. Buccal lappets without suckers; tentacles short, delicate; **clubs small, narrow, median manal suckers small (6 to 8% of head width)**. Arms are medium to short; left ventral arm hectocotylized, with 6 to 8 pairs of normal suckers proximally, followed distally by 2 longitudinal series of fine papillae.

Size: Small to medium-sized squid; maximum mantle length 184 mm in males, 140 mm in females.

Geographical Distribution: Eastern Atlantic Ocean, from approximately 60°N to 20°S: western Baltic Sea (sporadic), North Sea and Celtic Sea, to the western coast of Ireland, south to the Sahara Banks, where the limits of its distribution probably are located at Cape Blanc. Throughout the Mediterranean Sea, except its easternmost part, i. e. not represented in Turkish waters or the Sea of Marmara (Fig. 82).

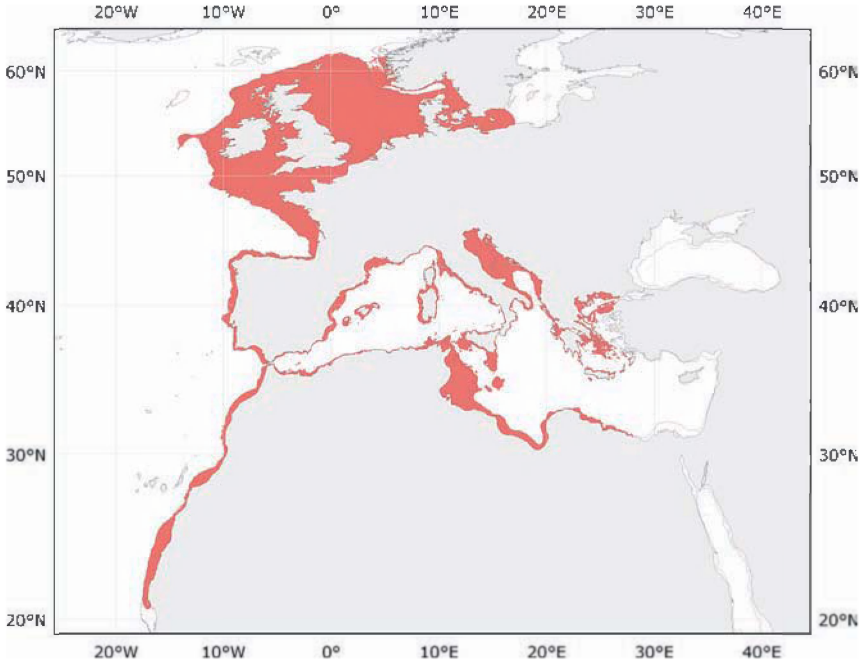


Fig. 82 *Alloteuthis subulata*

🟥 Known distribution

Habitat and Biology: Associated mostly with sandy and muddy bottoms but also present on hard substrata, i.e. coralligen, *Alloteuthis subulata* occurs from coastal shallow waters (less than 50 m) down to about 500 m, even though captures below 300 m are sporadic. It is reported as the most abundant cephalopod in the North Sea and the adjacent Skagerrak, where it forms dense aggregations over sandy and muddy bottom in shallow areas. It also is recorded in high quantities in the Celtic Sea and Irish waters, where it concentrates in inshore areas; it is rather common in the English Channel coastal waters, and it often is reported as abundant in Portuguese waters. It is less common in the Mediterranean Sea, where it is considered rare in some areas, and it generally is less frequently caught than the congeneric and sympatric

A. media. Seasonal migrations occur in the North Sea, where mature males and females arrive together in inshore waters in spring/early summer and juveniles leave in autumn and early winter to migrate into the Atlantic Ocean.

Sexual dimorphism consists mainly of the longer tail that characterizes adult males. Maturation occurs at a wide size range, as in the congener ***A. media***, with males maturing earlier than females and probably living longer. Animals start to mature at about 30 to 50 mm mantle length and in Portuguese waters manle length at 50% maturity (ML 50%) is 75 to 80 mm in females and 70 to 75 mm in males. An extended spawning period characterizes the English Channel population, where three main spawning peaks occur in spring, summer and autumn. Once mature, males start to mate and release spermatophores and continue to do so for the rest of their life span; this implies the possibility to mate with females of different cohorts. Mating in the laboratory occurred only head-to-head (or buccal-crown-to-buccal-crown) and spermatophores usually were placed on the ventral portion of the buccal membrane.

Eggs are small. Also, egg capsules are small, 20 to 40 mm long, and balloon-shaped, attached by “stalks” to hard substrata. Embryonic development lasts 2 to 3 weeks at temperatures of 15° to 18°C, and the small hatchlings, 1.5 to 2.2 mm mantle length, have a planktonic life phase of a few weeks before they become demersal. Growth rates are slower than those of the congener ***A. africana***, and in general, both species are considered among the slowest growing, in terms of percentage increase of body weight per day, of the family Loliginidae.

Life span is estimated to be about 1 year in the English Channel, much longer than that on the West African shelf, where it is estimated to be about 6 months.

Interest to Fisheries: ***Alloteuthis subulata*** is a bycatch in trawl fisheries throughout its range; in the Mediterranean Sea it is taken at 20 to 120 m depths over sandy-muddy bottoms. It is sold at most Mediterranean seafood markets along with the congeneric species ***A. media***, marketed fresh and frozen. Separate statistics are not reported and the species is considered of variable commercial interest depending on the geographic location.

Local Names: ITALY: Calamaretto puntuto.

Remarks: Effective schooling behaviour in response to light, predators, food and other external stimuli was observed in the laboratory (Lima *et al*., 1995). Recent genetic analyses indicate that ***A. media*** and ***A. subulata*** may represent extremes of a morphological gradient in a single species, or perhaps that these entities, in a different taxonomic arrangement, will turn out to be a species complex (Laptikhovsky *et al*., 2005). More recent molecular analyses support a sister-species relationship between ***A. subulata*** and ***A. media*** (Anderson *et al*., 2008). Morphometric analyses by the same authors confirm that central club sucker size can be used to separate ***A. subulata*** from ***A. media*** (Andersen *et al*., 2008).

Literature: Roper *et al*. (1984), Nesis (1982, 1987), Guerra (1992), Arkhipkin and Nekludova (1993), Belcari (1999b), Laptikovsky *et al*. (2002b, 2005), Anderson *et al*. (2006, 2008), Hastie *et al*. (2009).

Doryteuthis Naef, 1912

Doryteuthis Naef, 1912b, *Zoologischer Anzeiger*, 39(25):741–745 [742].

Type Species: *Loligo plei* (Blainville, 1823).

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Hectocotylus on left ventral arm IV with proximal suckers unmodified; ventral crest absent; suckers of reduced size and sucker stalks elongated to form papillae on dorsal or both dorsal and ventral series. **Fins posterior**. **Eggs small to moderate sized, less than 4 mm long**. Spermatophore cement body short. Photophores absent.

Geographical Distribution: American waters of the western Atlantic and eastern Pacific Oceans.

Remarks: Two subgenera currently are recognized. Since the type species of the formerly monotyic genus belongs to the subgenus ***Doryteuthis***, the subgenus ***Doryteuthis*** is treated first in this work.

Literature: Vecchione *et al.* (2005), Vecchione (2008c).

Key to the subgenera of *Doryteuthis*

1a. Modified portion of hectocotylized arm extends to arm tip; edges of gladius vane thickened; . . . . ***Doryteuthis (Doryteuthis)***

1b. Modified portion of hectocotylized arm does not extend to arm tip; edges of gladius vane not thickened . . . . ***Doryteuthis (Amerigo)***

Subgenus ***Doryteuthis*** Naef, 1912

Doryteuthis Naef, 1912b, *Zoologischer Anzeiger*, 39(25): 741–745 [742].

Type Species: *Doryteuthis (Doryteuthis) plei* (Blainville, 1823).

Doryteuthis (Doryteuthis) plei (Blainville, 1823)

Fig. 83; Plate IV, 23; Plate V, 24–25

Loligo plei Blainville, 1823, *Journal Physique Chimie d'Histoire Naturelle*, 96: 116–135 [132]. [Type locality: Martinique, West Indies, western North Atlantic Ocean].

Frequent Synonyms: *Loligo plei* Blainville, 1823, *Loligo pleii* Blainville, 1823.

Misidentifications: *Loligo pealeii* (formerly, multiple authors).

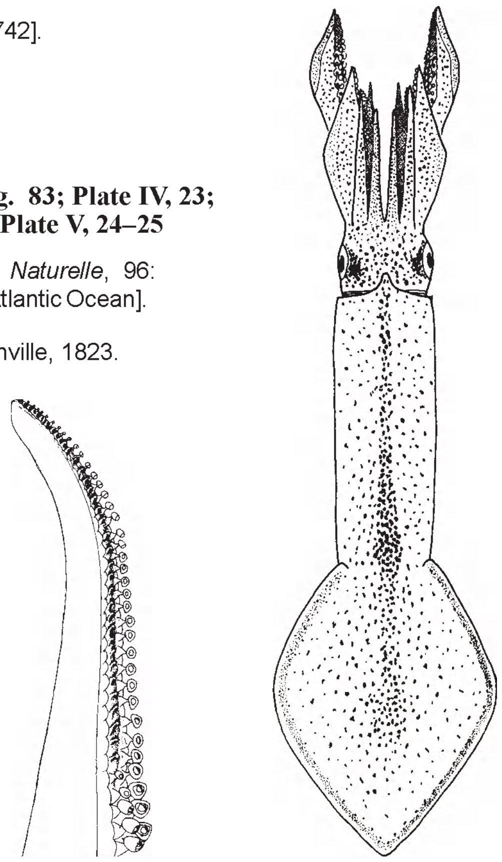
FAO Names: En – Slender inshore squid; **Fr** – Calmar flèche; **Sp** – Calamar flecha.

Diagnostic Features: Mantle long, slender, cylindrical, the posterior end acutely pointed; fins rhomboidal, their sides fairly straight, widest point curved. Low, narrow, midventral ridge often present, particularly on males. **Left ventral arm hectocotylized in mature males by a modification of distal half to fourth of arm that extends to arm tip**; one half to three-fourths (42 to 82) of suckers in dorsal row much smaller than half the size of their ventral counterparts; modified (small) suckers on small, narrow, triangular pedicels. Gladius slender, feather-shaped; ratio of greatest width of vane of gladius to greatest width of rachis 1.5 to 2.7; edge of vane straight (often slightly curved in females), thick, and ribbed (especially mature males). **Suckers present on ventral buccal lappets**. Eye not unusually large; diameter of externally visible eyeball 14 to 19% of mantle length, diameter of dissected lens 2 to 7% of mantle length. **Colour**: (dark) reddish brown dorsally, darkest along dorsal midline of mantle; lighter, more yellowish background colour ventrally with reddish brown overlay; often with reddish brown longitudinal stripes on anterior ventrolateral mantle of males.

Size: Medium-sized squid; maximum mantle length 370 mm in males, 260 mm in females.

Geographical Distribution: Western Atlantic Ocean, in continental shelf and upper slope waters from Cape Hatteras (36°N) (very rarely strays north to southern New England) to northern Argentina (35°S), often in association with the warm Brazil Current; this includes the Gulf of Mexico, the Caribbean Sea, Bermuda, Bahamian and Caribbean Islands (Fig. 84).

Habitat and Biology: This squid occurs from the surface to about 370 m depth, though it occurs mostly shallower than 200 m; apparently concentrates near the bottom during the day and disperses into the water column at night, when it can be dip-netted at the surface. Some sexual dimorphism is evident in the species: the gladius is wider in females, while male gladii usually have straighter margins with stronger lateral ribs. Ventral longitudinal ridges are more often present in males than females, and mature males often have ventrolateral stripes of chromatophores along the ventral mantle.



hectocotylus **dorsal view**

Fig. 83 ***Doryteuthis (Doryteuthis) plei***

Fig. 84 ***Doryteuthis (Doryteuthis) plei***

🟥 Known distribution

Maturity occurs over a broad range of sizes depending on season and locality, the smallest mature males are 38 mm mantle length, the smallest females 42 mm mantle length, whereas they can remain immature up to 148 mm (males) and 143 mm (females); 50% maturity occurs at 175 and 155 mm mantle length in males and females of the northeastern Venezuelan waters, and at 194 and 141 mm mantle length for males and females off southern Brazil's offshore waters (Santa Catarina). In that area, however, studies on the coastal squid population give much lower values (i.e. 147 mm ML for males and 97 mm ML for females), suggesting the existence of a population distinct from the offshore squids. Immature and mature specimens of a broad range of sizes may be caught in the same net-haul. Mature squid are present throughout the year, but 2 seasonal peaks occur in the populations studied: in spring and autumn in the Caribbean Sea, in late spring-early summer and autumn off the northeastern Venezuelan coasts, and in summer and winter in the southern Brazilian waters. Mating and spawning occur year round, but observations on specimens kept in aquaria indicate post-spawning mortality. Underwater observations reveal no immediate mortality to occurr after spawning, while observations on the sex-ratio distribution of the southern Brazilian population after the spawning events indicate post-spawning mortality. It is probable, though, that the extent of the spawning phase varies depending on several different factors. Also, due to the wide geographical range covered, the duration of the species' life cycle may vary, depending on geographic location and the specific environmental constraints that affect growth. At present, reproductive patterns and size structure of ***D. plei*** landed along the southern Brazilian coasts indicate an annual cycle for the species there, in agreement with earlier estimates for populations farther north. However, statolith and age studies on the northwestern Gulf of Mexico population (i.e. on samples from a much warmer and more productive region) revealed a very rapid, non-asymptotic growth and a life span of about 6 months. Combined analyses of gladius and statoliths suggest a "compromise" of about nine months as the probable life span for this species off southern Brazil. ***Doryteuthis plei*** feeds on crustaceans, small fishes and squids. It is preyed upon by a variety of vertebrates, including fishes, dolphins, fur seals and penguins.

Interest to Fisheries: ***Doryteuthis plei*** is caught throughout its geographic range, but separate statistics are not kept where it may co-occur with ***D. pealeii***. The former species comprises most of the cephalopod fishery in Venezuela, and a small fishery occurs in Yucatan. In the Bahamian and Caribbean Islands undoubtedly it is the most frequently captured commercial species of Loliginidae, and it has been an important component of the trawl fishery bycatch in the southern Brazilian waters for many years; there, when the crisis in the shrimp fishery forced the fleet to find alternative target species in the bycatch to reduce operation costs, interest in squids increased and ***D. plei*** now is the subject of directed small-scale fisheries both inshore and offshore. The principle gear includes otter trawls and dipnets. It is used as food and bait.

Local Names: USA: Arrow squid; VENEZUELA: Luria.

Remarks: Whitaker (1978), Hixon (1980a) and Sanchez *et al*. (1996) computed several indices in order to separate ***D. plei*** from ***D. pealeii***; the most reliable is the ratio of gladius width to rachis width (GW/RW), combined with the overall shape of the gladius, including the presence or absence of marginal ribs (present in ***D. plei***). In particular, the GW/RW ratios range from 1.9 to 2.7 in ***D. plei*** and from 2.1 to 3.8 in ***D. pealeii***, and the separation of the 2 species is best accomplished with a GW/RW ratio of 2.7. However, the 2 species are so similar morphologically, that a very careful examination of the collected samples always is recommended, especially in the areas where they are sympatric. The broad geographic range of ***D. plei*** makes it an interesting candidate to investigate adaptations to different environmental/oceanographic regimes, such as plasticity in growth and reproduction rates among different populations. Available information indicates that a small, isolated population exists in Bermuda waters, and an investigation on ***D. plei*** in the Gulf of Mexico revealed a genetic break between the northwestern Gulf of Mexico and the northeastern Gulf-western Atlantic populations (Herke and Folz, 2002).

Literature: Cohen (1976), Roper *et al*. (1984), Arocha and Urosa (1991), Sanchez *et al*. (1996), Perez *et al*. (2002), Herke and Folz, (2002), Jackson and Forsythe (2002), Vecchione (2002, 2008c).

Doryteuthis (Doryteuthis) roperi (Cohen, 1976)

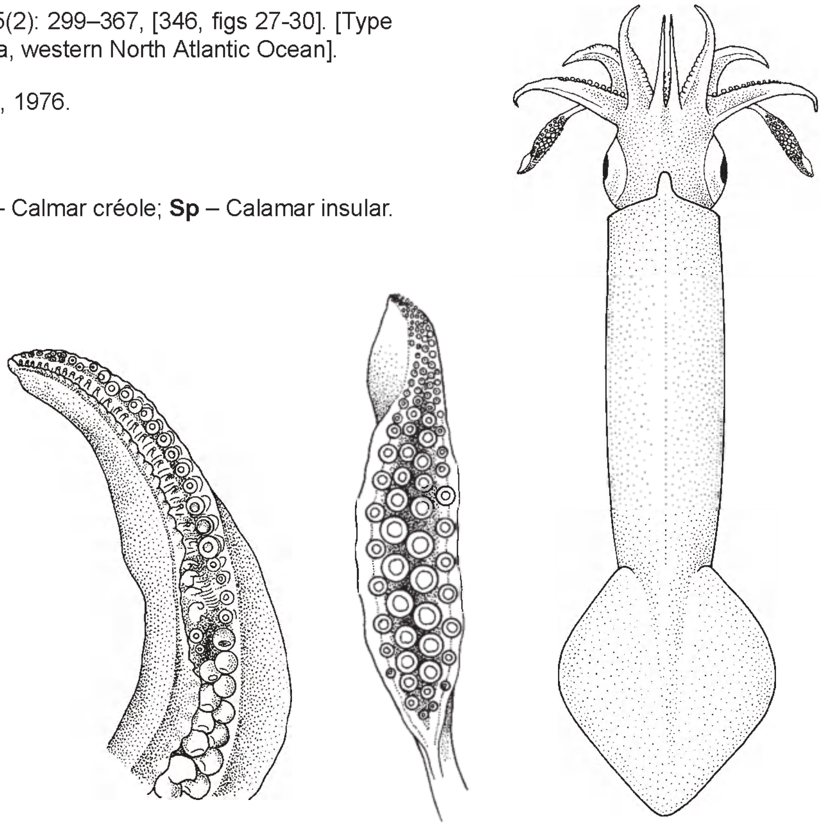
Fig. 85

Loligo roperi Cohen, 1976, *Malacologia*, 15(2): 299–367, [346, figs 27-30]. [Type locality: 25°42'30"N, 79°20'W, Caribbean Sea, western North Atlantic Ocean].

Frequent Synonyms: *Loligo roperi* Cohen, 1976.

Misidentifications: *Doryteuthis plei*.

FAO Names: En – Island inshore squid; **Fr** – Calmar créole; **Sp** – Calamar insular.



hectocotylus

tentacular club

dorsal view

Fig. 85 *Doryteuthis (Doryteuthis) roperi*

Diagnostic Features: Mantle long, slender, cylindrical; tapers to an acute posterior point. Fins rhomboidal, with curved lateral and anterior margins, that give them a heart-shaped or oval appearance in some specimens; **fin length about 33 to 39% mantle length**. Tentacles short, robust; clubs expanded, about 14 to 21% mantle length, with <25 transverse series of suckers. **Left ventral arm hectocotylized for >50% of arm length** (57 to 62%); about 80% of suckers in dorsal series modified to minute size, set on broadly triangular bases. Reddish brown chromatophores over the entire mantle, larger and more closely spaced on posterior half of dorsal side.

Size: Small-sized species, maximum mantle length 72 mm.

Geographical Distribution: Western Atlantic Ocean: Caribbean Sea and Gulf of Mexico (Fig. 86).

Habitat and Biology: The island inshore squid probably is widely distributed on the continental shelf of the Caribbean Sea, but its vernacular name reflects its apparent association with the islands therein. The species has been repeatedly recorded on the Flower Garden Banks, in the northwest Gulf of Mexico. Here, seasonal aggregations of juvenile and adult squid are observed during the annual coral spawning event (about 7 to 10 days after the first full moon in August and in September if there is a split spawning). Ancillary observations suggest that squid may be attracted by coral spawning, or the squid may spawn then as well. Alternatively, they may aggregate to utilize the prolific food resources made available by the coral spawning event. Maturation occurs at a small size: the smallest mature males measure 44 mm mantle length, the smallest mature females are 43 mm mantle length. Some sexual dimorphism occurs: the margins of the vane of the gladius are straighter in males, more tapered in females; the fins of most males are more rhombic than those of most females and males have a midventral ridge on the mantle.

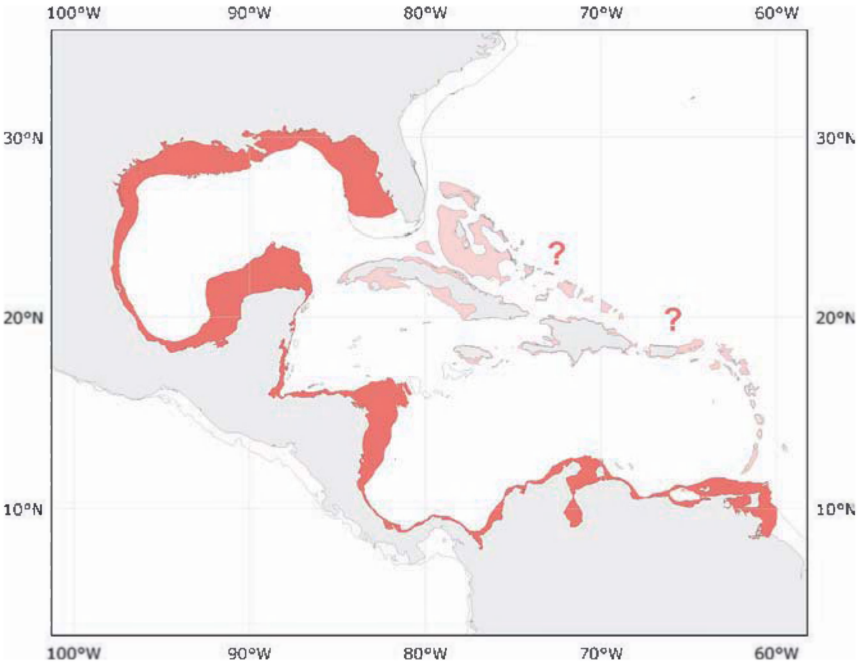


Fig. 86 *Doryteuthis (Doryteuthis) roperi*

🟥 Known distribution 🟥 Probable presence

Interest to Fisheries: The island inshore squid is taken by dip net at the surface at night, and it also is caught by trawl nets at depths between 50 and 300 m. However, its small size limits its interest to fisheries.

Local Names: None available.

Remarks: Because this small loliginid is easily confused with ***Loligo plei***, it may be more widespread than current records indicate.

Literature: Cohen (1976), Roper *et al*. (1984), Debose and Nevitt (2006), Vecchione (2002, 2008c).

Subgenus ***Amerigo*** Brakoniecki, 1986

Amerigo Brakoniecki, 1986, *Ph.D. Dissertation, University of Miami, Coral Gables, FL*, 163 p. [106].

Type Species: *Doryteuthis (Amerigo) gahi* (d'Orbigny, 1835).

Doryteuthis (Amerigo) gahi (d'Orbigny, 1835)

Fig. 87

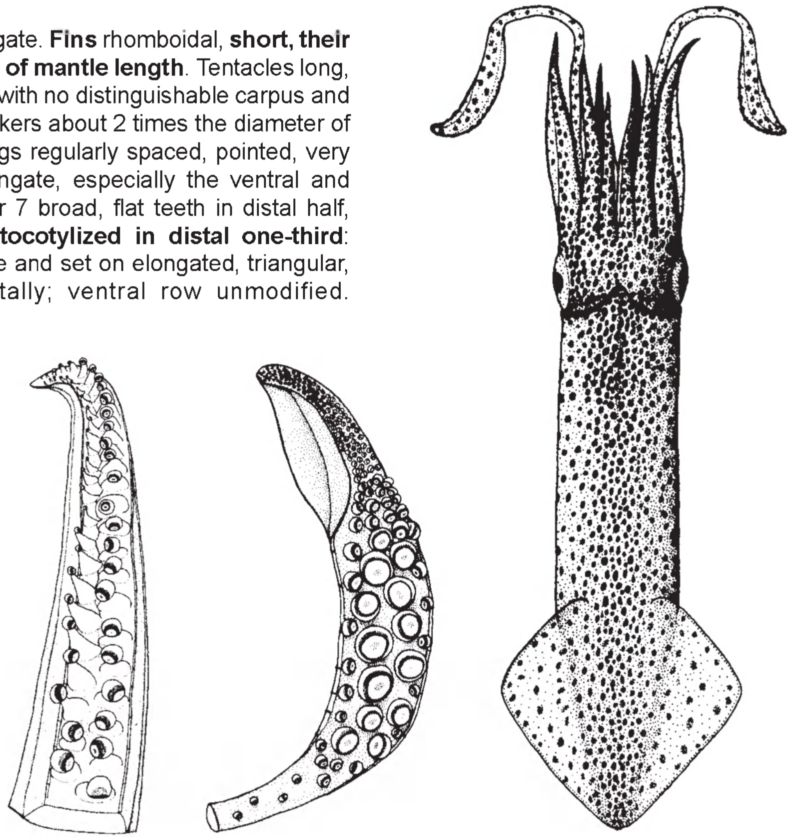
Loligo gahi d'Orbigny, 1835, *In* 1834-1847, *Voyage dans l'Amerique Meridionale*, 5(3): 1–758. [60, pl 3 figs 1–2]. [Type locality: Valparaiso, Chile, eastern South Pacific Ocean].

Frequent Synonyms: *Loligo gahi* d'Orbigny, 1835, *Loligo patagonica*, Smith, 1881.

Misidentifications: None.

FAO Names: En – Patagonian squid; **Fr** – Calmar patagon; **Sp** – Calamar patagónico.

Diagnostic Features: Mantle moderately elongate. **Fins** rhomboidal, **short, their length usually about 40% to 45%** (up to 53%) **of mantle length**. Tentacles long, slender; tentacular clubs narrow, unexpanded, with no distinguishable carpus and relatively small suckers on manus; median suckers about 2 times the diameter of the marginal suckers; teeth on club sucker rings regularly spaced, pointed, very numerous: 25 to 35 (possibly 45). Arms elongate, especially the ventral and ventrolateral arms; arm sucker rings with 6 or 7 broad, flat teeth in distal half, proximal half smooth; **left ventral arm hectocotylized in distal one-third**: suckers in dorsal series greatly reduced in size and set on elongated, triangular, swollen pedicles that grade smaller distally; ventral row unmodified. Chromatophores present on the oral/ventral surface of all arms, including hectocotylus. **Hatchling chromatophore general pattern**: 3 or 4 red chromatophores mixed with a similar number of yellow ones on each tentacle; 2 red chromatophores on each arm IV; 3 or 5 (generally 4), red chromatophores present on the "cheek patch" areas; 6 brown chromatophores arranged as a hexagon commonly found on dorsal head surface; 5 brown chromatophores form a pentagon in the centre, frequently present on the dorsal mantle surface, with yellow ones close to the posterior margins; numerous red chromatophores on the ventral surface of the mantle, arranged to form a more or less regular grid of oblique lines. However, variability occurs in chromatophore number and pattern, especially in the "cheek patch" area.



hectocotylus **tentacular club** **dorsal view**

Fig. 87 *Doryteuthis (Amerigo) gahi*

Size: Medium-sized squid; maximum reported mantle length 340 mm for females and 400 mm for males.

Geographical Distribution: Eastern Pacific Ocean, from northern Peru to southern Chile and southwestern Atlantic Ocean, from the Gulf of San Matias (Argentina, about 42°S) to Tierra del Fuego. The northern limits on both coasts are uncertain, but in the Pacific it is reported in the waters off Puerto Pizarro (about 4°S, southern Guayaquil Gulf, northern-most Peru), while in the Atlantic it extends on the continental slope to about 36°S, following the cold waters of the Malvinas (Falkland) currents (Fig. 88).

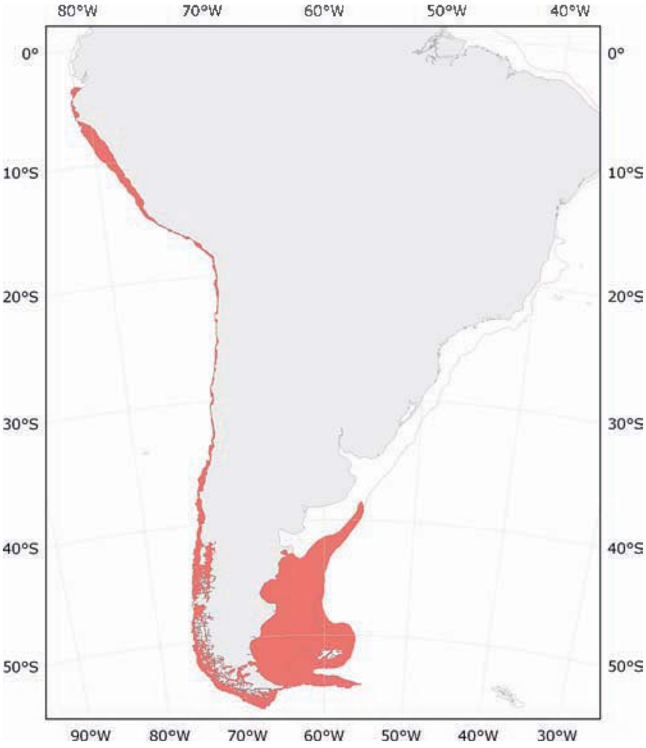


Fig. 88 ***Doryteuthis (Amerigo) gahi***

🟥 Known distribution

Habitat and Biology: ***Doryteuthis (Amerigo) gahi*** supports an important fishery on the Patagonian shelf. Due to the economic importance of the fishery, considerable research has focused on the populations that inhabit this area of the distributional range, and present knowledge on the biology of the species is derived mainly from data obtained in the Falkland Interim Conservation Zone (FICZ). Much less is known about the Pacific populations. The Patagonian squid occurs from the surface to about 600 m depth, but it is most commonly found within the 300 m isobath. Information on the Falkland population indicates that ontogenetic migrations occur in that area: the species spawns in shallow water and migrates down the continental shelf and slope after hatching for feeding and maturation. Animals then return to shallow water to spawn. Sexual segregation occurs during these migrations: while the greatest numbers of juveniles (<100 mm mantle length), both males and females, are consistently caught in waters of <100 m to the south and east of East Falkland, larger squid (>100 to 110 mm mantle length) on the feeding grounds are segregated by sex and depth, the females at 250 to 300 m, the males at 170 to 250 m. Males emigrate from their shallower feeding grounds to the spawning grounds earlier than the deeper-feeding females and the sex ratio evens out by the middle of the spawning season on the shallow spawning grounds (30 to 100 m). Interannual changes in the spatial distribution and abundance of the species also occur in relation to changes in the strength, oceanographic features and meander locations of the Falkland Current. This current meets the continental slope east of the Falkland Islands, causing a strong upwelling of the Sub-Antarctic Superficial water mass, where the main feeding grounds of the squids usually are located. However, in years of intensified current, a part of the population is displaced farther north and aggregates on the shelf at about 45°S to 47°S. Data about migrations in the Pacific waters off Peru and Chile are not available, but a migratory pattern for the species in the Callo area of Northern Peru has been hypothesized. In the Falkland population females have a larger mantle circumference than males, whereas only some differences in hard structures occur between males and female of the Peruvian population and no significant difference at all is evident between the 2 sexes in the Chilean population. Size at maturity is extremely variable; the observed range of mantle lengths at full maturity for males and females in the Falkland population is 80 to 380 mm and 70 to 300 mm mantle length respectively.

Maturation and growth of the reproductive organs seem to take place using energy derived from the squids' food, not at the expense of somatic tissue, and both processes continue during the migration from the feeding grounds to the spawning grounds. Mating first occurs on the feeding grounds where part of the male population remains after maturation, to meet with the maturing females on their way back to inshore waters. A 2-phase copulation seems to occur, with the first mating (sperm deposition in the sperm reservoirs on the buccal membrane) probably taking place on the feeding grounds and triggering the process of female maturation. Mature females then migrate to the spawning grounds, where the second mating occurs, with sperm deposition within the mantle cavity, thus allowing fertilization of eggs during spawning. Spawning is intermittent with egg deposition in batches as in other loliginids, and females remain on the spawning grounds until death. The number of ripe eggs in the oviducts of mature females varies with the size of the animals, from 90 to 200 in females of 80 to 100 mm mantle length to 4 000 to 4 500 in females of 280 to 300 mm mantle length. A high Potential Fecundity (PF) occurs with 1 800 and 35 000 eggs present (PF=0.56 ML 1.86). Actual fecundity is about 50% of total fecundity. Eggs are oval in shape and their size is intermediate for loliginids, those of the Atlantic populations are between 1.4 to 1.9 mm and 1.8 to 2.8 mm; the larger eggs are laid in winter. Eggs from the Chilean population are slightly larger, with diameters between 2.3 and 3.2 mm, as were those from 1 egg mass found in the Bridges Islands, Beagle Channel, Tierra del Fuego at 2.3 to 3.0 mm. Inshore spawning sites occur in shallow waters (0 to 20 m) all around the coastline of the South Falkland Islands and along the Patagonian Coast, from the Bridges Islands up to Gulf San Matias (about 42°S). However, collections of hatchlings in deeper waters (i.e. 86 miles, north of Nuevo Gulf, Argentina, at about 40°S), suggest that the spawning grounds may extend to greater depths, at least in the northern area of the distribution. Around the Falkland Islands, the eggs are found attached exclusively to kelp stipes of the species *Lessonia* spp. and *Macrocystis pyrifera*, preferably on short, solitary kelp strands, often at the outer (seaward) edge, with ambient water temperatures of 3.86° to 9 °C. Along the Patagonian coast eggs are found attached to various hard substrata, such as ropes, shells, fishing lines and gravel in sites where the SST ranges from 5°C (in the Beagle Channel in August) to close to 23°C (in the Nuevo Gulf in February). Freshly laid egg masses are bright white; egg capsules are mainly 50 to 60 mm in length and contain an average of 70 fertilized eggs. Egg masses are formed by a variable number of capsules, from less than 10 to more than 300; this variability depends on the size and condition of the female and on the deposition of multiple egg masses on a common mass by more than one female, as observed in other loliginids. Year-round spawning occurs at the northern limit of the distribution in the Nuevo Gulf, while two main spawning seasons, in May to June and in October to November, exist around the Falkland Islands. ***Dorytheuthis gahi*** spawns in colder waters than any other loliginid species, with normal egg development active at a temperature as low as 3.86°C, considerably less than in other loliginid species and less than that observed under experimental conditions in the laboratory. The duration of the embryonic development is negatively correlated with water temperature in squids; it requires 125 days at a very low temperature (one of the longest times among loliginids), while it is much shorter at higher temperatures (30 to 35 days at about 13°C). Consequently, the 2 cohorts observed in the Falkland Islands area differ in the duration of the embryonic development, so that the 5 to 6 months difference in the spawning time diminishes to only about 2 to 4 months difference in hatching time. This strategy enables recruits from both cohorts to take advantage of the spring-early summer zooplankton bloom that occurs in the Southwest Atlantic Ocean. The mantle length of hatchlings incubated in an aquarium varied between 2.3 and 3.7 mm, being inversely correlated with the mean incubation temperature; the newly hatched squids display a marked positive phototaxis and swim actively. Studies on juvenile distribution in the Falkland Island waters show that juveniles aggregate close to the bottom and are more available to the sampling gear by night than by day. Data from statolith analysis indicate a life span of about 1 year for the species throughout the distributional range; males may live longer than females (up to about 15 months), and it is assumed that catastrophic mortality of most of the population occurs soon after spawning. As in most of the squid species studied to date, feeding is likely to be opportunistic, with the animals eating all possible pelagic prey, with an apparent preference for euphasiid crustaceans in the population of the Falkland Islands. Peak feeding activity takes place around mid-day and early afternoon. Predators include several fish species, other squids, albatrosses, penguins, mammals (dolphins and sea lions).

Interest to Fisheries: ***Doryteuthis gahi*** is the second most important loliginid squid in the commercial fisheries world wide. The Falkland Islands international fishery is mainly concentrated in the south and east of the Falkland Island Interim Conservation and Management Zone. It was the world's largest fishery for a loliginid species until 1996, when it was overtaken by the Californian fishery for ***D. opalescens***. In the Falkland fishery there are 2 fishing seasons each year, from February to June and August to October. The 2 seasons result from the presence of the 2 main spawning groups. Squid from each spawning group recruit into the fishery at an age of about 6 months and are fished during the second half of their life cycle. At least 2, and more usually 3, cohorts of squid recruit to the fishery each year. Squid recruit in February, April/May, and August/September. The extensive commercial fishery concentrates mainly on the feeding grounds, at different depths according to season; consequently, the sexes are targeted differently at depths and in areas where the commercial fishery operates. The fishery has been regulated since the beginning of 1987, by using a target proportional escapement policy, which allows a level of fishing effort compatible with yearly conservation targets. Joint management by Argentina and the United Kingdom ensures that the fishery is closed at about the escapement limit.

Recent studies showed a strong negative relationship between sea surface temperature and recruitment intensity, and management strategies taking this relationship into account were proposed. Also, inverse patterns in abundance of ***Illex argentinus*** and ***D. gahi*** around the Falkland area were analysed and related to possible interspecific competition, in which ***I. argentinus*** likely represents a "limiting" factor ***D. gahi*** in some years, months and zones, either by direct (as a predator) or indirect (as a food competitor) impact. Undoubtedly, predicting squid recruitment using factors such as environmental data and predator abundance offers the potential to refine the licensed effort based on likely abundance.

Doryteuthis gahi also is fished by small-scale and industrial fisheries in Chilean waters, mainly in the southern area. Here the species is caught year-round, with maximum catches in summer and autumn. Also off the Peruvian coast landings of ***D. gahi*** are reported throughout the year, with 2 main seasons in spring (peak in March) and late summer (peak in September). In this region the catches are influenced by El Niño and La Niña events, where El Niño (associated rise in sea temperature) has a negative effect, while La Niña (lowered sea temperature) a positive one.

Local Names: ARGENTINA, CHILE, PERU: Calamar.

Remarks: The systematic position of ***Doryteuthis gahi*** (type locality: Valparaiso, Chile) had been long controversial. Considered the same species as ***Loligo patagonica*** Smith, 1881 (type locality: Alert Harbor, West coast of Patagonia) by several authors (e.g. Castellanos and Cazzaniga, 1979; Brakoniecki 1984b), the species were both considered to be valid species by other authors (e.g. Nesis, 1982, 1987). Observations on the egg size revealed that small differences exist between the Chilean and the southwestern Atlantic populations (e.g. Arkhipkin *et al*., 2000b, Baron, 2001, Guerra *et al*., 2001). Studies on morphological differences between ***D. gahi*** from the 2 oceans revealed significant differences between the Peruvian, Chilean and Patagonian populations. Differences were more accentuated between the population from the Falkland Islands and those from Peru and Chile than those between the 2 latter localities (Vega *et al*., 2002). Genetic studies also demonstrated that differences between the South East Pacific and South West Atlantic populations exist, supporting the suggestion that the 2 populations may represent distinct subspecies (Shaw *et al*., 2004).

As for the southwestern Atlantic populations, the similarity between ***D. gahi*** and ***D. sanpaulensis***, makes the identification of the 2 species difficult/uncertain, especially for juveniles and in the area where the 2 species overlap, i.e. between 42°S and 46°S. Recent morphological and meristic analyses indicate that indices of relative fin width (FW/ML) and relative gladius (GW/ML) are useful tools for the identification of the species. FW/ML can be used alone as a rapid and easy tool in the field: index values lower than 0.53 correspond to ***D. gahi***, while those higher are ***D. sanpaulensis*** (Pineda *et al*., 2002). Other characters useful on fresh, undamaged specimens are the body coloration and the pattern of chromatophores on the oral surface of arms IV: ***D. gahi*** is brownish dorsally and reddish ventrally, while ***D. sanpaulensis*** is reddish on both surfaces; no chromatophores are present on the arms of ***D. sanpaulensis***, while both sexes and all sizes of ***D. gahi*** possess chromatophores, even on the hectocotylus (Pineda *et al*., 2002). Less easily used but very useful nonetheless are statolith size and proportions in the 2 species: the statoliths of ***D. gahi*** are significantly larger than those of ***D. sanpaulensis***, and they have a very prominent dorsal dome and a comparatively long and thin rostrum (Pineda *et al*., 1998b). Additional observations on the the relative growth of beaks in the 2 species indicate differences that and can be used to discriminate between the 2 species, whereas the beak morphometry is similar (Pineda *et al*., 1996).

Literature: Brakoniecki (1984b), Roper *et al*. (1984), Hatfield and Rodhouse (1991), Pineda *et al*.(1998a, b), Brunetti *et al*. (1999), Villegas (2001), Vega *et al*. (2002), Arkhipkin *et al*. (2006).

Doryteuthis (Amerigo) ocula (Cohen, 1976)

Fig. 89

Loligo ocula Cohen, 1976, *Malacologia*, 15(2): 299–367. [330, figs 15-30]. [Type locality: 22°59'N, 78°43'W, Caribbean Sea, western Atlantic Ocean].

Frequent Synonyms: *Loligo ocula* Cohen, 1976.

Misidentifications: *Doryteuthis pealei*.

FAO Names: En – Bigeye inshore squid; **Fr** – Calmar à gros yeux; **Sp** – Calamar ojigrande.

Diagnostic Features: Mantle bluntly pointed posteriorly. Fins rhomboidal, their lateral angles rounded, anterior lobes well developed; **fin length about 45 to 55% of mantle length**. **Eyes very large; visible part 15 to 21% of mantle length**. **Left ventral arm hectocotylized, modified in distal one-third to one-fourth but not to tip**; 10 to 12 suckers in dorsal series <1/2 diameter of ventral counterparts; 2 to 5 suckers proximal to reduced suckers are enlarged; all modified suckers on swollen, triangular bases. Tentacles robust; clubs expanded, about 24 to 35% of mantle length.

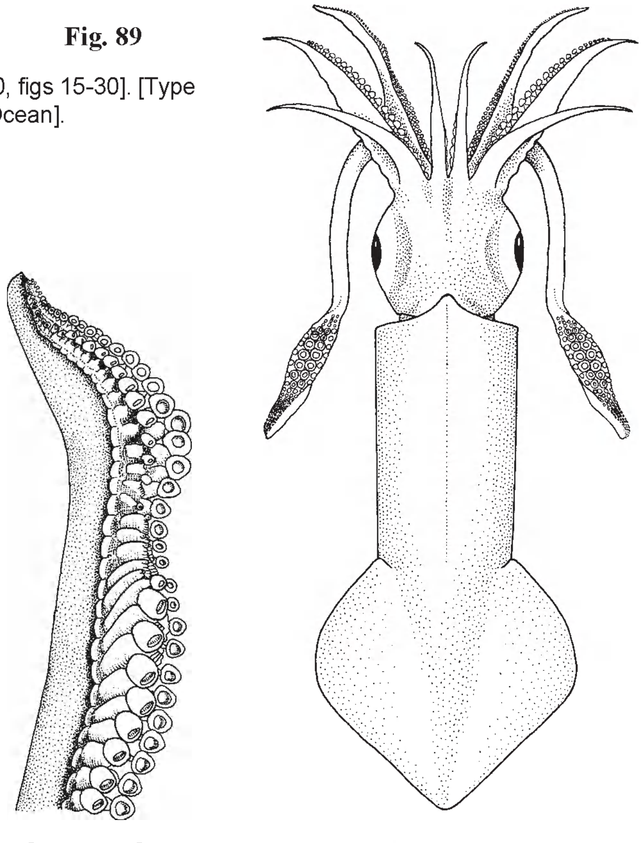
Size: Small-sized species; maximum reported mantle length 127 mm.

Geographical Distribution: Western Atlantic: Caribbean Sea around Cuba (Fig. 90).

Habitat and Biology: Found in depths of 250 to 360 m. Its biology is unknown.

Remarks: This small loliginid is known only from the original description, but because it is easily confused with ***Loligo pealeii*** it may be more widespread than current records indicate.

Literature: Cohen (1976), Roper *et al*. (1984), Vecchione (2002, 2008c).



hectocotylus **dorsal view**

Fig. 89 ***Doryteuthis (Amerigo) ocula***

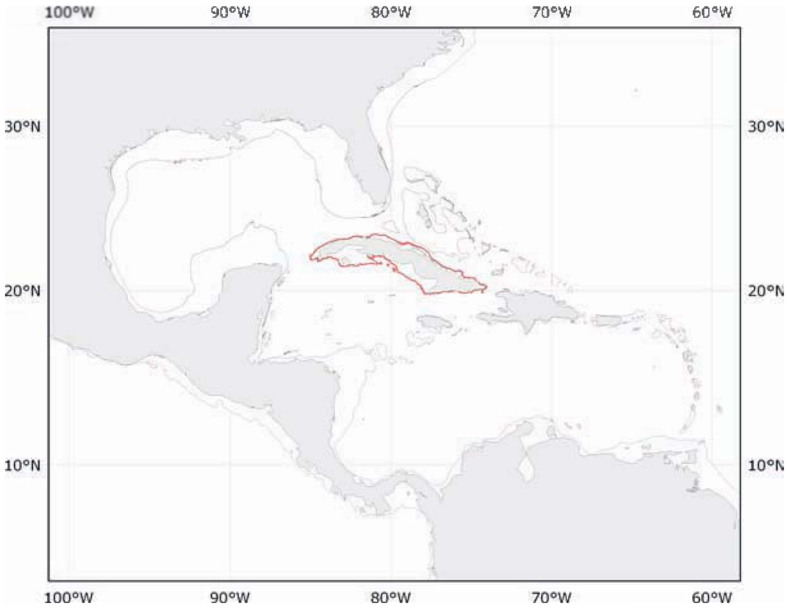


Fig. 90 ***Doryteuthis (Amerigo) ocula***

🟥 Known distribution

Doryteuthis (Amerigo) opalescens (Berry, 1911)

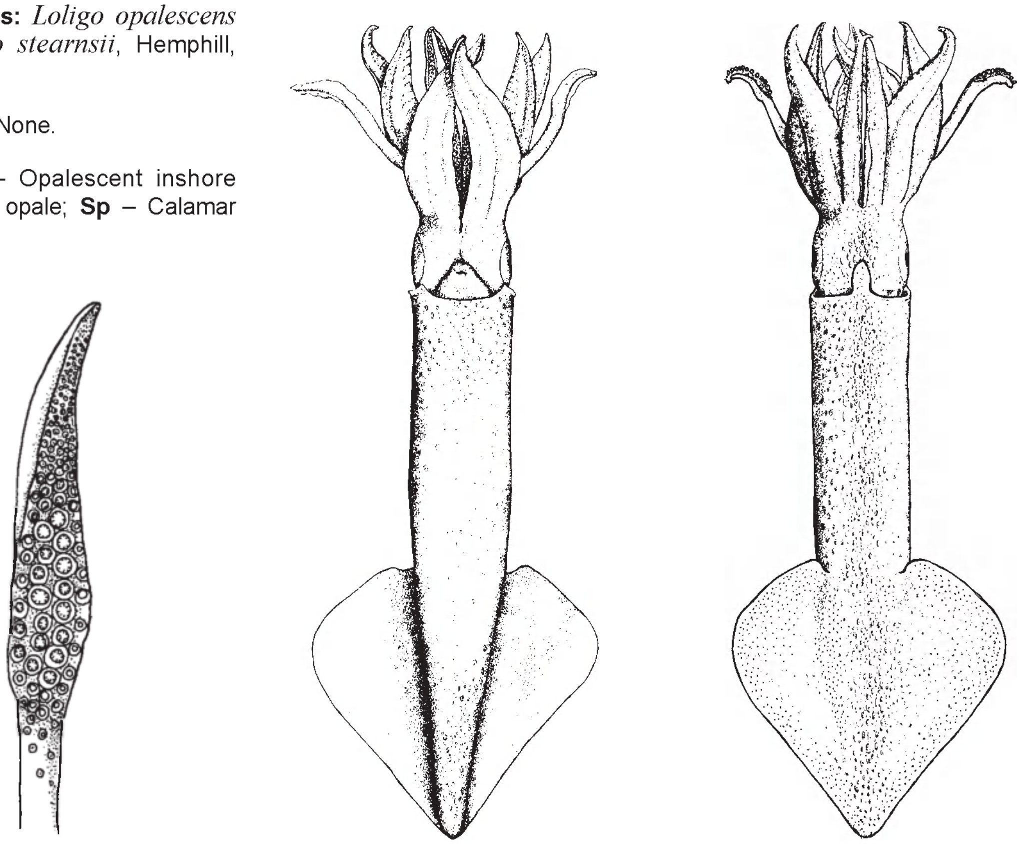
Fig. 91; Plate IV, 18–19

Loligo opalescens Berry, 1911b, *Proceedings of the United States National Museum*, 40(1838): 589–592. [591]. [Type locality: Puget Sound, Washington, USA, eastern North Pacific].

Frequent Synonyms: *Loligo opalescens* Berry, 1911, *Loligo stearnsii*, Hemphill, 1892.

Misidentifications: None.

FAO Names: En – Opalescent inshore squid; **Fr** – Calmar opale; **Sp** – Calamar opalescente.



tentacular club

ventral view

dorsal view

Fig. 91 ***Doryteuthis (Amerigo) opalescens***

Diagnostic Features: Mantle slender, width 20 to 33% of mantle length. **Fin length and width approximately equal, 38 to 52% of mantle length**. Tentacular **clubs narrow, unexpanded**; sucker rings with about 30 blunt teeth. Arms short; arm sucker rings with 9 to 12 blunt teeth. **Left ventral arm hectocotylized along distal one-third** by great reduction in sucker size and enlargement of stalks into papillae. Ink sac elongate.

Size: Small to medium-sized squid; most commonly reported sizes range between 130 and 190 mm mantle length, averaging between 140 and 170 mm mantle length. Maximum reported total length 305 mm.

Geographical Distribution: Endemic to the California Current region. Range from souteastern Alaska (58°N) to southern tip of Baja California, Mexico (22°N). However, abundance is generally low north of Vancouver Island, British Columbia, Canada (Fig. 92).

Habitat and Biology: ***Doryteuthis opalescens***, also known as the California market squid, inhabits most of the coastal waters over the continental shelf off western North America, from the surface to depths of 500 m within 200 miles off shore. Adult squid move to deep waters during the day, but return to the surface at night, mostly to hunt. Squid distribution, growth and life cycle success in this geographic

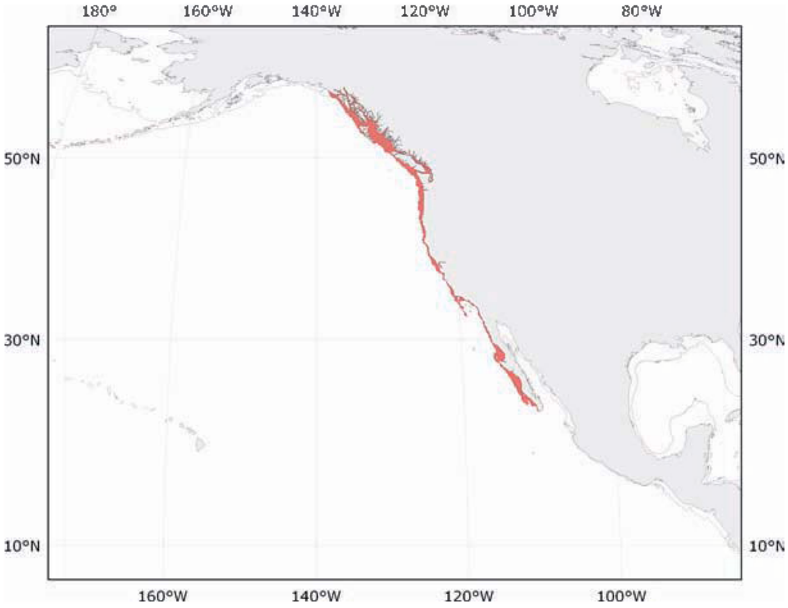


Fig. 92 ***Doryteuthis (Amerigo) opalescens***

🟥 Known distribution

area are related to the oceanography of the eastern Pacific Ocean, in which warmer, oxygen-rich surface waters lie above the deep zone of cold, nutrient-rich but oxygen-poor waters transported into the Pacific Basin from Antarctic origins. The very complex California Current System extends from Oregon to Baja California and generates eddies and meanders that affect the distribution of paralarval and juveniles. Upwelling of cold, rich water along the coast affect squid growth and abundance. This system, in turn, is affected by the El-Niño and La Niña events that occur farther south, both resulting in strong fluctuations of squid abundance and distribution.

Sexual dimorphism exists: females have distinctly shorter and thinner arms and tentacles than males, and smaller heads; this results in a more massive appearance of males, that enables easy indentification of adult males and females. Males grow larger than females and squid size is positively correlated with La Niña (colder waters-lower metabolic rates) and upwelling (high productivity-rich food resources available) events. Conversely, during the El Niño events, squid are smaller and less abundant due to the combined effects of high metabolic rates (increased temperatures) and lower levels of available prey (decreased ocean productivity). Size at maturity varies; the smallest mature female observed in the field mesured 81 mm mantle length, the smallest mature male 72 mm mantle length; even smaller sizes are noted for animals cultured in the laboratory (i.e. 60 mm mantle length for females and 71 mm for males). However, female and male squid may remain immature to a mantle length of 140 and 130 mm, respectively.

Maturation and growth of the reproductive organs seem to occur from energy derived directly from food, not at the expense of somatic tissue, judging from the excellent condition of the squid entering the spawning areas, with animals described as “fat and heavy, with glossy, unmarked skin and thick and firm mantles” (Fields, 1950). Reproduction is seasonal and spawning takes place at different seasons within the distributional range. In southern California spawning occurs in winter, from approximately December to March; farther north, in Monterey Bay, the spawning season extends from April to November, with a major peak in April; off Central California a main spawning peak occurs in October. Off Bamfield, British Columbia, spawning peaks occur in spring. Even farther north off Vancuver Island, spawning does not occur every year, but, when it does, it takes place in late summer.

Spawning aggregations may result in millions of individuals aggregating on the spawning grounds. In Monterey Bay, however, small spawning groups (about 30 to 200 squids) commonly are formed from the much larger schools aggregated above in the water column (i.e. thousands or tens of thousands of squid). In situ observations indicate that this particular spawning activity occurs during daytime, and no mass die-off seems to occur after spawning; instead, squids actively rejoin the larger schools aggregated above. These animals apparently are in excellent condition, corroborating results of other studies on loliginids that spawn intermittently. This phenomenon of daytime spawning and absence of mass die-off of spawned-out loliginid squid is contrary to earlier perceptions. Mating behaviour is unique among loliginid squids: the male grasps the female from her ventral side and holds her for minutes or hours in a nearly vertical position; both copulation and deposition of egg capsules occur in this posture, with the paired animals lowering themselves together to the egg bed. In living animals tissues are milky and translucent, with a faintly bluish tone. When mating, the male’s mantle is pale but the arms and some of the head are dark red, while the female’s colour does not vary. Mottled gold and brown is a common colour pattern for excited animals and squids become very dark if disturbed.

In the laboratory, ***Doryteuthis opalescens*** exhibits dominance behaviour during spawning. A single dominant male prevents other males from approaching the egg mass he guards. Females are allowed to approach the egg mass. The dominant male uses postural and colour displays directed toward the intruding male. Similar dominance behaviour and displays have not yet been observed in the ocean.

Eggs are oval, about 2.0 to 2.5 mm in length, 1.3 to 1.6 mm in width; sizes usually are proportional to the female size, and the eggs are enveloped in a thick corion. Eggs are arranged irregularly in elongated capsules, the outer layer of which is an acellular matrix 1 to 2 mm thick that contains a dense culture of bacteria, the probable source of which are the nidamental glands. These bacteria may aid in carotenoid production and egg protection by forming antibiotics and toxic products. This may partly explain why such low predation occurs on the readily accessible and highly visible egg masses attached to the substrate. Average capsule length is about 80 mm and each capsule is anchored by a thin, transparent stalk to the substrate (sandy bottom) or to other capsules. The number of eggs per capsule varies, but mean values number between 150 and 200 eggs. Freshly laid capsules are white, but they soon become brown, infested with worms and debris, and often have damaged sheaths. Often mixed masses of older brown capsules occur later in the centre of a mass surrounded by more recently deposited white capsules; this confirms that aggregate egg masses are formed over an extended interval of time.

Egg development requires 30 to 35 days at 13.6°C but shortens to as little as 21 days at 16°C. Oxygen levels are critical for embryonic development. Hatching occurs mainly at night and newly hatched squid (2.5 to 3.2 mm mantle length) are active swimmers and display a positive phototaxis in the laboratory. In the natural environment paralarvae are most abundant adjacent to oceanic fronts associated with uplifted isotherms, and their distribution is strongly affected by tidal currents; this keeps them within 3 kilometers of shore long enough to allow them to feed on the abundant coastal plankton.

Growth is highly influenced by environmental constraints, with males responding quicker to changes in the environment than females, most probably due to the much greater reproductive investment of females in terms of relative body weight percentages. Individuals reach maturity at 6 to 9 months, and even though, spawning activity may be prolonged, contrary to previous belief, their lifespan is completed within less than one year.

Opalescent squids are active predators that feed upon a wide range of prey, including crustaceans, fishes, polychaetes and cephalopods. Slight differences in prey preference may occur, depending on growth, habitat, sex and maturity stage, but these squids are basically opportunistic feeders. The diet, therefore, changes in relation to water depths and location.

Market squid are preyed upon by a variety of fishes and higher-level predators and are the principal forage items for several species of fishes, birds and mammals. Therefore they are very important in the food web off California.

Interest to Fisheries: The California market squid has been harvested since the 1860s, and since 1993 it has become the largest fishery in California, both in terms of tonnage and value. In the 1999–2000 season fishermen landed 105 005 tonnes of California market squid, with an ex-vessel (wholesale) revenue of USD 36 million, the highest ever attained in the California fisheries. After the decline of the anchovy fishery decades ago, ***Doryteuthis opalescens*** probably constitutes the largest biomass of marketable species off California. They typically are harvested on shallow nearshore spawning grounds; specialized light boats shine high intensity lights on the water to attract and congregate the squids near the surface, then seiner boats capture them with purse-seine nets. The fishery originated in Monterey Bay, and has expanded to southern California, where the majority of squid captures currently occur around the California Channel Islands, from Pt. Dume to Santa Monica Bay and in southern Monterey Bay. Landings continued to increase in recent decades, as the fishing activity intensified, with fishermen from Alaska, Washington and Oregon also participating. A strong relationship between total landings and important El Niño events has been noted. Squid landings collapsed twice, following strong El Niño events in 1982–83 and 1997–98, whereas only slight decreases occurred after weak ones.

Due to the paramount importance of this fishery some management measures have been enacted, but they have been limited only to weekend closures, to allow a weekly 48-hours period of undisturbed spawning. In addition, since 2000, light boat and seine vessel operators have been required to complete logbooks for the California Department of Fish and Game, so that Catch Per Unit Effort (CPUE) for the market squid can be estimated. Due to (1) the increasing market demand, (2) the fact that the fishery is concentrated on the spawning grounds and (3) the knowledge that spawning represents the final phase of the squids life and that squid abundance is strictly related to environmental conditions, unwarranted concern about effective management actions recently has increased. Spatial closures have been suggested to protect at least a few spawning sites and guarantee some undisturbed reproduction. The recent establishment of the marine reserve system in the Channel Islands should protect about 13% of initial squid spawning grounds. Paralarval density index was found to correlate strongly with subsequent adult squid abundance on the spawning grounds. Therefore, catch limits for the fishery could be set according to paralarval abundance surveyed about nine months prior to spawning and fishing.

Local Names: USA: California market squid.

Remarks: Information on the extent of genetic differentiation among exploited populations is crucial for the conservation of the species. Due to the extensive distribution of ***Doryteuthis opalescens*** the existence of more than one population or genetically distinct stocks, isolated by seasonal or geographical spawning differences, has been postulated (e.g. Ally and Keck, 1978, Kashiwada and Recksiek, 1978a,b, Bettinger *et al*., 1985, Hixon, 1983). However, recent observations indicate that no significant difference was detected within the sampled population over about 2 500 km of the North American west coast, suggesting that unrestricted gene flow prevents population differentiation in the market squid (Reichow and Smith, 1999, 2001). This may be due to the relatively narrow continental shelf in the area, which restricts inshore/offshore migrations and expands north/south movements and distribution.

Literature: Fields (1965), Karpov and Caillet (1978, 1979), Kashiwada and Recksiek (1978a,b), Hixon (1983), Yang *et al*. (1986), Vojkovich (1998), Reichow and Smith (2001), Zeidberg and Hamner (2002), Jackson and Domeier (2003), Forsythe *et al*. (2004), Zeidberg *et al*.(2004, 2006), Vecchione (2008c).

Doryteuthis (Amerigo) pealeii (Lesueur, 1821)

Fig. 93; Plate IV, 20–22

Loligo pealeii Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101, 7 pls, [92, pl 8]. [Type locality: South Carolina, western North Atlantic Ocean].

Frequent Synonyms: *Loligo pealeii* Lesueur, 1821, *Loligo punctata* DeKay, 1843, *Loligo pallida* Verrill, 1873, *Loligo pealii* Verrill 1874, *Loligo pealeii* var. *borealis* Verrill, 1880, *Loligo pealeii* var. *pallida* Verrill, 1881.

Misidentifications: *Doryteuthis plei*, particularly in the southern end of the geographic range of *D. pealeii.*

FAO Names: En – Long-finned inshore squid; **Fr** – Calmar totam; **Sp** – Calamar comun.

Diagnostic Features: Mantle long, moderately slender, cylindrical, the posterior end acutely pointed; **fins rhomboidal, their sides nearly straight**. Gladius long, rather wide, feather-shaped, ratio of greatest width of vane of gladius to greatest width of rachis 2.7 to 3.7 in females, 2.4 to 2.9 in males; edge of vane curved (sometimes straight in males), thin, rarely ribbed. Eyes not unusually large, diameter of externally visible eyeball 8 to 18% mantle length, and diameter of dissected lens 2 to 6% mantle length. **Left ventral arm** of mature male **hectocotylized by modification of the distal third to fourth of arm, but the modification does not extend to arm tip**; fewer than 12 suckers in dorsal row smaller than half the size of their counterparts in the ventral row; **bases or pedicels of some of the modified suckers rounded, narrowly triangular**. **Colour**: reddish brown, darker and more vivid dorsally, lighter, less pigmented ventrally.

Size: Medium- to large-sized squid; maximum mantle length 465 mm for males and 303 mm for females. However, sizes in the western central Atlantic are considerably smaller than in northern waters: males do not exceed 300 mm mantle length (less than 200 mm average), and females do not exceed 130 mm mantle length.

Geographical Distribution: Western Atlantic Ocean continental shelf and upper slope waters, from Newfoundland (Holyrood, 47° 30'N, 53° 06'W) to the Gulf of Venezuela, including the Gulf of Mexico and the Caribbean Sea. (Does not occur around islands, except as rare strays to islands close to continental shelf or slope) (Fig. 94).

Habitat and Biology: ***Doryteuthis pealeii*** distribution represents the second broadest geographical distribution and greatest range of environmental temperature adaptation of any loliginids in the northwest Atlantic, after that of ***Doryteuthis plei***. Typically neritic, in the northwest Atlantic, North of Cape Hatteras, ***D. pealeii*** migrates inshore and northward in late spring and early summer into shallow coastal waters to spawn; by late autumn to early winter the squid migrate southward and into deeper waters along the edge of the continental shelf, where they over-winter. These inshore-offshore and north-south movements are mainly related to the avoidance of water temperatures of 8°C or below. Large concentrations of squid are associated with frontal zones with strong temperature gradients, and they are concentrated mostly along the warm-water side. Hence the definition of “member of the migratory, warm-water group of species, centred primarily in mid-Atlantic waters” (Murawski, 1993), which makes seasonal migrations. Along with water temperature, variations in atmospheric forcing associated with the North Atlantic Oscillation (NAO) also affects the species distribution. Conspicuous in the Mid Atlantic Bight from Cape Cod to Cape Hatteras, offshore and to the north, ***D. pealeii*** coexists with the short finned squid, ***Illex illecebrosus***. Inshore, from Delaware Bay south, it shares waters with the thumbstall squid, ***Lolliguncula brevis*** and with the island inshore squid, ***Doryteuthis plei***, with which it often is confused and misidentified. Conflicting information exist on depth segregation of the three loliginids in the areas where they co-occur.

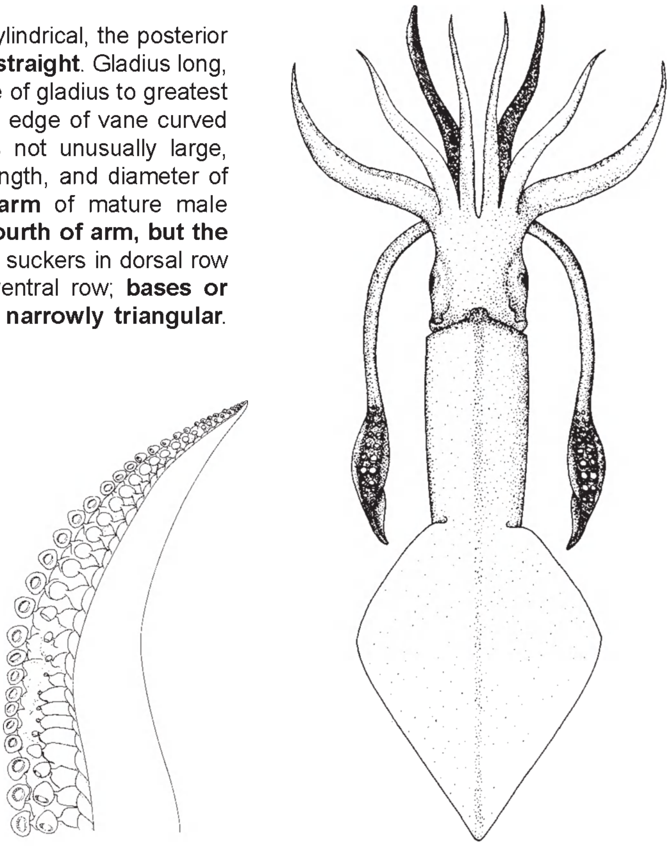

tentacular club **dorsal view**

Fig. 93 ***Doryteuthis (Amerigo) pealeii***

Fig. 94 ***Doryteuthis (Amerigo) pealeii***

🟥 Known distribution

The depth distribution of ***D. pealeii*** ranges from shallow surface waters (i.e. 0 to 10 m) down to 393 m, about the maximum acknowledged depth for most loliginids. Generally demersal, ***D. pealeii*** disperses upward into the water colum at night, and daily movements off the sea bottom are known from trawl samples at all depths and seasons.

Sex ratio in the studied populations is consistently close to 1:1, although males and females are not necessarily equally represented in older age groups. Males grow larger than females, and a distinctive sexual dimorphism has been documented frequently. More males than females have a midventral ridge on the mantle, and this is is more pronounced in males; also, some large mature males have longitudinal reddish brown chromatophore stripes along the ventrolateral margins of the mantle. However, even though the 2 sexes are significantly different statistically in many characters, the differences are small; aside from size, these differences are distinctive only in 2 characters: females have a broader gladius vane and fewer gill filaments than males.

The size at which 50% of the North Atlantic population reaches maturity is about 200 mm mantle length. However, sexual maturity is relatively independent of size and more “environmentally controlled”. Minimum mantle length of mature males and females was 61 and 73 mm, respectively, for specimens from the Caribbean, while the largest immature specimens came from Martha’s Vineyard, Massachussets, and measured 219 and 208 mm, respectively. These and other observations support the hypothesis that latitude and environment affect maturation and spawning. Mating and egg laying have been observed frequently in aquaria. Prior to copulation there is a notworthy mating behaviour to establish a hierarchy, with bright, conspicuous colour displays and arm movements. Males engage in agonistic bouts to gain females, and egg masses play a role in this behaviour. Visual detection of eggs and physical contact stimulate male-to-male aggression, probably through a heat labile factor embedded within squid egg capsules that acts as a chemosensory cue. Mating occurs both in the head-to-head posture, which results in the transfer of spermatophores to the female buccal area, and in a parallel posture; in the latter case males pick up bundles of spermatophores from the muscular penis with the hectocotylus and transfer them inside the female mantle cavity, near the opening of the oviduct. Spawning observations in the field report a complex social structure associated with the egg laying behaviour. After mating, ***D. pealeii*** males and females remain paired and several pairs form a semicircle; 1 pair at a time proceeds with the egg laying process, where the male interwines arms with the female then actually delicately moves both of them over and among the egg fingers, while the female produces the egg capsules. No agonistic behaviour occurs after the pairs are formed. However, field video reveals that smaller, non-consort, “sneaker” males obtain extra-pair copulations, thus participating in the egg fertilization event. The high potential of multiple paternity within eggs capsules derives from such a behaviour, and the subsequent high degree of genetic mixing, result in a stronger sexual selection within the population.

Spawning occurs year-round, with 2 major spawning seasons: 1 in winter, the majority of which occurs in the southern end of the species’ range, in near-shore waters on the continental shelf south of Cape Hatteras, North Carolina; another in spring-summer, on the shelf waters off southern New England, north of Cape Hatteras, usually as far as George’s Bank and Cape Cod. However, unusual environmental conditions may favour northern extention of distribution and spawning (e.g. into the Gulf of Maine and to Newfoundland, as in 2002).

Actual reproductive output varies greatly in wild-caught females kept in an aquarium, with a maximum of 53 000 eggs laid, with the highest mean number over 15 000. Neither size nor age consistently affect fecundity, and multi-ovipositing occurs, where females can lay realtively small clutches of eggs at short intervals or large clutches several weeks apart. Females maintained in isolation from males can lay fertilized eggs, demonstrating the use of stored sperm and deposition lasting over periods of 15 or more days. All these elements indicate that ***D. pealeii*** is a multiple spawner, with ovideposition extending over weeks or months.

Eggs are yolky and ovate, about 1.0 to 1.6 mm long. They are laid in gelatinous finger-like strands or capsules, each one about 8 to 10 cm long, 3.5 to 5.0 cm in diameter, and amber coloured; each capsule contains up to 180 eggs arranged in spiral arrays. Capsules are provided with a sticky filament on one end, which females use to attach them together in masses (“sea mops”), typically anchored to a solid substrate (rock, shells, man-made objects) at depths from a few to 250 m. These egg masses frequently are found on anchor lines, in fish traps and other places that indicate that they are deposited over a short period of time, often overnight.

Normal embryonic development occurs at temperatures between 12º and 23°C, with mean hatching times of 27 to 10 days, respectively. Hatching is nearly synchronous. Newly hatched ***D. pealeii*** measure about 1.8 mm mantle length and they immediately swim to the water’s surface, regardless of illumination intensity. Planktonic paralarvae and juveniles are abundant in surface waters of the Mid-Atlantic Bight in spring, summer and autumn and usually are confined to coastal waters, except when current conditions result in offshore transport. The appearance of schooling behaviour at a size of 5 to 8 mm mantle length may indicate the transition from the planktonic to the juvenile and adult neritic phase of the life cycle.

Laboratory growth in the first phase of the life cycle is fast, and the increase of body mass per day is significantly higher in squid reared at a higher temperature, providing strong evidence of phase-specific temperature sensitivity in squid growth. Thus, wild squid hatched in early summer would be 2 and 3 times the weight, at the same age, of squid hatched in spring and early autumn, because of their exposure to warmer summer temperatures. This temperature-differential mechanism allows later-hatched cohorts to catch up with older squid in size and maturity through seasonally increasing water temperature.

Until recently, ***D. pealeii*** was thought to have a life span of up to 3 years and several different models were used to describe growth from field data (e.g. length frequency distributions); these included linear, cyclic, von Bertalannfy and exponential models and more than 1 growth phase was suggested by some authors. Subsequent application of statolith aging techniques indicates that the species grows more rapidly than previously thought and has a life span of less than 1 year . Growth in length and weight is exponential, and males grow faster and achieve larger sizes than females.

As is the case for many other squid species, the long finned squid feeds on a variety of prey, including fishes, cephalopods, crustaceans and other invertebrates. Diet changes with the ontogenetic development; the smallest juveniles (10 to 40 mm mantle length) feed mainly on copepods, while larger ones (40 to 80 mm mantle length) eat macroplankton (e.g. euphausids) and begin to feed on fish larvae. Young crabs, shrimps and polychaetes are eaten by squid larger than 80 mm mantle length, then young fishes (e.g. silver hake, mackerel, herring, manhaden) and other squids start to dominate, and become the major prey items in adult squid. The highest feeding activity occurs in daylight, and seasonal variation in the feeding rate was observed, with highest feeding activity in the summer. Also, seasonal and geographic variation occurs in the diet composition, depending on the availability of prey items at specific times and places. Size-structured patterns of food consumption were observed, wherein each size-group of squid has its own optimum size of prey (i.e. from 4 to 24% of predator length), piscivory being greater in larger squid. In turn, ***D. pealeii*** is preyed upon by many vertebrates, including fishes (e.g. gadids, skates, lambrids, tunas, sharks) as well as marine mammals and seabirds.

Recent studies indicate that ***D. pealeii*** is a major component in the flow of biomass from pelagic species to predator fish species on the continental shelf off the eastern United States and southeastern Canada, which in turn is a large fraction of the overall energy budget of the shelf ecosystem off the northeast coast of the United States. The tonnage of squid consumed by predatory fishes approaches or exceeds fishery landings, and may even approach and exceed the current estimates of maximum sustainable yield. Therefore, composition and abundance of predators may have important implications on long-term fishery yields of squid.

Interest to Fisheries: ***Doryteuthis pealeii*** is one of the five important commercial species of squids of the northeastern fisheries region of the United States. Small coastal fisheries expanded with the entry of distant waters fleets during the late 1960s and 1970s and catch quotas were established in 1974 by the International Commission for Northwest Atlantic Fisheries–ICNAF. It is caught principally by otter trawls and inshore trapnets. Utilized as food and for bait, it is fished primarily north of Cape Hatteras, although catches also occur in the northern Gulf of Mexico, Yucatan, Columbia and Venezuela. Currently, this is one of the few loliginid species for which specific fishery statistics exist (Jereb and Roper, 2005).

Local Names: None available.

Remarks: Whitaker (1978), Hixon (1980a) and Sanchez *et al*. (1996) computed several indices in order to separate ***D. pealeii*** and ***D. plei***, the most reliable of which is the ratio of gladius width to rachis width (GW/RW) combined with the overall shape of the gladius, including the presence or absence of marginal ribs (absent in ***D. pealeii***). In particular, the GW/RW ratios range from 1.9 to 2.7 for ***D. plei***, and from 2.1 to 3.8 for ***D. pealeii***, and the separation of the two species is best accomplished with a GW/RW ratio of 2.7. However, the 2 species are so similar morphologically that a very careful examination of the collected samples always is recommended, especially in the areas where they are sympatric.

Long considered to be a unit stock, although heterogeneous populations were known to exist (Garthwaite *et al*., 1989), the ***D. pealeii*** fishery was conducted, assessed and managed accordingly (e.g. Sissenwine and Tibbets, 1977, Lange, 1981, Lange and Sissenwine, 1983, Lange *et al*., 1984, Brodziak and Rosenberg, 1993). Recently, however, a genetic break between the northern Gulf of Mexico and the Atlantic Ocean populations was demonstrated (Herke and Foltz, 2002) and subsequently the existence of multiple genetic stocks within the Atlantic population was confirmed (Buresch *et al*., 2006). This phenomenon, along with the rapidly developing offshore fisheries (up to 90% of total landings), the development of a new export market for juveniles (< 50 mm mantle length) and the discovery that this species grows very rapidly and completes its life cycle in less than 1 year, requires that a more cautionary and comprehensive population-based management policy be implemented to ensure a sustainable fishery. Once based on total annual allowable catch and already considered inadequate in the late 1990s (e.g. Macy, 1995a,b, Brodziak, 1998), concise management clearly will need special attention from now on.

As one of the best-studied loliginid species, the literature on ***D. pealeii*** is substantial and includes studies on anatomy, physiology, morphology, biology, behaviour, life cycle and fishery, as well as medical applications (see the Appendix).

Literature: Drew (1911, 1919), Mesnil (1977), Cohen (1976), Summers (1983), Roper *et al*. (1984), Brodziak and Rosenberg (1993), Macy (1995a), Brodziak and Hendrickson (1999), Dawe *et al*. (2001), Hatfield *et al*. (2001), Hatfield and Cadrin (2002), Herke and Foltz (2002), Buresch *et al*. (2006), Dawe *et al*. (2007), Vecchione (2008c).

Doryteuthis (Amerigo) surinamensis (Voss, 1974) **Fig. 95**

Loligo surinamensis Voss, 1974, *Zoologische Mededelingen Rijksmuseum van Natuurlijke Historie et Leiden*, 48(6): 43–53. [43, figs 1–3]. [Type locality: 30 miles northeast of lightship "Suriname River", off the coast of Suriname, western South Atlantic Ocean].

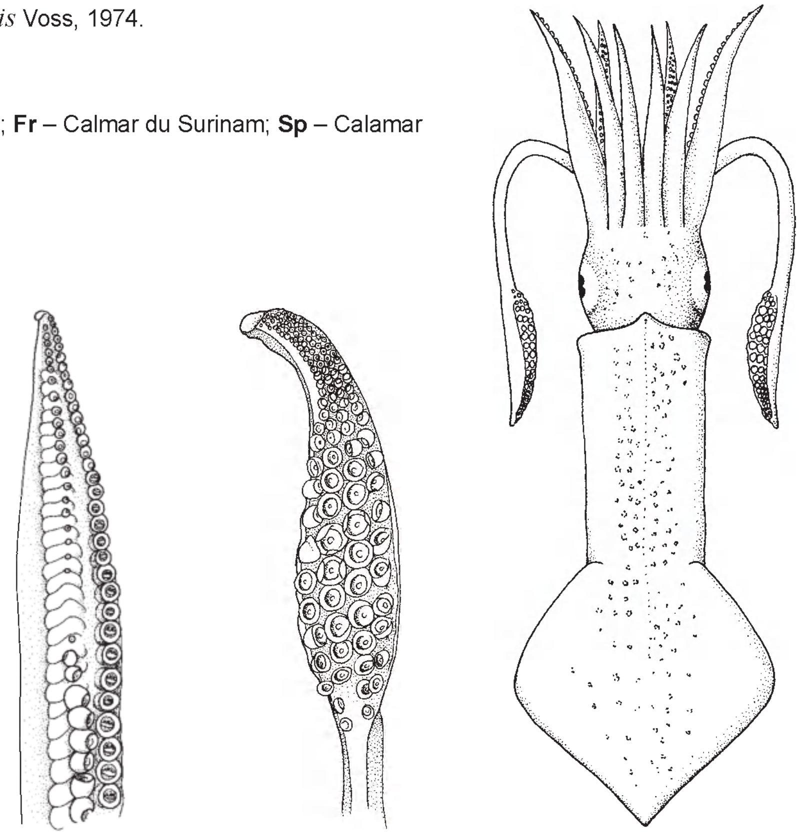
Frequent Synonyms: *Loligo surinamensis* Voss, 1974.

Misidentifications: *Doryteuthis pealeii.*

FAO Names: En – Suriname inshore squid; **Fr** – Calmar du Surinam; **Sp** – Calamar Surinamés.

Diagnostic Features: Mantle moderately broad, about 25% of mantle length. **Fins broadly rhombic**, with rounded lateral angles; **fin length about 50% of mantle length**. Tentacular **clubs expanded, about 30 % of of tentacle length**. Arms of moderate length, about 45% of mantle length. **Left ventral arm of males hectocotylized in distal portion** beginning at 22nd to 24th dorsal sucker pair; suckers at arm tip unmodified; modified suckers reduced in size and set on enlarged, transversely flattened bases. Sucker rings on unmodified ventral arms with sharply pointed teeth. Numerous small to large brown and reddish brown chromatophores on mantle and head, both dorsally and ventrally, more numerous on dorsal side.

Size: Small-sized squid: maximum reported mantle length 118 mm.



hectocotylus tentacular club dorsal view

Fig. 95 *Doryteuthis (Amerigo) surinamensis*

Geographical Distribution: Southern Caribbean Sea: currently, reported only from around the mouth of the Suriname River, Suriname (Fig. 96).

Habitat and Biology: Apparently a shallow living species; known depth range 27 to 37 m.

Remarks: Because this squid is easily confused with ***Doryteuthis pealeii***, its range may be more extensive than indicated by the limited published reports.

Literature: Voss (1974), Roper *et al.* (1984), Vecchione (2002, 2008c).

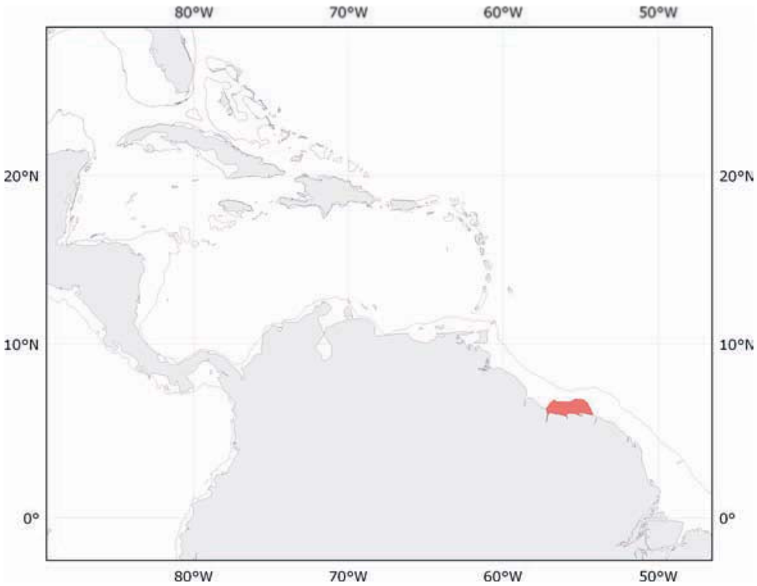


Fig. 96 *Doryteuthis (Amerigo) surinamensis*

🟥 Known distribution

Subgenus undescribed

Doryteuthis sanpaulensis (Brakoniecki, 1984) Fig. 97

Loligo sanpaulensis Brakoniecki, 1984b, *FAO Fisheries Synopsis*, 125(3): 1–277. [102, text-figs 3–5]. [Type locality: 41°47’S, 63°35’W, western South Atlantic Ocean].

Frequent Synonyms: *Loligo brasiliensis* Blainville, 1823.

Misidentifications: *Doryteuthis plei*, *Doryteuthis gahi*.

FAO Names: En – Sao Paulo squid; **Fr** – Calmar de Sao Paulo; **Sp** – Calamar de Sao Paulo.

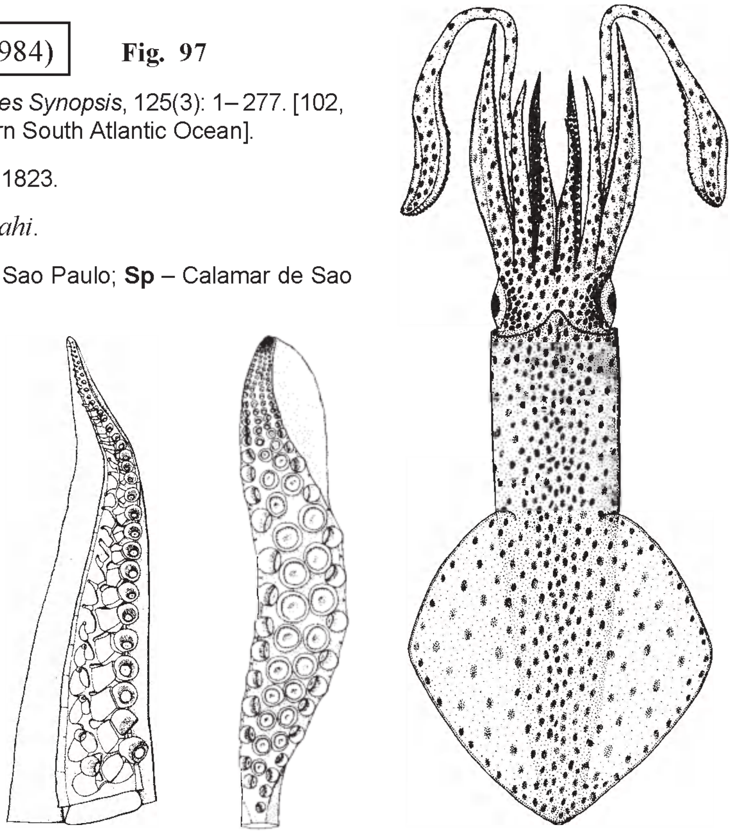

hectocotylus tentacular club dorsal view

Fig. 97 *Doryteuthis sanpaulensis*

Diagnostic Features: Mantle moderately long. **Fins rhombic, relatively long, 55% of mantle length** (exceptionally **to 65%**), widest at midpoint; anterior and posterior margins nearly straight; lateral angles rounded. Tentacles long; clubs expanded, distinct manus and dactylus present, but no distinguishable carpus; marginal suckers relatively large, median manal suckers only about one-third larger than marginal suckers; club sucker rings with about 25 pointed, separated teeth, smaller and more widely spaced proximally. Arms moderately long, arm length indices larger in females than in males; arm sucker rings with 5 to 7 broad truncate teeth distally, smooth proximally. **Left ventral arm hectocotylized along distal 45% of arm length** by great reduction in size of suckers in dorsal row that are set on conical to elongate thickened pedicels; suckers on ventral row normal but pedicels are slightly elongate and thickened. Gladius long and slender; edges of vanes with no lateral thickening or at most broad, diffuse thickenings. **Hatchling chromatophoric features**: 4 chromatophores on each tentacle, 2 red interspersed with 2 yellow, up to 3 red ones observed in largest hatchlings; only 1 red on each arm IV; cheek patch areas: 2 red commonly present, up to 3 observed. Other chromatophore arragements: ventral mantle – numerous red chromatophores (from 20 to 40) arranged in 6 horizontal rows, 3 or 4 yellow ones in a longitudinal row on each side; dorsal mantle – always devoided of dark chromatophores, 3 yellow ones arranged in an “arrow” pointing out to the posterior end, and 1 yellow chromatic phase frequently present at one of the lateral margins.

Size: Medium-sized squid; maximum reported mantle length 220 mm (specimen from Argentinian waters, sex unknown); common size 160 mm mantle length for females, 200 mm mantle length for males.

Geographical Distribution: Southwestern Atlantic Ocean: from southern Brazil to northern Patagonia (Argentina), approximately from 20°S to 46°S but precise limits are unknown (Fig. 98).

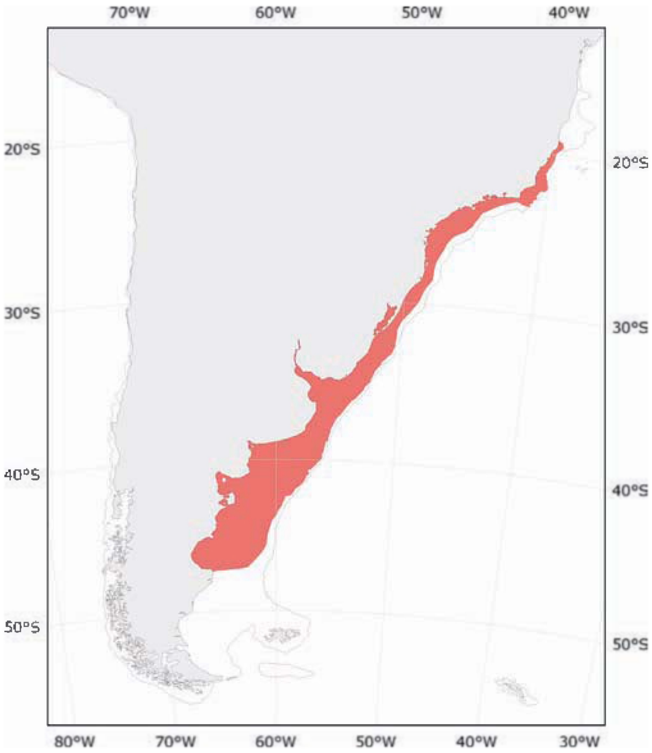


Fig. 98 *Doryteuthis sanpaulensis*

🟥 Known distribution

Habitat and Biology: ***Doryteuthis sanpaulensis*** is widely distributed in coastal waters off southern Brazil and Argentina, where it is the most abundant loliginid squid. It ranges in depth down to about 120 m. Inshore abundance is greater in less saline waters, while offshore higher concentrations are consistently coupled with the cold and food-rich areas of water mass fronts, such as the Subtropical Convergence off southern Brazil, where Subtropical Waters and the northern part of the Malvinas Current (i.e. Subantarctic Waters) converge, as well as in the upwelling area of the South Atlantic Central waters off Cabo Frio, Brazil, the northern limit of known distribution.

Size at 50% maturity is very variable along the species distributional range, ranging between 40 mm and 78 to 80 mm for females in southern Brazil and northern Patagonia and between 23 and 90 mm for males from southern Brazil. However, no geographic gradient is evident. Spawning duration also is variable, and probably is related to latitude. Northern populations have long, almost year-round spawning seasons, with 2 peaks, in winter or winter/spring and summer. The midrange population of Mar del Plata (Argentina) spawns from spring to autumn, with highest activity in spring/summer in some years and early winter in other years. In northern Patagonia, the southernmost distribution area, low water temperatures restrict spawning to late spring-summer (occasionally early autumn) and to shallow-water bottoms, when the monthly average of the SST ranges between 15° and 17°C. Spermatophores are small and slender (SpLI between 3.7 and 7.4) with a smooth, slender cement body. Eggs are small, 1.2 to 1.3 mm maximum length and approximately oval in shape. They are laid in typical loliginid capsules on sandy or muddy bottoms. The number of capsules in egg masses varies between 10 and 400. Embryonic development occurs normally at temperatures between 16° and 19°C, whereas below 13° and above 23°C all embryos die after hatching. These observations that temperatures below 13°C are fatal to the embryos, agree with the egg mass findings from January to April/May in coastal shallow waters, when water temperature of the mixed upper layer (tens of meters thick) is about the same as that of the surface level. Embryonic development in captivity was completed in 16 days at 19°C. Newly hatched paralarvae measure between 1.4 and 1.7 mm mantle length and display a marked positive phototaxis, swimming actively with swinging movements. The paralarval chromatophore pattern is characteristic and enables species identification. Hatchling abundance/concentration is higher in coastal areas where upwelling occurs.

Doryteuthis sanpaulensis feeds mainly on fishes and crustaceans, but also cephalopods, including conspecifics. Predators include a wide range of fishes, squids, both conspecifics and ***Illex argentinus***, and marine mammals, birds and sharks. The Sao Paulo squid is particularly important in the diet of the La Plata and Franciscana dolphins, several fur seal species, the Magellanic penguin and the benthic dog shark.

Interest to Fisheries: This species is commonly taken as bycatch in trawl fisheries that target ***Loligo plei*** in its northern area of distribution and ***Loligo gahi*** in the southern area. Also, it is a common bycatch component of artisanal fish trapping and trawling that target coastal fishes and shrimps.

Local Names: ARGENTINA, BRAZIL, URAGUAY: Calamar.

Remarks: The similarity of ***Doryteuthis sanpaulensis*** with ***D. gahi*** makes the identification of the 2 species difficult and uncertain, especially in the case of juveniles and in the area where the 2 squids are sympatric, i.e. between 42°S and 46°S. Morphological and meristic analyses indicate that indices of fin width over mantle length (FW/ML) and gladius width over mantle length (GW/ML) are useful to help identify the species. FW/ML can be used alone as a rapid, easy differentiation tool in the field: index values lower than 0.53 correspond to ***D. gahi***, while those higher are ***D. sanpaulensis*** (Pineda *et al*., 2002). Other characters useful on fresh, less damaged specimens are the body coloration and the pattern of chromatophores on the oral surface of arms IV: ***D. gahi*** is brownish dorsally and reddish ventrally, while ***D. sanpaulensis*** is reddish on both surfaces; no chromatophores are present on ***D. sanpaulensis*** arms IV, while in both sexes and all size ranges studied chromatophores are found on ventral arms in ***D. gahi***, even on the hectocotylus (Pineda *et al*., 2002). Statolith morphology is less easy to use but useful nonetheless to distinguish the 2 species: the statoliths of ***D. sanpaulensis*** are significantly smaller than those of ***D. gahi*** at a given mantle length; they have a rounded dorsal dome and a short rostrum, whereas those of ***D. gahi*** have a very prominent dorsal dome and a comparatively long and thin rostrum (Pineda *et al*., 1998b).

Literature: Brakoniecki (1984a,b), Andriguetto and Haimovici (1991, 1996, 1997) Pineda *et al*.(1998a,b, 2002), Baron (2001, 2003a,b), Baron and Re (2002a,b), Vidal (2006a,b), Martins and Perez (2006a,b, 2007), Vecchione (2008c).

Heterololigo Natsukari, 1984

Heterololigo Natsukari, 1984a, *Venus, Japanese Journal of Malacology*, 43(3): 229–239 [234].

Type Species: *Loligo bleekeri* Keferstein, 1866.

Diagnostic Features: Tentacular **clubs narrow, with small, nearly uniform suckers in 4 series**. **Arms very short**; suckers with blunt teeth around distal ring. Hectocotylus with proximal suckers unmodified; suckers of reduced size and sucker stalks elongated to form papillae in dorsal series; **dorsal series of papillae and trabeculae at distal tip of modified hectocotylus form bicuspid lamelliform flaps** separated from ventral series of suckers by serrated membrane; no fusion between papillae and protective membrane in the modified portion. **Eggs small to moderate sized, less than 4 mm long**. Spermatophore cement body short. Photophores absent.

Size: Medium to large-sized; maximum recorded mantle length 380 mm.

Geographical Distribution: Northwestern Pacific.

Remarks: Currently monotypic.

Heterololigo bleekeri (Keferstein, 1866)

Fig. 99

Loligo bleekeri Keferstein, 1866, *In* Bronn, *Die Klassen und Ordnungen des Thier-reiches: Weichthiere (Malacozoa)*, 1 500 p., 136 pls. [1402, pls.122,127]. [Type locality: "Japan"].

Frequent Synonyms: *Loligo bleekeri* Keferstein, 1866, Okutani, 1980, Nesis, 1982; *Doryteuthis bleekeri* Naef, 1912, Okutani, 1973.

Misidentifications: None.

FAO Names: En – Spear squid; **Fr** – Calmar lancette; **Sp** – Calamar lanceolato.

Diagnostic Features: Mantle very elongate, narrow, a fleshy ridge along ventral midline, indistinct in females. **Fins** posterior, **large, thick, length two-thirds of mantle length**. Tentacles short; tentacular clubs narrow, suckers small, nearly uniform in size, those of medial 2 series of manus only slightly larger than marginal series; manal sucker rings with about 30 long blunt, separate teeth, the 10 to 14 distal ones the largest. **Arms very short and small in relation to body size; left arm IV hectocotylized in distal one-third to one-fourth** where arm tip is thickened and blunt; modified sucker stalks become longer with thicker bases towards tip; suckers become very minute and rudimentary in the modified section, especially in the dorsal row, with very thickened basal papillae; dorsal basal papillae very greatly thickened, then transformed into tightly arranged, bicuspid, lamelliform flaps; a narrow, serrated membranous fleshy crest separates the 2 series of modified sucker papillae. **Hatchling dorsal chromatophore arrangement very characteristic**: a hexagon of red chromatophores surrounds a yellow one on the dorsal surface of the head and 6 red chromatophores are arranged in a rhombic design on the dorsal surface of the mantle.

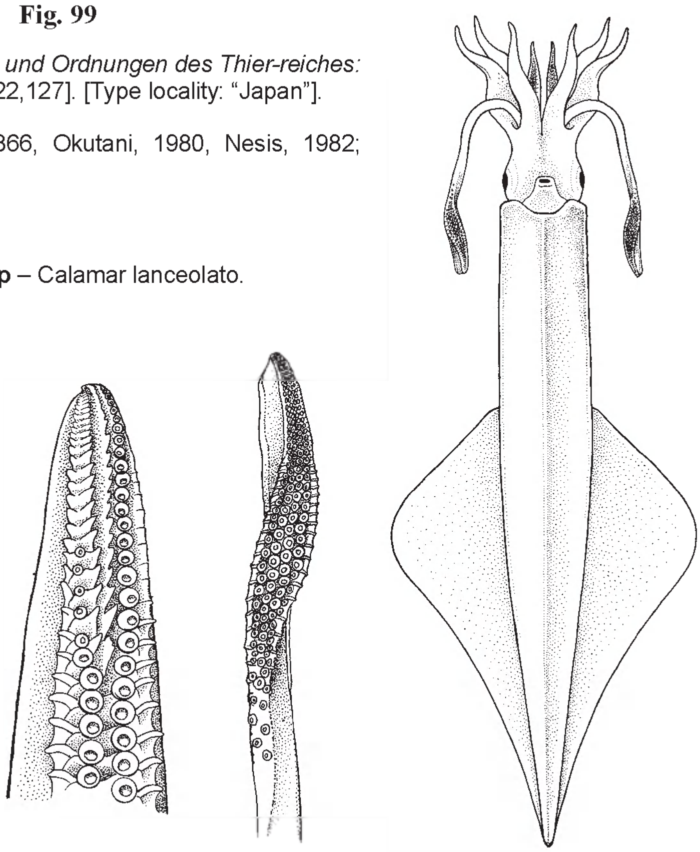

hectocotylus **tentacular club** **ventral view**

Fig. 99 ***Heterololigo bleekeri***

Size: Medium to large-sized squid; maximum recorded length 380 mm mantle length for males and 301 mm mantle length for females. Commonly at 200 to 250 mm mantle length.

Geographical Distribution: Japan: from southern Kyushu (about 30°N) to the Kuril Strait (about 51°N); however, its northern limit commonly is located off Hokkaido waters (about 43ºN to 44°N). Present along the coast of Korea and in the East China Sea and Yellow Sea.Then it is not endemic to Japan (Fig. 100).

Habitat and Biology: The spear squid occurs from surface waters to depths of approximately 150 m; it has never been recorded beyond the continental shelf. However, where its distribution overlaps with that of ***Photololigo edulis***, ***H. bleekeri*** is distributed farther offshore in deeper waters. The centre of the distribution occurs in the northern Sea of Japan off the Aomori Prefecture. Adult squid migrate southward following water temperatures between 7º and 15°C, optimal for spawning.

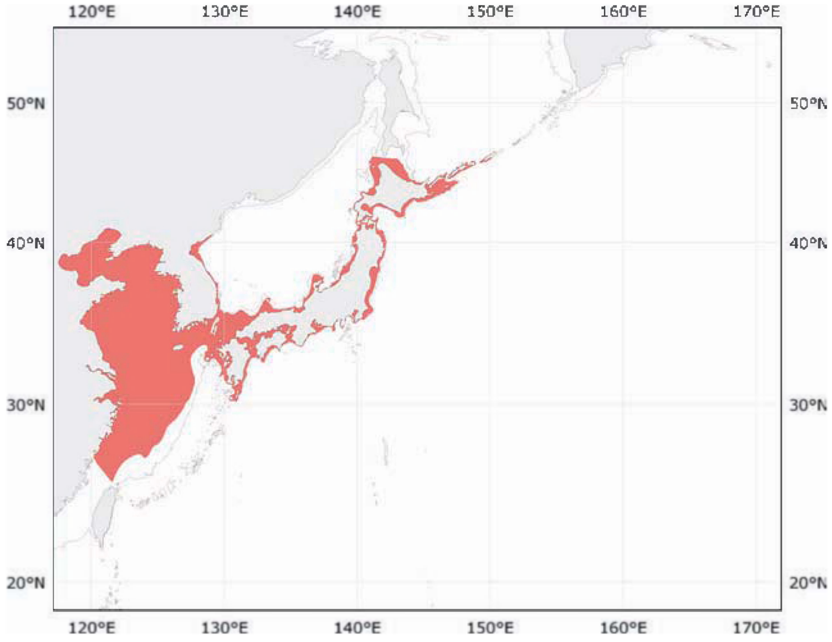


Fig. 100 ***Heterololigo bleekeri***

🟥 Known distribution

A slight sexual dimorphism occurs in adult squid. Males have a slightly more slender mantle, smaller heads and shorter arms than females of the same mantle length. Males grow larger than females and mature earlier; the smallest mature males recorded measured 100 mm mantle length, the smallest females 130 mm mantle length; all males and females are mature at 250 mm and 200 mm mantle length, respectively.

With the onset of maturity, squids migrate from the offshore areas to shallow waters near-shore, for mating and spawning. The spawning season extends over a rather long period, beginning earlier in the southern portion of the distribution area, where squid start spawning in December and continue spawning until May, whereas in the north, spawning starts in April and may last until October-November. The water temperature during the spawning season ranges between 7º and 15°C. Mating occurs mainly in the side-to-side position and occasionally in the head-to-head position. Spermatophores are attached to the buccal membrane and, more conspicuously, in the mantle cavity close to the opening of the oviduct.

Eggs are laid in clusters attached to seaweeds or the surface or undersurface of various hard substrates such as rocks, artificial reefs, wreckage, etc. at about 20 to 30 m depth. In the presence of these substrates, spawning also may occur in waters deeper than usual, to 60 to 70 m. While a record of egg cases being laid on the sand of an experimental tank also exists, in the natural environment eggs of the spear squid are never found on sandy bottom. Observations in aquaria indicate that females lay between 500 and 2 000 eggs per spawning event, and they spawn at least 2 to 4 times before they die. Newly laid eggs are ovate, amber coloured and measure 2.5 to 3.1 mm in length, and 1.8 to 2.1 mm in width. Eggs are arranged in typical loliginid egg cases, between 50 and 140 mm long and 5 to 10 mm wide. The mean number of eggs per egg case varies between 50 to 60 and 100. Data from the west coast of Kyushu as well as observations in captivity indicate that embryonic development lasts 83 days at 10°C, 38 days at 15°C, and 21 days at 22°C; development is inhibited below 7°C and above 25°C. Newly hatched paralarvae have a mean mantle length of 3.4 mm and a mean total length of 6.5 mm and undergo a short planktonic life before acquiring the demersal life-style.

Age determination by statolith analysis indicates a maximum life span of 351 days for females and 385 days for males.

Heterololigo bleekeri feeds opportunistically on crustaceans, fishes and molluscs; however, ontogenetic differences occur, with juveniles eating mostly copepods, young squids between 50 and 90 mm mantle length preying mostly on crustaceans, and adult squid over 200 mm mantle length feeding on fishes and other cephalopods.

Observations on differences in the spawning season peaks and migration routes lead to the hypothesis of the existence of 2 different populations in northern Japan. However, studies on population genetics indicate a low level of genetic diversity, that confirms the existence of a single population in the waters around Japan.

Interest to Fisheries: ***Heterololigo bleekeri*** is the most extensively utilized loliginid squid in Japan. It is caught by bottom trawl, set nets, trap nets, jigging, hand-held dip nets, gill nets and blanket nets. While trawlers are not selective, other fishery techniques target mainly mature, spawning squid, so that fishing seasons coincide more or less with the time of maturation and spawning and fishing varies according to location and fishing method. This species is widely caught in most Japanese coastal waters except south of Kyushu (i.e. in Okinawa seas), in the Inland Sea and east of Hokkaido. Catches fluctuate widely in relation to climatic conditions because the species prefers cool water regimes. In the southwestern Japan Sea, in particular, catches decreased sharply after the late 1980s, due to a climatic shift from cool to warm conditions in the Tshushima Warm Current and to the increased exploitation rate of the last decade, such that concern about a possible collapse of the stock exists. Management measures have been considered, including closures of some areas to the fishery and construction of artificial spawning beds to increase spawning yield and to create a favourable environment for newly hatched squid. The feasibility of aquaculture presently is under intensive study and the species has been reared in captivity for up to two months.

Local Names: JAPAN: Sasaika, Chiyokl, Sayanaga, Shakuhachiika, Tenashi, Teppo, Tsutsuika, Yariika.

Remarks: The eggs and egg cases of ***Heterololigo bleekeri*** resemble those of ***Photololigo edulis***. However, other than always being attached to hard substrates, the eggs of ***H. bleekeri*** are larger and the egg cases are smaller, less transparent and contain fewer eggs. Accordingly, newly hatched spear squid also are considerably larger than hatchlings of ***P. edulis***. Studies on the embryonic development of the spear squid indicate that the major developmental pattern is essentially identical to that of ***Doryteuthis pealeii*** and ***Loligo forbesii*** (Baeg *et al*., 1992) and similar to that of ***Doryteuthis gahi*** (Guerra *et al*., 2001), though the latter has smaller embryos. Records of the species from Ambon (Indonesia) exist (Joubin, 1894), but the spear squid never has been reported in Taiwan and/or the South China Sea; (e.g. Voss and Williamson, 1971, Dong, 1978, Tung, 1978 in Natsukari and Tashiro, 1991); therefore, these records are doubtful.

Literature: McConathy *et al*.(1980), Roper *et al*. (1984), Natsukari and Tashiro (1991), Reichov and Smith (2001), Ito (2002), Ikeda *et al*. (2005), Okutani (2005), Tian (2007), Vecchione (2008d).

Loliolus Steenstrup, 1856

Loliolus Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 4: 185–216. [193].

Type Species: *Loliolus hardwickei* (Gray, 1849).

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Arm sucker rings with square plate-like teeth around entire margin. **Hectocotylus with ventral crest** formed by fusion of protective membrane with ventral row of papillae; original form of conical papillae completely obscured. Mantle **without posterior tail-like elongation**. **Fins posterior**. **Eggs small**. Spermatophore cement body short. Photophores absent.

Size: Small-sized squid; mantle length up to 150 mm.

Geographical Distribution: Indo-West Pacific waters.

Remarks: Two subgenera currently are recognized. Since the type species of the formerly monotypic genus belongs to the subgenus ***Loliolus***, the subgenus ***Loliolus*** is treated first in this work.

Literature: Vecchione *et al.* (2005), Vecchione (2008f).

Key to the subgenera of *Loliolus*

1a. Suckers along entire length of hectocotylized arm modified, no unmodified suckers on proximal arm . . . . ***Loliolus (Loliolus)***
1b. Less than entire arm modified by hectocotylization, proximal part with unmodified suckers . . . . ***Loliolus (Nipponololigo)***

Subgenus ***Loliolus*** Steenstrup, 1856

Loliolus Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 4: 185–216. [193].

Type Species: *Loliolus (Loliolus) hardwickei* (Gray, 1849).

Loliolus (Loliolus) hardwickei (Gray, 1849)

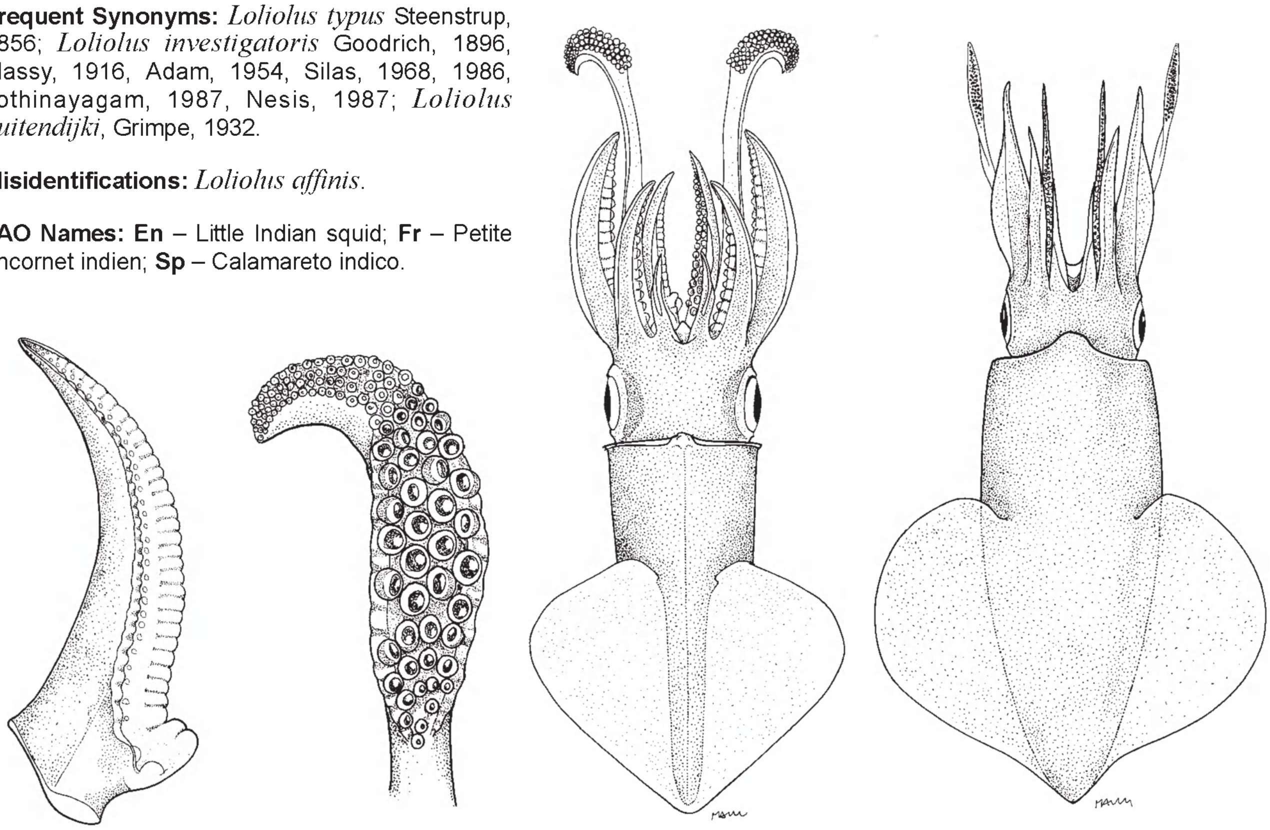
Fig. 101

Loligo hardwickei Gray, 1849, *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Artepedia*, 164 pages, London. [69]. [Type locality: India].

Frequent Synonyms: *Loliolus typus* Steenstrup, 1856; *Loliolus investigatoris* Goodrich, 1896, Massy, 1916, Adam, 1954, Silas, 1968, 1986, Jothinayagam, 1987, Nesis, 1987; *Loliolus buitendijki*, Grimpe, 1932.

Misidentifications: *Loliolus affinis*.

FAO Names: En – Little Indian squid; **Fr** – Petite encornet indien; **Sp** – Calamareto indico.



hectocotylus **tentacular club** **dorsal view of male** **dorsal view of female**

Fig. 101 ***Loliolus (Loliolus) hardwickei***

Diagnostic Features: Mantle short, stout; **fins large, heart-shaped**, with anterior and lateral edges rounded, **width up to 76% of mantle length**; head short, a little narrower than the mantle width. Arms rather short, subequal, usually shorter in females than males. Arm sucker rings with only 2 to 7 large, low, stout, broad teeth on the distal margin, their number varies depending on the arm and the sex of the specimen. **Left ventral arm hectocotylized in males by the modification of both ventral and dorsal series of suckers along its entire length**: suckers are missing, except at the very tip where 2 or 3 minute suckers may be present; ventral sucker stalks enlarged and fused entirely with the ventral trabeculate membrane to form a fleshy ridge. Modified suckers on dorsolateral and ventrolateral arms of males larger in dorsal series than in ventral series. Tentacles short. Clubs small, scarcely expanded; club suckers subequal; largest club sucker rings with 20 to 40 small, acute or bluntly triangular teeth around the entire margin. One pair of small papillae on the ink sac in males, absent in females.

Size: Small-sized squid; maximum reported size 88 mm mantle length (a male captured at the mouth of the River Hughli, India). Common at about 30 mm mantle length in males and over 60 mm mantle length in females.

Geographical Distribution: A tropical species of the Indian Ocean waters, from the Northern Persian Gulf, along the coasts of India and Burma (Myanmar), and throughout Indonesia. A single specimen was reported from the Chinese coast, opposite Taiwan. Never recorded in either northern or southern subtropical waters (Fig. 102).

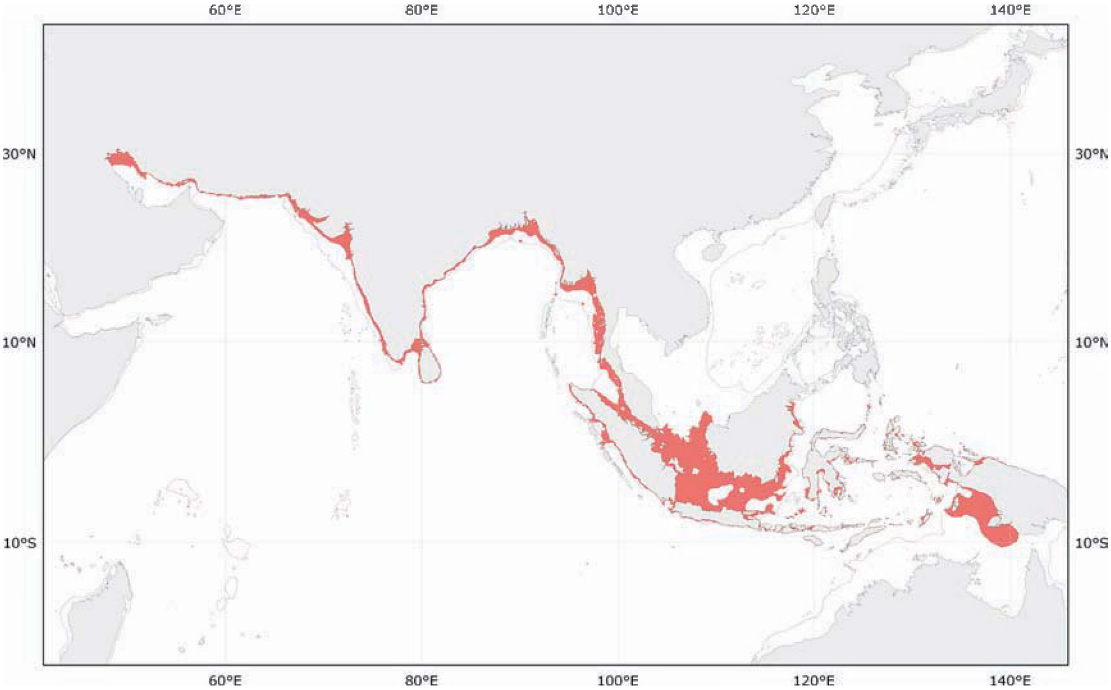


Fig. 102 ***Loliolus (Loliolus) hardwickei***

🟥 Known distribution

Habitat and Biology: Very little information is available on the biology of ***Loliolus hardwickei***, which is not considered by the major available references on Indian Ocean squid biology. This probably is because this species has little importance for the commercial fisheries, in spite of its common occurrence in the area. ***Loliolus hardwickei*** is known to inhabit estuarine and coastal waters to a maximum recorded depth of 30 m. Males and females reach sexual maturity at a size of about 30 to 40 mm mantle length.

Interest to Fisheries: In spite of its common occurrence in the Indo-Pacific region, few data on catch statistics are available; artisanal fisheries may occur in local situations. ***Loliolus hardwickei*** (as ***L. investigatoris***) is reported among the cephalopod resources of the northern part of the Arabian Sea, i.e. the Guajarat coast, and the eastern coast of India.

Local Names: None available.

Remarks: None.

Literature: Massy (1916), Silas (1986), Lu *et al.* (1985), Norman & Lu (2000), Jereb and Roper (2006), Vecchione (2008f).

Loliolus (Loliolus) affinis Steenstrup, 1856

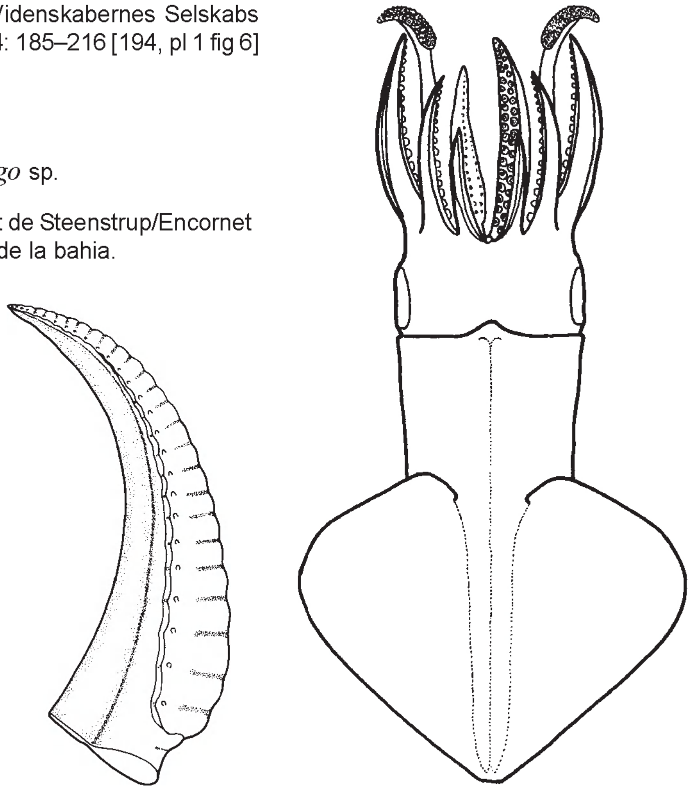
Fig. 103

Loliolus affinis Steenstrup, 1856, Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk, 4: 185–216 [194, pl 1 fig 6] [Type locality: Indian Ocean].

Frequent Synonyms: None.

Misidentifications: *Loliolus hardwickei*, *Nipponololigo* sp.

FAO Names: En – Steenstrup's bay squid; **Fr** – Encornet de Steenstrup/Encornet de la baie; **Sp** – Calamareto de Steenstrup/Calamareto de la bahia.



hectocotylus dorsal view

Fig. 103 *Loliolus (Loliolus) affinis*

Diagnostic Features: Mantle slightly flattened dorsoventrally, with a bluntly rounded tip. **Fins large, heart-shaped, width up to 98% of mantle length**. Head broad, short, as wide as mantle width, eyes large. Arms short; arm suckers larger in males. Modified suckers on dorsolateral and ventrolateral arms of males larger in ventral series than in dorsal series. Arm I largest suckers show 3 or 4 truncate teeth on distal margin; proximal margin smooth or irregular. **Left ventral arm hectocotylized in males, generally equal to or shorter than right ventral arm**; suckers and sucker stalks entirely absent in ventral row; ventral protective membrane broad, thickened; trabeculae on ventral row greatly thickened, fused by the broad, fleshy, ventral protective membrane. Tentacles relatively short, clubs small, slightly expanded, carpal suckers absent. Club sucker dentition shows truncate, conical teeth in juveniles, that change to square, plate-like teeth in adults. Medial manal suckers with 15 to 20 small, blunt, well-spaced teeth on entire margin. One pair of small papillae on the ink sac in males, absent in females.

Size: Small-sized squid; maximum mantle length 47 mm.

Geographical Distribution: Widely distributed in coastal waters of the Indo-Malayan region, from the eastern Bay of Bengal to the Andaman Sea, Thailand, Indonesia, and Cambodia. Confined to tropical areas; never extends to northern or southern subtropical zones (Fig. 104).

Habitat and Biology: This species occurs in shallow coastal habitats to depths of 13 to 15 m. It probably is a schooling species. Smallest mature males measure 22 mm mantle length; size at maturity of females uncertain. A general statement about mature individual size of 35 mm mantle length in the waters of Thailand, may include females as well as males, since females are larger than males.

Interest to Fisheries: Occasionally caught in demersal trawl catches in the Gulf of Thailand among larger loliginids; it may be confused with juveniles of other larger, more commercially important, species.

Local Names: None available.

Remarks: None.

Literature: Lu *et al*. (1985), Chotiyaputta (1993a,b), Okutani (2005), Vecchione (2008f).

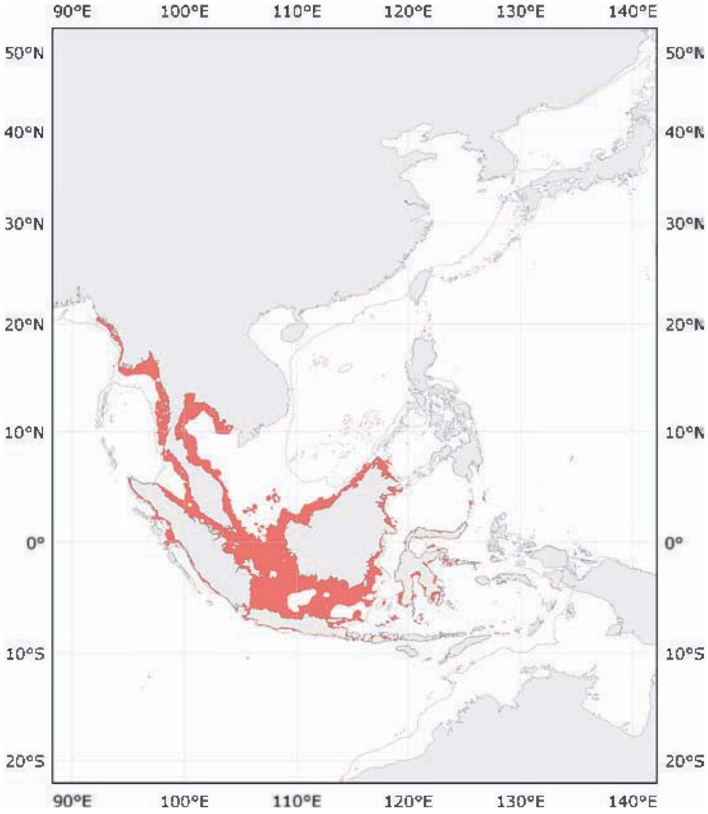


Fig. 104 *Loliolus (Loliolus) affinis*

🟥 Known distribution

Subgenus *Nipponololigo* Natsukari, 1983

Nipponololigo Natsukari, 1983. *Venus*, 42(4):313-318, 6 figures. [313].

Type Species: *Loliolus (Nipponololigo) beka* (Sasaki, 1929).

Loliolus (Nipponololigo) beka (Sasaki, 1929)

Fig. 105

Loligo beka Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University*, 20 (supplement):1–357 [121, text-figs 70–72, pl 13 fig 5]. [Type locality: Kojima Bay, western Honshu, Japan, western North Pacific Ocean].

Frequent Synonyms: *Loligo sumatrensis*, Appellöf, 1886 (non Orbigny, 1839).

Misidentifications: *Loliolus uyii* (Wakiya and Ishikawa, 1921).

FAO Names: En – Beka squid; **Fr** – Calmar cracheur; **Sp** – Calamar beka.

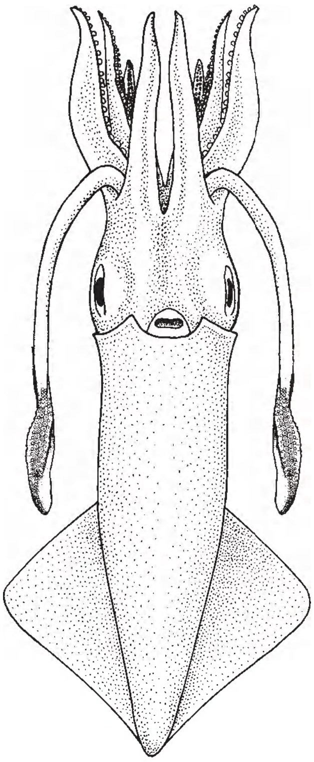


Fig. 105 *Loliolus (Nipponololigo) beka*

Diagnostic Features: Mantle short, slender; **fins rhomboidal with round lateral angles, both fin length and width more than 50% of mantle length, up to 60%**. Arms slightly longer in males than in females, with larger suckers; arm sucker rings with a smooth plate-like tooth extending up to one-third of the proximal margin and 2 to 7, wide, broad squared teeth along the distal margin. **Left ventral arm hectocotylized in males with about 6 to 9 pairs of normal suckers on the proximal end and the distinctive ventral row of palisade-like, fused, fleshy papillae that form a wall-like crest on the distal portion** (about two-third of the arm length). Tentacular clubs expanded, lanceolate; medial manal suckers twice the diameter of the lateral suckers, with 18 to 20 (30) sharp teeth on the sucker rings.

Size: Small-sized squid; maximum mantle length 87 mm (female).

Geographical Distribution: Temperate to tropical western Pacific Ocean; all along the southeast Asian coastal waters, from southern Japan and Hainan Island to the Gulf of Thailand and the Andaman Sea (Fig. 106).

Habitat and Biology: The depth distribution is undetermined. This species occurs in coastal and estuarine waters, particularly bays. Studies on the diet indicate that the Beka squid feeds mainly on benthic species of crustaceans and on juveniles of the small yellow croaker, *Pseudosciaena polyactis*. It is preyed upon by several fish species that inhabit estuarine waters.

Interest to Fisheries: The Beka squid is captured in trawls and light-luring nets in the Gulf of Thailand, and it is mentioned as one of the main fishery resources of the estuarine waters of the Pearl River, northeast of Hainan, East China Sea.

Local Names: INDIA (Tamil Nadu): Oosikanava; JAPAN: Beka.

Remarks: This is the smallest species within the subgenus ***Nipponololigo***.

Literature: Natsukari (1983), Okutani *et al*. (1987), Nateewathana (1992), Li *et al*. (1995), Yang and Tan (2000), Li *et al*. (2000), Norman and Lu (2000), Okutani (2005), Vecchione (2008f).

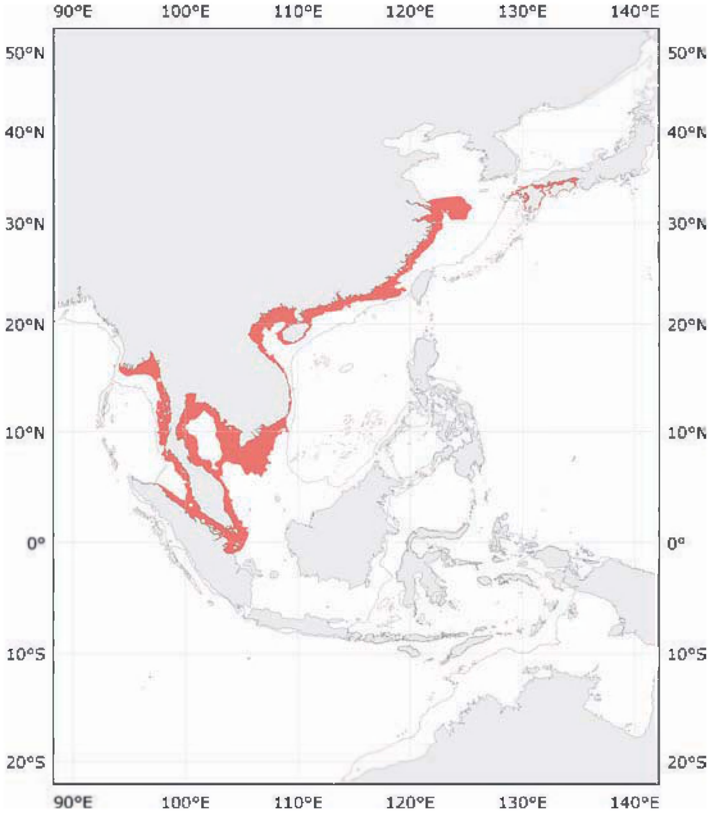


Fig. 106 *Loliolus (Nipponololigo) beka*

🟥 Known distribution

Loliolus (Nipponololigo) japonica (Hoyle, 1885)

Fig. 107

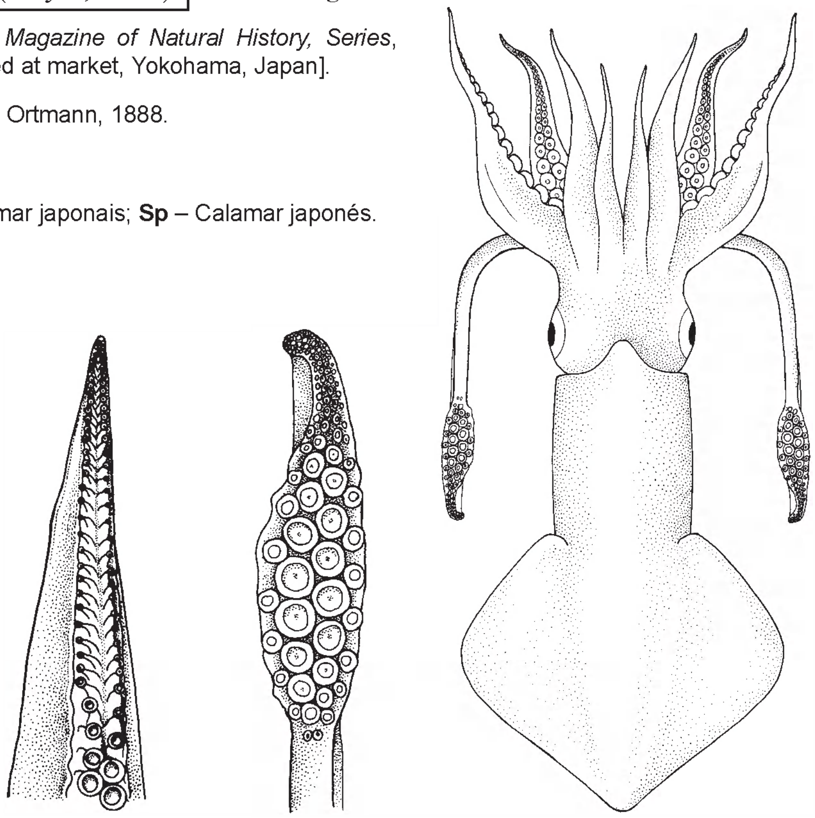
Loligo japonica Hoyle, 1885, *Annals and Magazine of Natural History, Series*, 5(16):181–203. [187]. [Type locality: purchased at market, Yokohama, Japan].

Frequent Synonyms: *Loligo tetradynamia*, Ortmann, 1888.

Misidentifications: None.

FAO Names: **En** – Japanese squid; **Fr** – Calmar japonais; **Sp** – Calamar japonés.

Diagnostic Features: Mantle relatively small, stout, conico-cylindrical. **Fins rhomboidal, about 50% of mantle length**. Tentacular clubs expanded, lanceolate, **the 12 enlarged medial manus suckers 2 or 3 times the diameter of marginal ones**, with 20 to 30 closely set, low, rounded teeth. Arms II and III enlarged, thickened, largest sucker rings large, with 7 to 13 low, broad, blunt teeth. **Left ventral arm hectocotylized in distal half to two-thirds**, by sucker stalks modified into papillae, **most with minute, rudimentary suckers on tips**; papillae of ventral row especially swollen, somewhat flattened, fused together forming a wall-like crest; papillae of dorsal row more elongate, separate, conical. Several normal suckers on proximal, non-modified portion. Distalmost section of the arm not modified.



hectocotylus tentacular club dorsal view

Fig. 107 *Loliolus (Nipponololigo) japonica*

Size: Small-sized squid; maximum recorded mantle length 130 mm (female, northeastern Honsu) and 150 mm (sex not reported, Yellow Sea).

Geographical Distribution: Temperate to tropical western Pacific Ocean, from the Yellow Sea and East China Sea to southern Vietnamese waters and northward around Japan, to southern Hokkaido (Fig. 108).

Habitat and Biology: This species is most abundant in shallow waters. Spawning takes place during summer and autumn in depths between 1 and 10 m. During this period the squid form large aggregations.

Interest to Fisheries: This species supports local fisheries during spring and summer north of mid-Honshu, Japan, as well as in China and Viet Nam. It is reported as one of the most abundant species in the catches off Quingdao (Sangdon Province), China, East Yellow Sea, and, occasionally, off the southeastern coast of Honshu, Japan, Pacific Ocean. It is taken with set nets and small trawls, but it is uncertain whether small individuals can be attracted with light and then jigged. The squid is marketed fresh and frozen. The flesh is of excellent quality and often is eaten raw.

Local Names: JAPAN: Bouzuika, Hiika, Jhindouika, Koika.

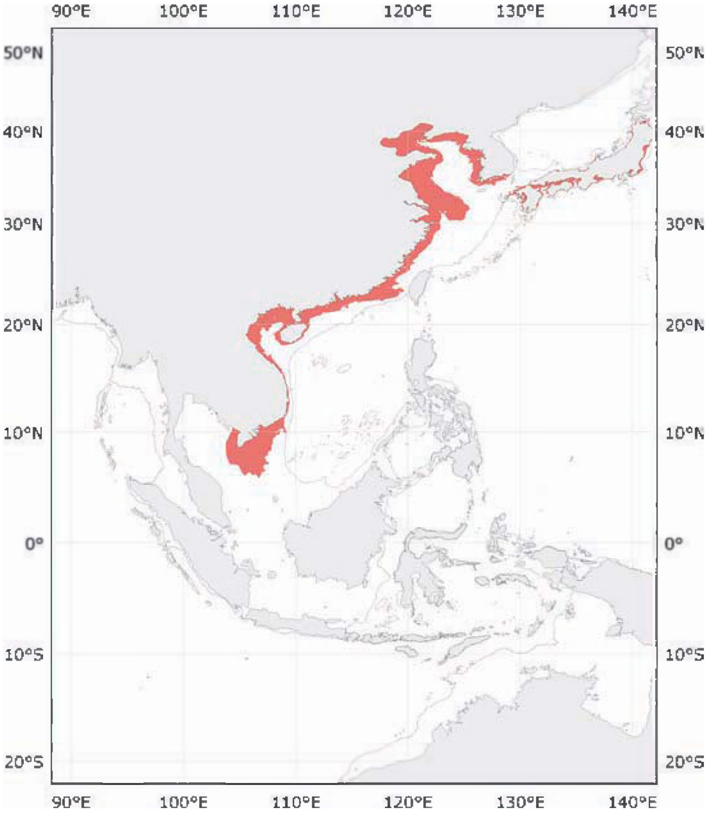


Fig. 108 *Loliolus (Nipponololigo) japonica*

🟥 Known distribution

Remarks: The gladius length index (GLI: gladius width/gladius length x 100) was found to be the most useful character to discriminate juveniles of ***Loliolus japonica*** and ***Uroteuthis edulis*** smaller than 12 mm mantle length, in the areas where the 2 species co-occur (Okutani *et al.*, 1975). Due the importance of this species to local fisheries, preliminary considerations were made on the methods of forecasting catches in the Yellow Sea and Bohai Sea (Ge and Qiu, 1991).

Literature: Natsukari (1983), Okutani *et al.* (1976a, 1987), Norman and Lu (2000), Okutani (2005), Ren *et al.* (2005), Vecchione (2008f).

Loliolus (Nipponololigo) sumatrensis (D'Orbigny, 1835) **Fig. 109**

Loligo sumatrensis D'Orbigny, 1835 *In* Ferussac and D'Orbigny, 1834-1848, *Histoire Naturelle Generale et Particuliere Cephalopodes Acetabuliferes Vivants et Fossiles*, 96 pages + lvi pages + 361 pages, Atlas with 144 plates. Paris. [317, Calmar pl. 13, figs 1-3]. [fide Tillier and Boucher-Rodoni (1994:101); taxon dated from plate]. [Type locality: Sumatra Island, Indonesia, eastern Indian Ocean].

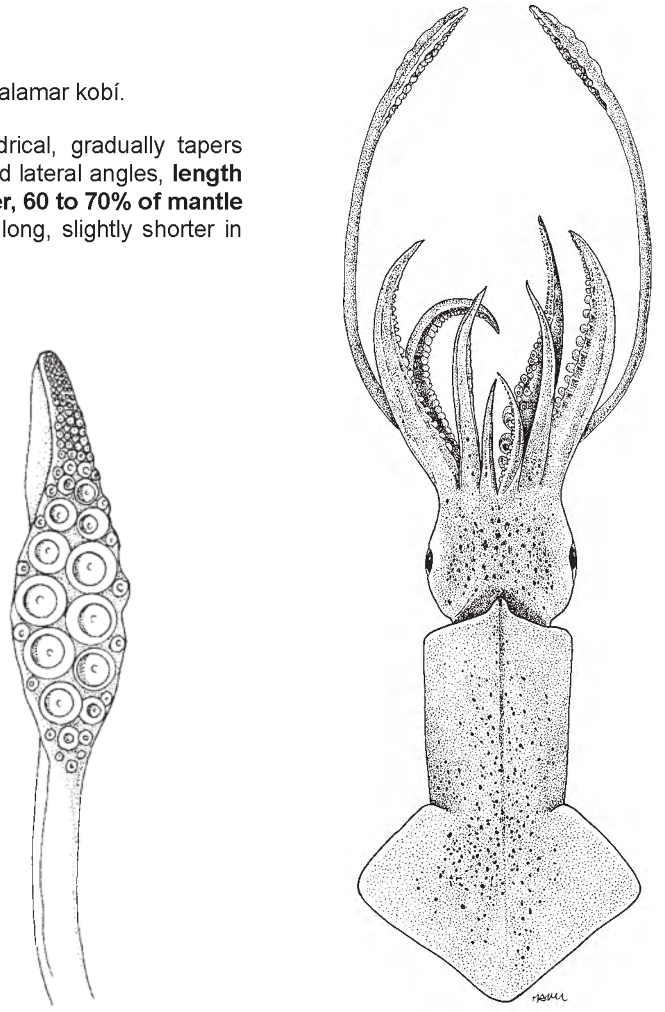
Frequent Synonyms: *Loligo kobiensis*, Hoyle, 1885, Roper *et al.* 1984, *Loligo yokoyae*, Ishikawa, 1926, *Loliolus rhomboidalis*, Burgess, 1967, *Nipponololigo kobiensis*, Natsukari, 1983.

Misidentifications: *Loliolus beka*, *Loliolus uyii.*

FAO Names: En – Kobi squid; **Fr** – Calmar kobì; **Sp** – Calamar kobí.

Diagnostic Features: Mantle short, slender, subcylindrical, gradually tapers posteriorly into a blunt point. **Fins rhomboidal** with round lateral angles, **length about 60 to 65% of mantle length, width slightly larger, 60 to 70% of mantle length**. Head small, with large eyes. Arms moderately long, slightly shorter in females; arm sucker rings with 6 to 9 low broad squared teeth. Arm III sucker rings with 5 to 10 low plate-like teeth; diameters less than those of the largest tentacular sucker rings which are smooth or have low serrations around only part of their diameter. **Left and right ventral arms modified in males**. **Most of the left ventral arm is hectocotylized, up to 87% distal to the first 3 pairs of normal suckers**, sucker stalks of the left arm modified as low stump-like papillae in the dorsal series and broad thick palisade-like papillae in the ventral series, reducing in size distally. **Right ventral arm with 3 or 4 pairs of much enlarged suckers proximally.** Suckers on the other arms are similar in shape and size in males and females, except the proximal suckers in arm III of males, enlarged at sexual maturity. Tentacles weak, tentacular clubs expanded and rather strong in comparison; 6 to 8 medial manal suckers up to 4 to 5 times the diameter of lateral suckers and with smooth sucker rings; smaller marginal suckers with 6 to 15 small, sharp teeth.

Size: Small-sized species, maximum mantle length 120 mm; common in catches at 20 to 70 mm mantle length.



tentacular club ventral view

Fig. 109 *Loliolus (Nipponololigo) sumatrensis*

Geographical Distribution: Temperate and tropical western Pacific, from the southern Japanese and South Korean waters southwestward to Sumatra, China, Thailand, Philippines and Indonesia, westward to the Bay of Bengal, from the Andaman Sea to the east coast of India and the Maldive Islands (Fig. 110).

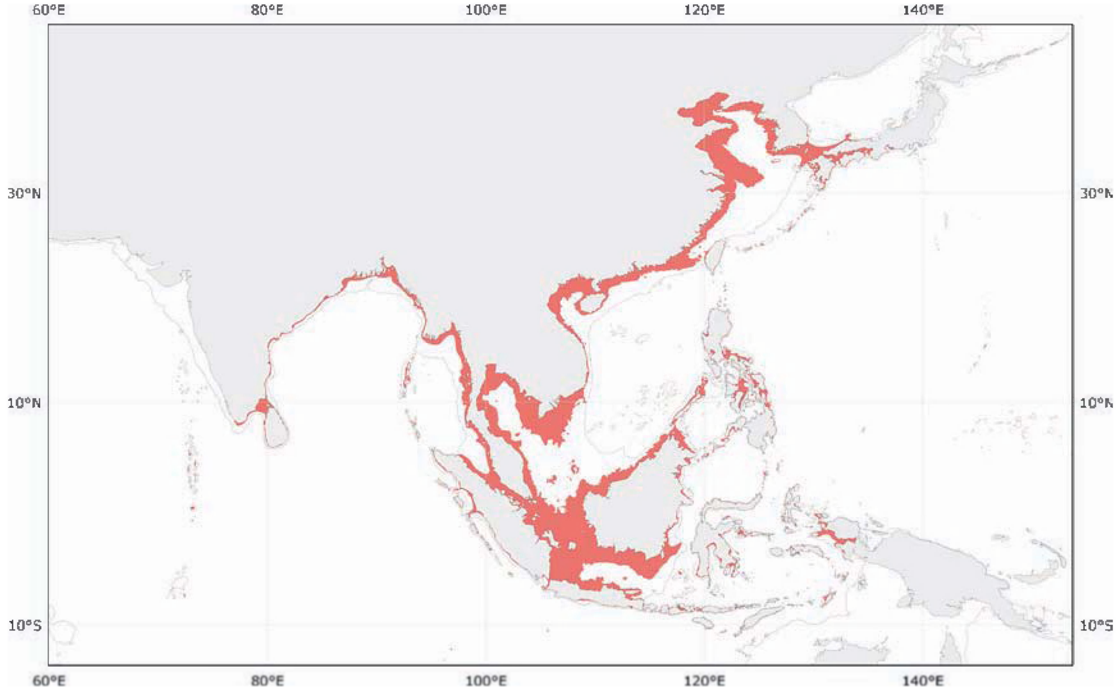


Fig. 110 ***Loliolus (Nipponololigo) sumatrensis***

🟥 Known distribution

Habitat and Biology: ***Loliolus (Nipponololigo) sumatrensis*** commonly inhabits coastal waters all loliginids are neritic and coastal waters. Its biology has not been specifically investigated, probably because of its marginal interest to fisheries. A synopsis of the available biological knowledge, however, is available for the Gulf of Thailand and the Andaman Sea populations where ***L. sumatrensis*** is common at sizes that range between 20 and 70 mm mantle length, and its spawning period extends year round. Egg capsules are leaf-like and contain about 100 eggs; hatchlings, 1.5 mm mantle length, are planktonic.

Interest to Fisheries: Taken as bycatch in trawl and light-luring fisheries for other squids in most of its distributional area (e.g. southwestern Japanese waters), the Kobi squid is highly abundant in the Gulf of Thailand and in the Andaman Sea, whereas it appears to be scarce in the Bay of Bengal. Attempts to rear this species in a large-scale culture system in Thailand provided initial data useful for potential commercial aquaculture production.

Local Names: THAILAND: Katoy squid.

Remarks: According to Manoch (1998) ***Loliolus uyii*** from the eastern side of the Gulf of Thailand is synonymous with ***L. sumatrensis***.

Literature: Burgess (1967), Natsukari (1983, 1984b), Okutani *et al*. (1987), Chotiyaputta (1993a), Okutani (2005), Jereb and Roper (2006), Vecchione (2008f).

Loliolus (Nipponololigo) uyii (Wakiya and Ishikawa, 1921)

Loligo uyii Wakiya and Ishikawa, 1921, *Dobutsu-Gaku Zasshi [Zoological Magazine, Tokyo]*, 33:279–292, 12 figures [286, fig. 12a–h]. [Type locality: Bay of Kagoshima, Kii, Japan, western North Pacific Ocean].

Frequent Synonyms: *Loligo gotoi* Sasaki, 1929, *Loligo tago*, Sasaki, 1929, *Loligo aspera* Ortmann, 1888.

Misidentifications: None.

FAO Names: En – Little squid; **Fr** – Calmar mignon; **Sp** – Calamar balilla.

Diagnostic Features: Mantle short, moderately stout, its width about 25% of the mantle length. **Fins rhomboidal**, their angles rounded, length **about 60% of mantle length**. Tentacular clubs slightly expanded, about 8 suckers in 2 median manal series greatly enlarged with smooth rings; medial and distal rings with 7 to 10 very low, broad, plate-like or semilunar teeth. **Arm III sucker rings with 3 to 6 low plate-like teeth**; diameters approximately equal to those of the largest tentacular sucker rings which are smooth. **Left ventral arm hectocotylized along distal two-thirds with about 75 suckerless papillae**, those in dorsal series small, rounded, separate, but the ones on ventral row greatly swollen and connected into a ridge.

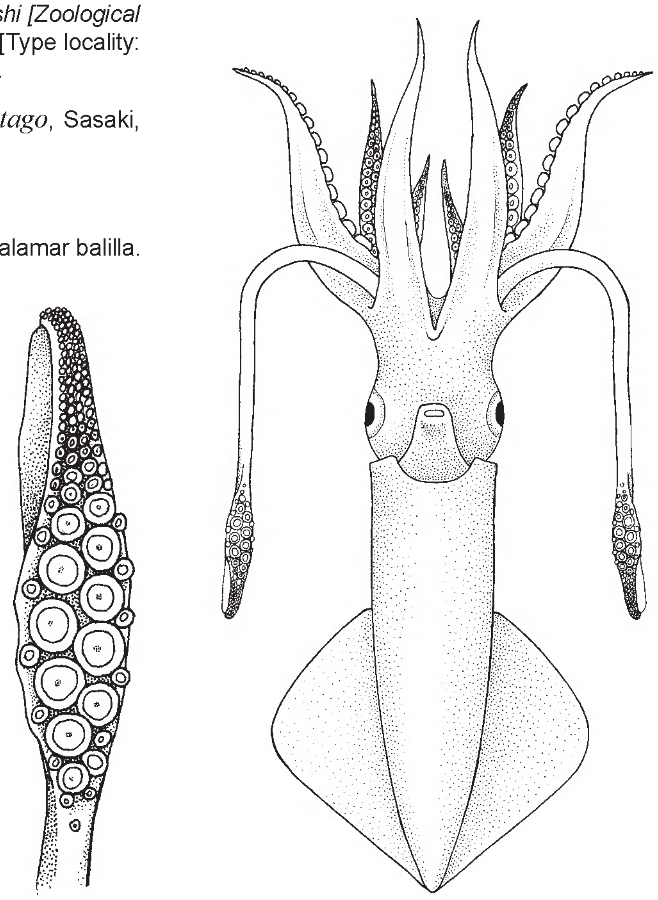
Size: Small-sized squid; maximum mantle length 113 mm (female).

Geographical Distribution: Temperate and tropical Indo-West Pacific Ocean: southwestern Japan, to the East and South China Seas, including Taiwan (Province of China) (Fig. 112).

Habitat and Biology: This species occurs to about 50 m depth.

Interest to Fisheries: Unknown.

Fig. 111



tentacular club

ventral view

Fig. 111 *Loliolus (Nipponololigo) uyii*

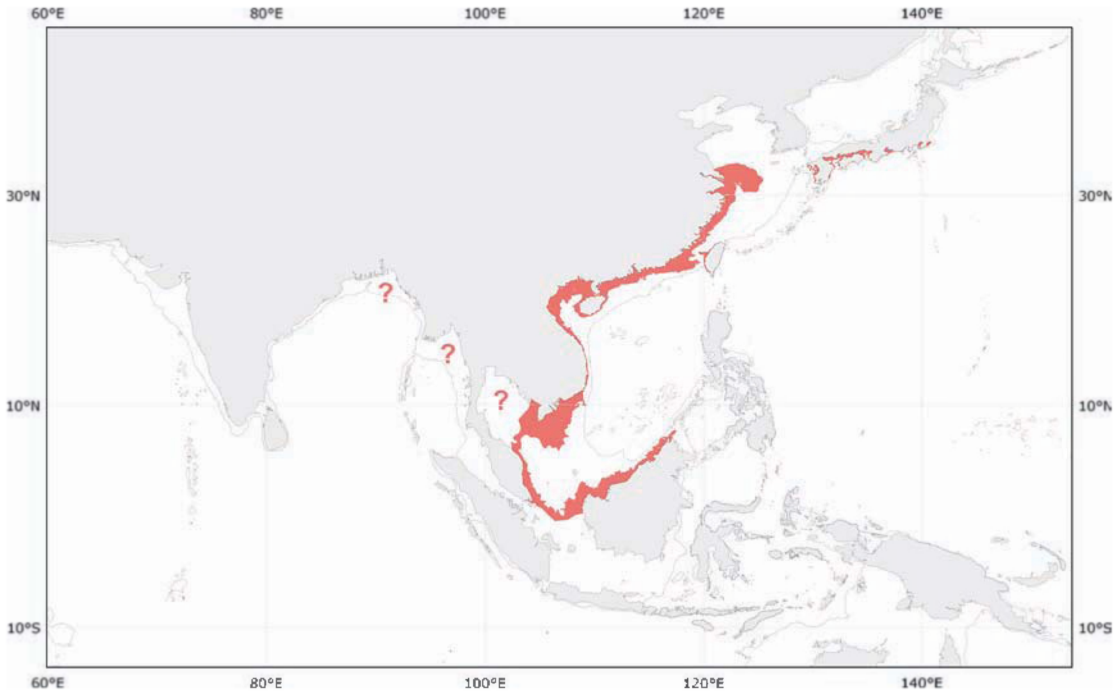


Fig. 112 *Loliolus (Nipponololigo) uyii*

🟥 Known distribution

Local Names: CHINA: Yau jai.

Remarks: Norman and Lu (2000) report the species distribution to extend to the gulf of Thailand. According to Manoch, 1998, records from the Gulf of Thailand should be attributed to ***Loliolus sumatrensis***. Records of this species from the Bay of Bengal also exist (Yothinayagam, 1987).

Literature: Natsukari (1983), Nesis (1982, 1987), Manoch (1998), Vecchione, *et al*. (1998b), Norman and Lu (2000), Okutani (2005), Vecchione (2008f).

Lolliguncula Steenstrup, 1881

Lolliguncula Steenstrup, 1881, *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, 1(3): 211–242. [242].

Type Species: *Lolliguncula brevis*.

Diagnostic Features: Tentacular **clubs expanded**, with suckers in 4 series. Arm sucker rings with square, plate-like teeth around entire margin. **Hectocotylus without crest**; suckers reduced, sucker stalks elongated to form papillae on either dorsal or both dorsal and ventral rows. Mantle without posterior tail-like elongation. Posterior of **fins broadly rounded; fins wider than long in adults**. Eggs small. Spermatophores with **long cement body**. Photophores absent.

Size: Small-sized species; maximum mantle length 120 mm.

Geographical Distribution: Tropical and subtropical West Atlantic, and tropical eastern Pacific Ocean.

Remarks: The genus ***Lolliguncula*** was established to distinguish ***L. brevis*** from the species of ***Loligo*** then known, based on body and fin shape and spermatophore deposition site. These characters have since proven to exhibit considerable variability, both within and among species. However, all of the species in this genus are united and distinguished from all other loliginids by the long cement body of their spermatophores. Variability exists in hectocotylus morphology, and this led Berry (1929) to erect the genus ***Loliolopsis*** and Brakoniecki (1986) to erect ***Afrololigo***. This variability is extreme in ***L. diomedeae***, but Brakoniecki (1986) has pointed out the similarities in hectocotylization between this species and the other species of ***Lolliguncula***. Many of the morphological characters of ***Afrololigo mercatoris*** are shared with species of ***Lolliguncula***, the genus in which it was originally described. However, DNA sequence analysis by Anderson (2000a) supports Brakoniecki's (1986) conclusion based on hectocotylus morphology that ***Afrololigo*** is a distinct genus (Vecchione, 2008a). Two subgenera currently are recognized. Since the type species of the formerly monotypic genus belongs to the subgenus ***Lolliguncula***, the subgenus ***Lolliguncula*** is treated first in this work.

Literature: Brakoniechi (1986), Anderson (2002a), Vecchione *et al*. (2005), Vecchione (2008g).

Key to the subgenera of *Lolliguncula*

1a. Modified portion of hectocotylus less than entire arm, proximal portion not modified . ***Lolliguncula (Lolliguncula)***
1b. Hectocotylus modified along entire arm. . . . . ***Lolliguncula (Loliolopsis)***

Subgenus ***Lolliguncula*** Steenstrup, 1881

Lolliguncula Steenstrup, 1881, *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, 1(3): 211–242. [242].

Type Species: *Lolliguncula (Lolliguncula) brevis* (Blainville, 1823).

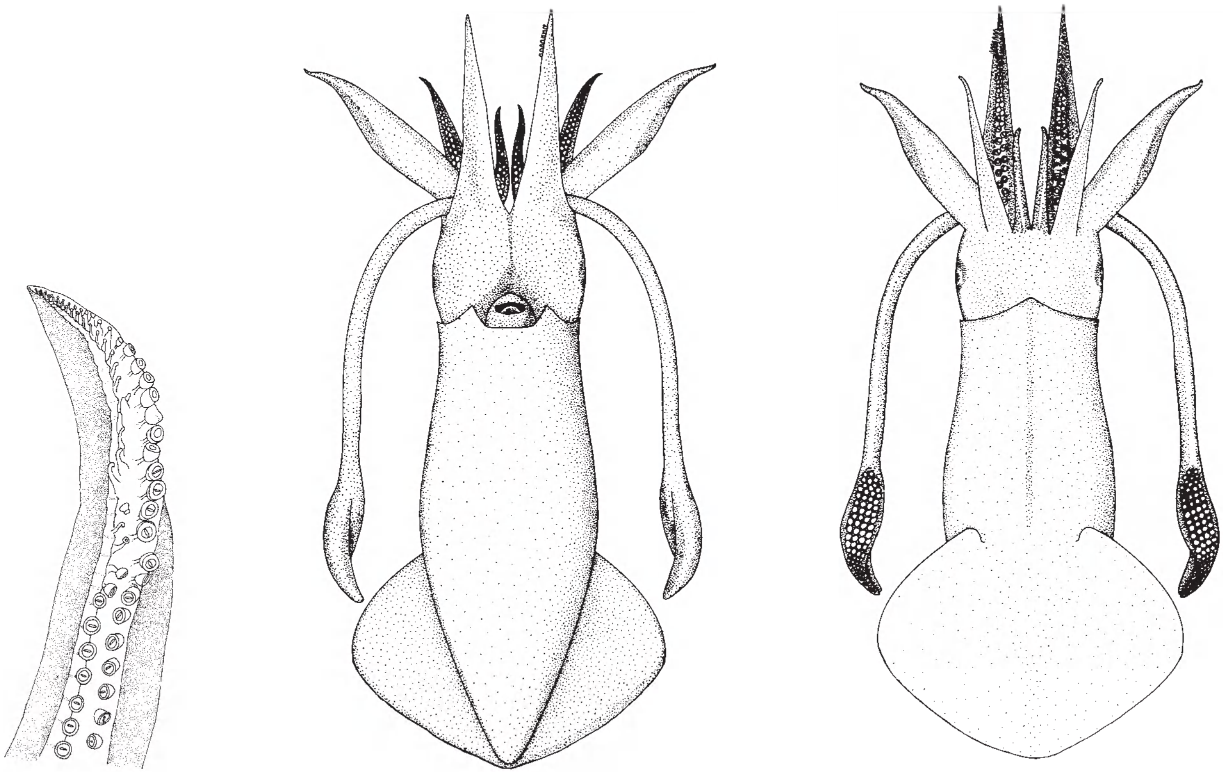
Lolliguncula (Lolliguncula) brevis (Blainville, 1823) **Fig. 113**

Loligo brevis Blainville, 1823, *Journal Physique Chimie d'Histoire Naturelle*, 96:116–135. [133]. [Type locality: Japan, western North Pacific Ocean].

Frequent Synonyms: *Loligo brevipinna* Lesueur, 1824, *Loligo hemiptera* Howell, 1867.

Misidentifications: *Loligo* spp.

FAO Names: En – Thumbstall squid; **Fr** – Calmar doigtier commun; **Sp** – Calamar dedal.



hectocotylus ventral view dorsal view

Fig. 113 *Lolliguncula (Lolliguncula) brevis*

Diagnostic Features: Mantle stout, bluntly rounded posteriorly, widest in midportion. **Fins short (50 to 55% of mantle length), broad, wider than long; fin width 75% of mantle length, very rounded. Modified portion of hectocotylized left ventral arm occupies distal third of arm and extends to arm tip**; about 24 suckers of dorsal series modified, the proximal 1 to 3 being greatly reduced in diameter, the remaining pedicels distally are greatly enlarged into long, slightly flattened papillae that gradually diminish in size distally; no large, puffy, glandular enlargement of basal area of arm between sucker series. **Colour**: dark reddish brown to brownish yellow with chromatophores over nearly entire animal; chromatophores most dense on ventral surface of mantle and head, except in very large specimens, in which the opposite occurs.

Size: Small-sized squid; maximum reported mantle length 120 mm for females, 85 mm for males.

Geographical Distribution: Western Atlantic Ocean, about 45ºN to 28ºS; from Nova Scotia, New Jersey and Delaware Bay, southward to Rio de Janeiro, Brazil, including Gulf of Mexico and Caribbean mainland; excluded from the Bahamas and Caribbean Islands except Cuba and Curaçao (Fig. 114).

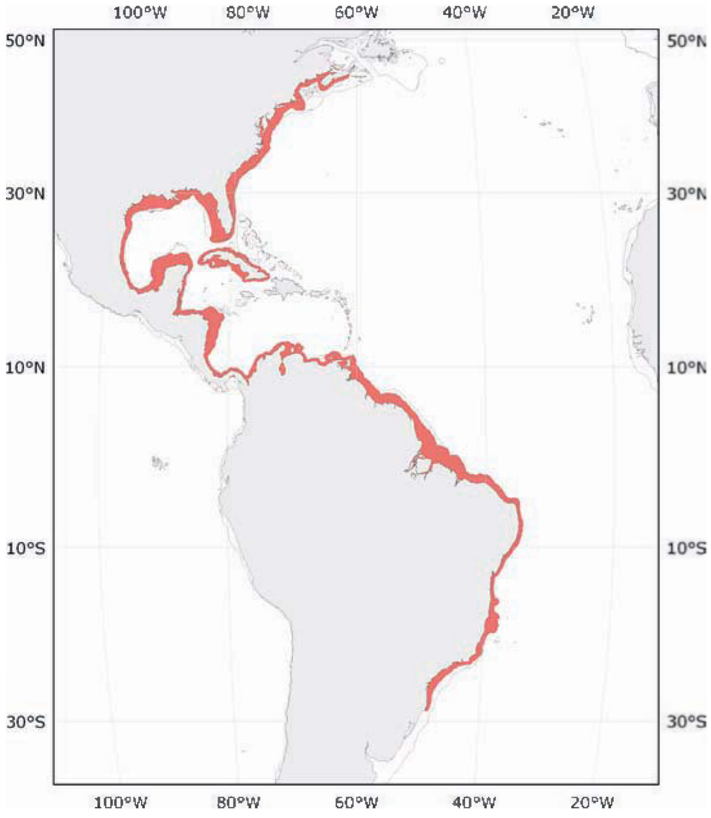


Fig. 114 *Lolliguncula (Lolliguncula) brevis*

🟥 Known distribution

Habitat and Biology: A shallow-water euryhaline species, ***Lolliguncula brevis*** generally is limited to very shallow waters. A notable exception among other cephalopods, the brief squid tolerates low salinities, down to 17.9 PSU, and it withstands a wide range of environmental conditions, having been collected over bottom water temperatures between 8.1º and 29.6°C, salinities between 17.9 and 35 PSU and dissolved oxygen levels between 1.9 and 14.6 mg/l mainly due to the unique characteristics of the species' hemocyanin. This allows the species to inhabit estuarine waters and bays; for example, ***L. brevis*** is an important component of the Chesapeake Bay ecosystem. Excursions into hypoxic waters, in particular, however short in duration, may provide advantage by avoiding predation or exploiting additional food niches.

Females grow larger and are more robust than males. Males mature earlier; 50% of the male population studied in the Gulf of Mexico becomes mature at approximately 40 mm mantle length; 50% of the female population are mature at about 70 mm mantle length. In Brazilian waters off Santa Catarina Island, autumn/winter spawners mature at larger sizes (males 36 mm mantle length; females 48 mm mantle length) than spring/summer spawners (males 29 mm mantle length; females 42 mm mantle length); however, immature animals may attain larger sizes. Mature individuals are found in all seasons and spawning occurs year round. Small eggs are laid in elongate, terminally rounded, individually-fixed gelatinous capsules attached to the bottom in shallow waters in the Northern Hemisphere, while in Brazilian waters club-like capsules about 1.6 mm long are laid in small clusters/clutches measuring about 65 mm in diameter. Paralarval individuals are most abundant near bottom in inshore coastal waters with a salinity of about 26 PSU and can already tolerate very low oxygen concentrations, having been collected in waters considered to be hypoxic.

Food consists of small crustaceans and fishes, and the Thumbstall squid is preyed upon by fishes and mammals.

Observations on squid attracted by light at night in Brazilian shallow waters, reveal that these small squid often are positioned in the boundary zone of zooplankton and small pelagic fish schools of *Anchoa* spp., also attracted by the lights; here they often display a very unusual behaviour, mimicking the colour, form and swimming pattern of the small fishes nearby, probably as an effective form of hunting technique as previously observed in another squid, ***Sepioteuthis sepioidea***. ***Lolliguncula brevis*** is known to associate with anchovies in Florida estuaries, where they prey upon these fishes; a similar relationship could take place in coastal bays off Brazil, as partially supported by the presence of fish remains in the few stomachs examined.

Interest to Fisheries: Caught sometimes in large quantities as bycatch in otter-trawl fisheries for shrimps and fishes. Catches are common around Cape Canaveral, Florida in winter and progressively farther northward to Cape Hatteras in spring and summer. In the Gulf of Mexico the species is widespread but major concentrations seem to occur in the waters of high productivity around the Mississippi River delta. Commonly present in the Pacific shrimp catches by Mexican trawlers, it is sold fresh in local markets along the Oaxaca coast; it also is abundant in the Venezuelan squid catches, mainly east of the Orinoco Delta, but also in shallow waters around Margarita Island and in the Gulf of Venezuela. Currently, however, no specific commercial fishery exists in spite of the great abundance of this species in several areas.

Local Names: USA: Western Atlantic brief squid, Bay squid, Brief squid; VENEZUELA: Chipiron.

Remarks: Recently, the validity of the species for the entire area of the distribution in the western Atlantic waters was questioned, based on differing morphological features (e.g. Simone, 1997, Martins and Perez, 2002, Zaleski, 2005) and differences in egg deposition (e.g. Perez and Vidal, 1997, Zaleski, 2005) in specimens from Brazil and the Gulf of Mexico. A taxonomic separation of squids from the North and the South Atlantic into two distinct species of ***Lolliguncula (Lolliguncula)*** was proposed (Zaleski, 2005, Zaleski and Perez, 2006), and it currently is under discussion (Vecchione, pers. comm.).

A morphological and morphometric analysis carried out on specimens from 11 localities along the Brazilian coast (Zaleski, 2005) indicated the dominant occurrence of a single species in the entire latitudinal range examined (8°S to 28°S). A few local "morphotypes" were distinguished, possibly in relation to the limited displacement capacity of adults, the low paralarval dispersal and the presence of bays and estuaries where the species may have encountered reproductive isolation, all elements that may have favored the observed intraspecific variation. Studies on ***Lolliguncula brevis*** from the Gulf of Mexico have determined the osmotic regulatory mechanism that enables this species to inhabit a wide range of salinities. (Lucero and Poulsen, 2005).

Literature: Hendrix *et al*. (1981), Roper *et al*. (1984), Vecchione *et al*. (1994), Jackson *et al*. (1997), Simone (1997), Bartol *et al*. (2002), Lucero and Poulsen (2005), Zaleski (2005), Zaleski and Perez (2006), Martins and Perez (2007), Vecchione (2008g).

Lolliguncula (Lolliguncula) argus Brakoniecki and Roper, 1985

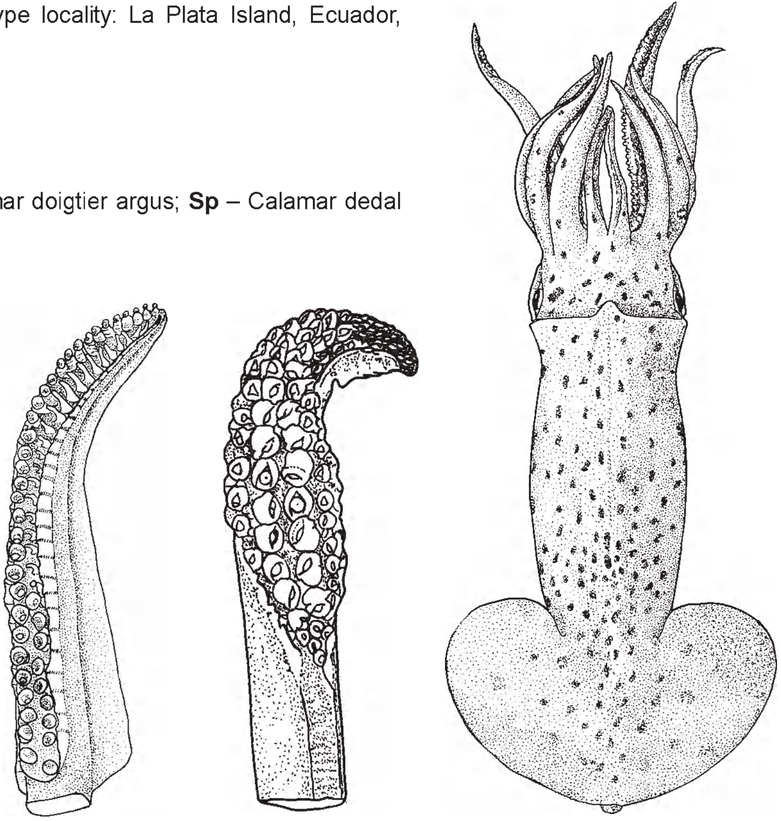
Fig. 115

Lolliguncula argus Brakoniecki and Roper, 1985, *Proceedings of the Biological Society of Washington*, 98(1): 47–53 [47, figs 1–2]. [Type locality: La Plata Island, Ecuador, eastern Pacific Ocean].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Argus brief squid; **Fr** – Calmar doigtier argus; **Sp** – Calamar dedal argus.



hectocotylus tentacular club dorsal view

Fig. 115 ***Lolliguncula (Lolliguncula) argus***

Diagnostic Features: Mantle short, stout (width usually >30% mantle length), bluntly pointed posteriorly; **fins small but wide, length <38% mantle length, width >1.5% mantle length**; tentacles short, compressed; clubs with enlarged manus suckers, marginal suckers about half size of median ones; arm suckers with about 5 blunt teeth on distal margin and proximal margin smooth. Suckers absent on buccal membrane lobes; enlarged proximal suckers present on dorsal and lateral arms. Only 1 ventral arm modified in males (no flap on arm opposite hectocotylus): **right ventral arm hectocotylized** with dorsal series of **distal two-thirds** modified into fleshy papillae lacking suckers.

Size: Very small-sized squid; maximum recorded mantle lengths 30 mm for males and 39 mm for females.

Geographical Distribution: Lower Gulf of California, Mexico to La Plata Island, Ecuador (Fig. 116).

Habitat and Biology: A coastal species, characterized by its small size at maturity (males 20.8–26.8 to 29.6 mm mantle length, females 20.6 to 32.3 to 38.8 mm mantle length).

Interest to Fisheries: Unkown. Probably misidentified with its congener ***Lolliguncula panamensis***, if captured.

Local Names: None available.

Remarks: It is the only known myopsid to have its primary hectocotylization on the right ventral arm instead of the left.

Literature: Brakoniecki and Roper (1985), Roper *et al.* (1995), Vecchione (2008g).

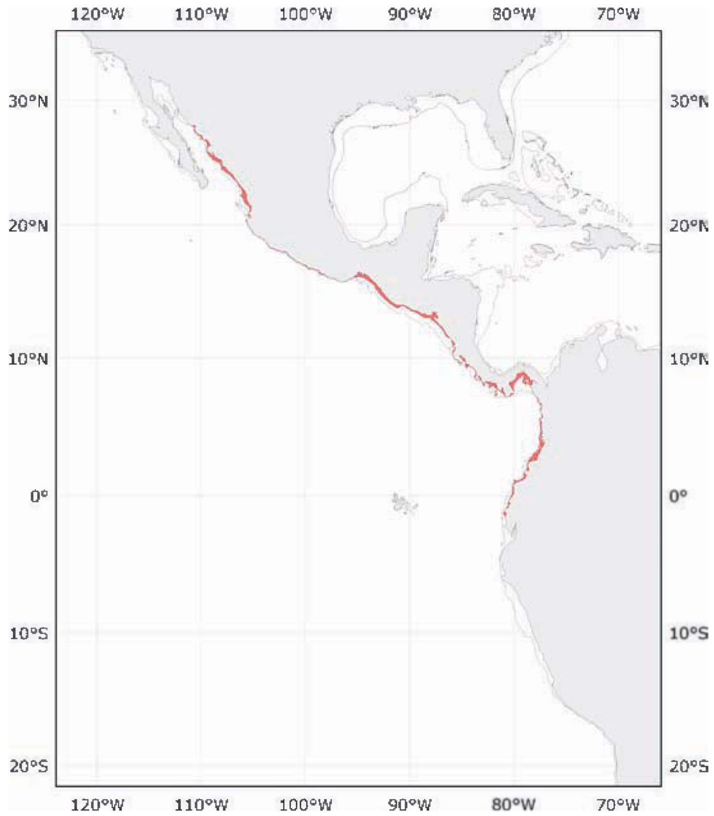


Fig. 116 ***Lolliguncula (Lolliguncula) argus***

🟥 Known distribution

Lolliguncula (Lolliguncula) panamensis Berry, 1911

Fig. 117

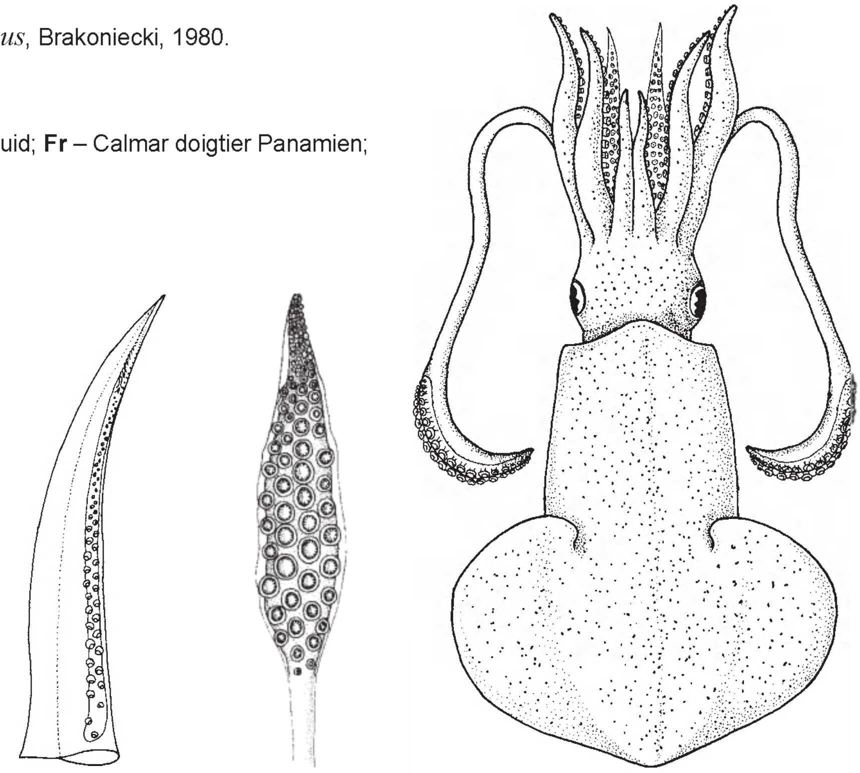
Lolliguncula panamensis Berry, 1911c, *Proceedings of the Academy of Natural Science of Philadelphia*, 63(1):100–105 [100, text-figs 1–7, pl 7]. [Type locality: Panama, eastern Pacific Ocean].

Frequent Synonyms: *Lolliguncula tydeus*, Brakoniecki, 1980.

Misidentifications:

FAO Names: En – Panama thumbstall squid; **Fr** – Calmar doigtier Panamien; **Sp** – Calamar dedal Panameño.

Diagnostic Features: Mantle stout (width usually >30% ML), bluntly rounded posteriorly. **Fins broad, width 50 to 90% mantle length** (usually 60 to 70%), **length usually greater than 38% mantle length**. Tentacles long, robust; clubs large, expanded, with enlarged suckers on manus, especially median series with 23 to 27 small, sharp, triangular teeth around ring (smaller proximally); arm suckers with 11 to 15 short, broad, truncate teeth, prominent distally and obscure proximally. Suckers present on buccal membrane lobes. **Only left ventral arm hectocotylized** (no flap on arm opposite hectocotylus), with **distal quarter** of dorsal series of suckers modified into long, fleshy papillae; small suckers along entire length; hectocotylus longer than opposite arm. No enlarged proximal suckers on dorsal and lateral arms.



hectocotylus tentacular club dorsal view

Fig. 117 *Lolliguncula (Lolliguncula) panamensis*

Size: Small-sized squid; maximum reported mantle length 110 mm in females and 80 mm in males.

Geographical Distribution: Eastern central Pacific Ocean from the western side of Baja California and Gulf of California, through Mexico to northern Peru (Fig. 118).

Habitat and Biology: The species occurs over a depth range to 120 m, but principally inhabits waters less than 50 m depth, at temperatures from 21° to 27ºC, and salinities between 15 and 23 PSU. Spawning takes place throughout the year, apparently in several batches. Maturation occurs at about 80 mm mantle length in females and 40 mm mantle length in males. Prey includes fishes (81%) and crustaceans (>15%).

Interest to Fisheries: Taken as bycatch in shrimp fisheries off Panama, Columbia and Ecuador, but not separately reported in catch statistics. The largest individuals are picked out of the catch, packed and frozen for export to Europe. In spite of their small size, some potential for commercial exploitation for these squids exists.

Local Names: USA: Panama brief squid.

Remarks: ***Lolliguncula panamensis*** and ***Lolliguncula (Loliolopsis) diomedeae*** overlap for most of their distributional ranges. The species description/distinction is based on morphological characteristics of males, but

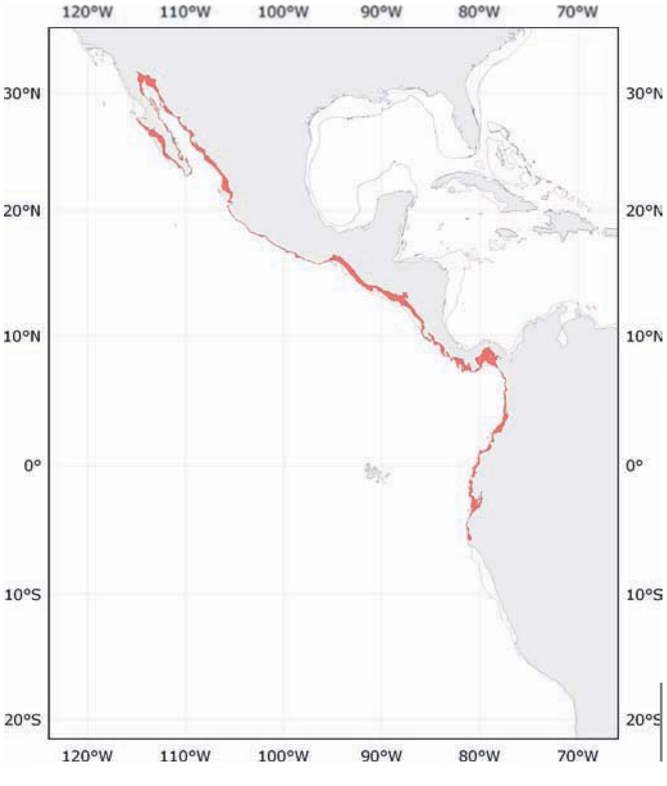


Fig. 118 *Lolliguncula (Lolliguncula) panamensis*

🟥 Known distribution

females or subadults are distinguishable in that the fins of ***L. panamensis*** are larger and longer than those of ***L. diomedeae*** and the body is comparatively larger and more robust (see Sanchez, 2003). Also, the 2 species rarely are caught in the same trawls, possibly a result of what has been defined a “competitive exclusion” (Barrientos, 1987), and they preferentially inhabit different depth ranges: ***L. panamensis*** is most abundant in waters less than 50 m, while ***L. diomedeae*** prefers deeper waters, from 50 to 200 m depth (Sanchez, 2003).

Literature: Roper *et al.* (1984), Barrientos (1987), Roper *et al.*(1995), Sanchez (2003), Vecchione (2008g).

Subgenus ***Loliolopsis*** Berry, 1929

Loliolopsis Berry, 1929, *Transactions of the San Diego Society of Natural History*, 5(18):263–282, 9 figs, 2 pls. [266].

Type Species: *Lolliguncula (Loliolopsis) diomedeae* (Hoyle, 1904).

Lolliguncula (Loliolopsis) diomedeae (Hoyle, 1904)

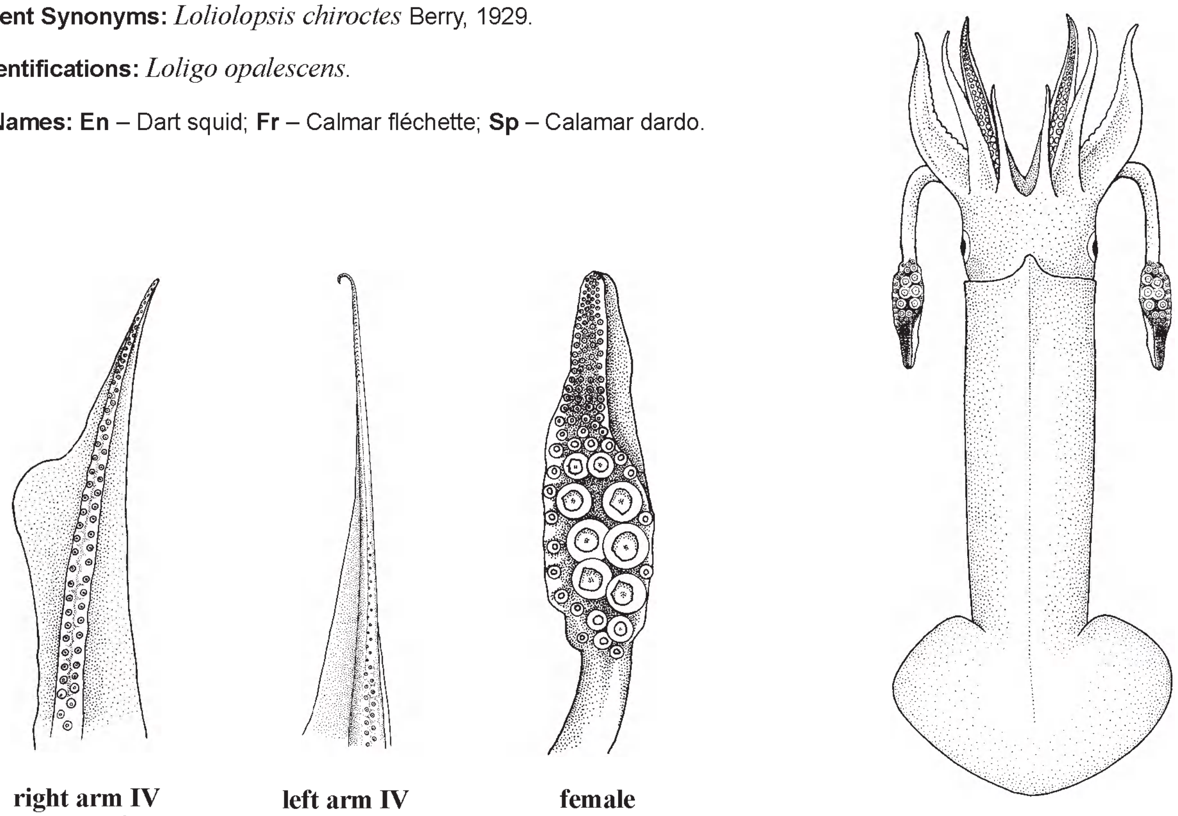
Fig. 119

Loligo diomedeae Hoyle, 1904, *Bulletin of the Museum of Comparative Zoology, Cambridge*, 43(1): 1–72, 12 plates [29, pls 5-6]. [Type locality: 16°47’30"N, 99°59’30"W, eastern Central Pacific Ocean].

Frequent Synonyms: *Loliolopsis chiroctes* Berry, 1929.

Misidentifications: *Loligo opalescens.*

FAO Names: En – Dart squid; **Fr** – Calmar fléchette; **Sp** – Calamar dardo.



right arm IV hectocotylized

left arm IV hectocotylized

female tentacular club

dorsal view of female

Fig. 119 ***Lolliguncula (Loliolopsis) diomedeae***

Diagnostic Features: Mantle elongate, **narrow** (width usually <30% mantle length), bluntly pointed posteriorly. **Fins short, length <50% mantle length** (usually 30 to 40%). **Sexes dimorphic**: female with larger body, relatively shorter arms and larger fins than males. **Both ventral arms conspicuously modified in males, left ventral arm hectocotylized**, greatly elongate with suckers minute at base and absent along rest of arm; sucker stalks modified into papillae; **right ventral arm with broad, membranous flap** and suckers of reduced size.

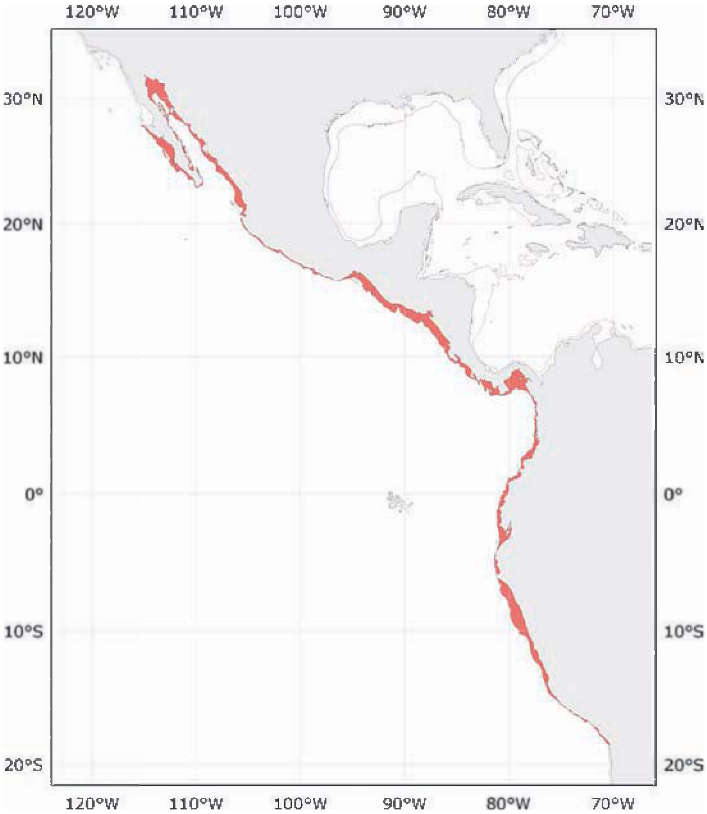


Fig. 120 ***Lolliguncula (Loliolopsis) diomedeae***

🟥 Known distribution

Size: Small sized-squid; maximum reported mantle length 115 mm.

Geographical Distribution: Eastern Central Pacific Ocean: from western side of Baja California and Gulf of California to Peru (Fig. 120).

Habitat and Biology: Frequently forms large aggregations in the Gulf of Panama. Females appear to outnumber males 2:1 and males remain smaller than females.

Interest to Fisheries: Taken as a bycatch in the Panamanian shrimp fishery, but usually discarded; small quantities reach the local market.

Local Names: USA: Dart squid.

Remarks: Hoyle (1904) described ***Loligo diomedeae*** based on a specimen collected off Acapulco, Mexico. Then, Berry (1929) described another loliginid species, that he named ***Loliolopsis chiroctes*** from multiple specimens, also from Baja California, on which he based his new genus ***Loliolopsis***. As these species are synonymous, Hoyle's species name has priority for the type species of Berry's genus. ***Lolliguncula diomedeae*** and ***L. panamensis*** overlap for most of their distributional range. The species description/distinction is based on morphological characteristis of males, but females or subadults are distinguishable in that the fins of ***L. diomedeae*** are narrower and shorter than those of ***L. panamensis*** and the body is comparatively thinner and has a fusiform shape (see Sanchez, 2003). Also, the 2 species are rarely caught in the same trawls, possibly a result of what has been definined a "competitive exclusion" (Barrientos, 1987), and they preferentially inhabit different depth ranges: ***L. panamensis*** is most abundant in waters less than 50 m, while ***L. diomedea***e prefers deeper waters, from 50 to 200 m depth (Sanchez, 2003).

Literature: Roper *et al*. (1984) Barrientos (1987), Roper *et al*. (1995), Sanchez (2003), Vecchione (2008g).

Pickfordiateuthis Voss, 1953

Pickfordiateuthis Voss, 1953, *Bulletin of Marine Science of the Gulf and Caribbean*, 2(4): 602–609. [602].

Type Species: *Pickfordiateuthis pulchella* Voss, 1953.

Diagnostic Features: Tentacular club with biserial suckers on manus. **Fins subterminal, oval**, with free anterior and posterior lobes. **Buccal membrane lappets lack suckers**. Photophores absent.

Size: Dwarf species, maximum recorded sizes between 20 and 26 mm mantle length.

Geographical Distribution: Bahama Islands and Florida Keys to Brazil in Atlantic; along coasts of Baja California in Pacific Ocean.

Remarks: ***Pickfordiateuthis pulchella*** was considered to belong to a monospecific family until Brakoniecki (1996) described a second species, ***Pickfordiateuthis vossi***, from the eastern Pacific and submerged the family into the older family of myopsid squids, Loliginidae. At least one other species of ***Pickfordiateuthis***, in addition to the 3 listed here, currently is not formerly named but designated by Brakoniecki (1996), based on specimens from the western Central Atlantic.

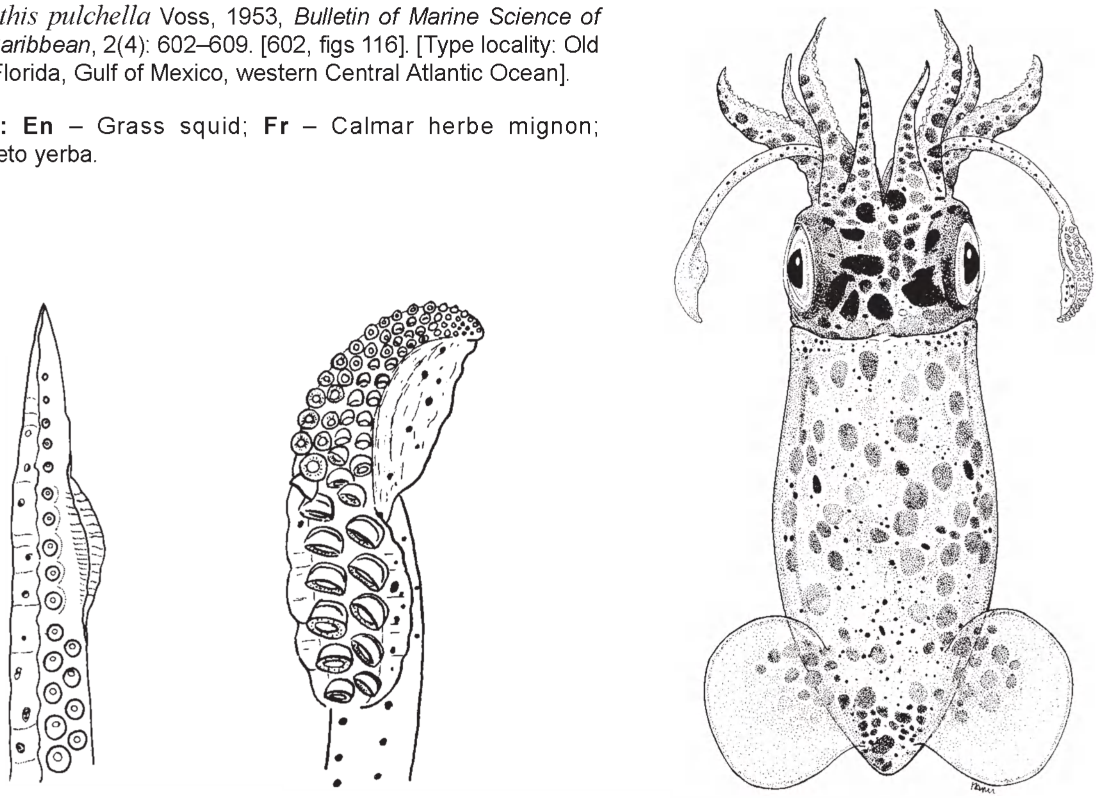
Literature: Voss (1953), Brakoniecki (1996), Vecchione (2008h).

Pickfordiateuthis pulchella Voss, 1953

Fig. 121; Plate V, 26

Pickfordiateuthis pulchella Voss, 1953, *Bulletin of Marine Science of the Gulf and Caribbean*, 2(4): 602–609. [602, figs 116]. [Type locality: Old Rhodes Key, Florida, Gulf of Mexico, western Central Atlantic Ocean].

FAO Names: En – Grass squid; **Fr** – Calmar herbe mignon; **Sp** – Calamareto yerba.



hectocotylus tentacular club dorsal view

Fig. 121 *Pickfordiateuthis pulchella*

Diagnostic Features: Mantle short, bluntly pointed posteriorly. **Chromatophores present on visceral membrane**. **Fins lateral, large**, eliptical to round, **sepiolid-like**. Manus of tentacular clubs with suckers in 2 series; dactylus suckers in 4 series.

Size: Very small sized squid; maximum recorded mantle length 22 mm.

Geographical Distribution: Tropical western Atlantic Ocean: South Florida, Florida Keys, Bahama Islands, Caribbean Sea islands and coasts, to Brazil (Fig. 122).

Habitat and Biology: Shallow tropical waters on patch reefs and seagrass beds. In spite of the accessible habitat, the squid is rarely captured and little is known of its biology.

Literature: Voss (1953), Brakoniecki (1996), Arango and Diaz (1996).

Fig. 122 *Pickfordiateuthis pulchella*

🟥 Known distribution

Pickfordiateuthis bayeri Roper and Vecchione, 2001

Fig. 123

Pickfordiateuthis bayeri Roper and Vecchione, 2001, *Bulletin of the Biological Society of Washington*, 10: 301–310. [302, figs 1–3]. [Type locality: Bahama Islands, western North Atlantic Ocean].

Misidentifications: *Loligo* sp.

FAO Names: En – Bayer's grass squid; **Fr** – Calmar herbe de Bayer; **Sp** – Calamar yerba de Bayer.

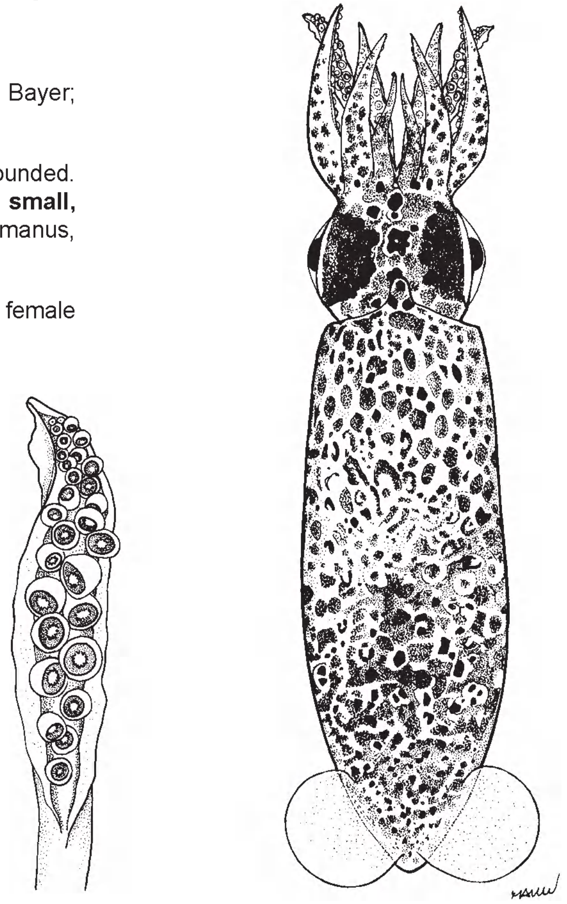
Diagnostic Features: Mantle elongate, posterior end broadly rounded. **Chromatophores absent from visceral membrane**. **Fins small, subterminal**. Tentacles short, thin. Club suckers in 2 series on manus, crowded on dactylus.

Size: A very small-sized squid, currently known only from the female type specimens, 23 and 26 mm mantle length.

Geographical Distribution: Western North Atlantic Ocean: Bahama Islands (Fig. 124).

Habitat and Biology: Type specimens collected from a swarm of squids at 110 to 113 m depth during descent by submersible. The squids ceased following the sub at about 274 m. Although the bottom depth at the dive site was about 1 km, the location was about 2 km off Abaco Island, so shallow water was nearby. Since both specimens were fully mature, mated, unspawned females, it was suggested that the occurrence of ***P. bayeri*** in that habitat, unusual for all known species of the genus, represents an offshore mating migration.

Literature: Roper and Vecchione (2001).



tentacular club

dorsal view

Fig. 123 *Pickfordiateuthis bayeri*

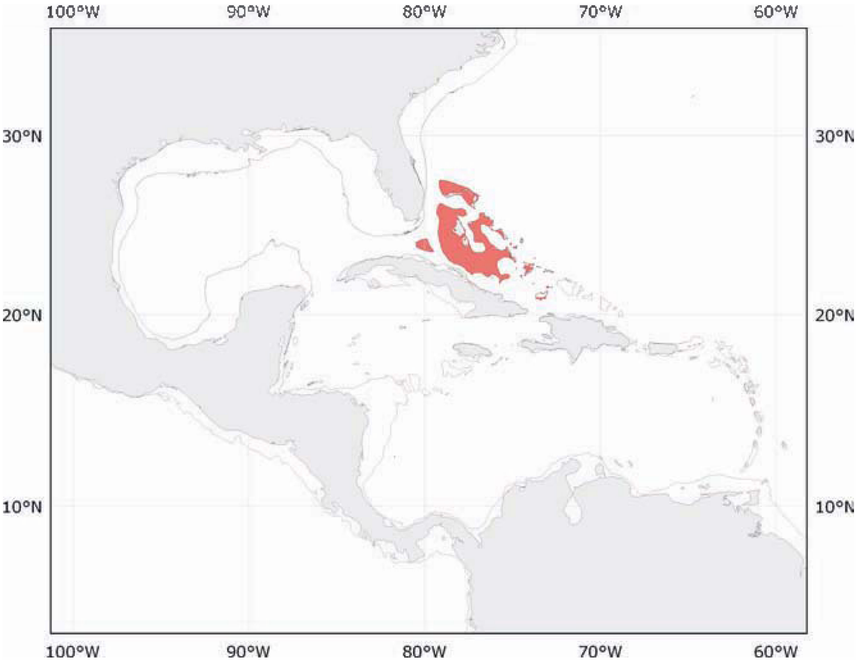


Fig. 124 *Pickfordiateuthis bayeri*

🟥 Known distribution

Pickfordiateuthis vossi Brakoniecki, 1996

Fig. 125

Pickfordiateuthis vossi Brakoniecki, 1996, *Bulletin of Marine Science*, 58(1): 9–28 [16, figs 4c, 5–7]. [Type locality: 24.6°N, 112.1°W, Bahia Magdelena, Mexico, eastern Central Pacificf Ocean].

FAO Names: En – Voss' grass squid; **Fr** – Calmar herbe de Voss; **Sp** – Calamar yerba de Voss.

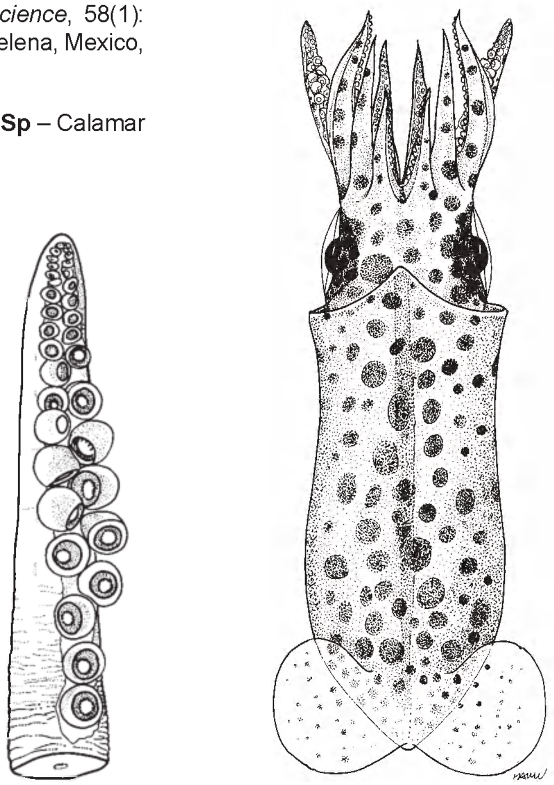
Diagnostic Features: Mantle elongate, posterior end broadly rounded. **Fins round, relatively large**, length about one-quarter mantle length. **Chromatophores absent from visceral membrane**. Left ventral arm hectocotylized on distal third in males; 6 to 9 normal pairs of proximal suckers, followed by absence of suckers in both series; stalks modified into long thick, papillae that decrease in size distally, then completely absent at arm tip. Tentacles short, stout, similar in appearance to arms; **clubs highly modified, elongate, with no visible manus or dactylus**; proximal suckers on clubs in single series, increase to 2 series on remainder of club.

Size: Very small-sized species; mazimum recorded size around 20 mm mantle length.

Geographical Distribution: Eastern Central Pacific Ocean: Pacific and Gulf coasts of Baja California; throughout the Sea of Cortez, Mexico (Fig. 126).

Habitat and Biology: Shallow waters near shore; females are larger than males at maturity; average female mantle length at maturity 15 mm, average male 13 mm.

Literature: Brakoniecki (1996).



tentacular club

dorsal view of female

Fig. 125 ***Pickfordiateuthis vossi***

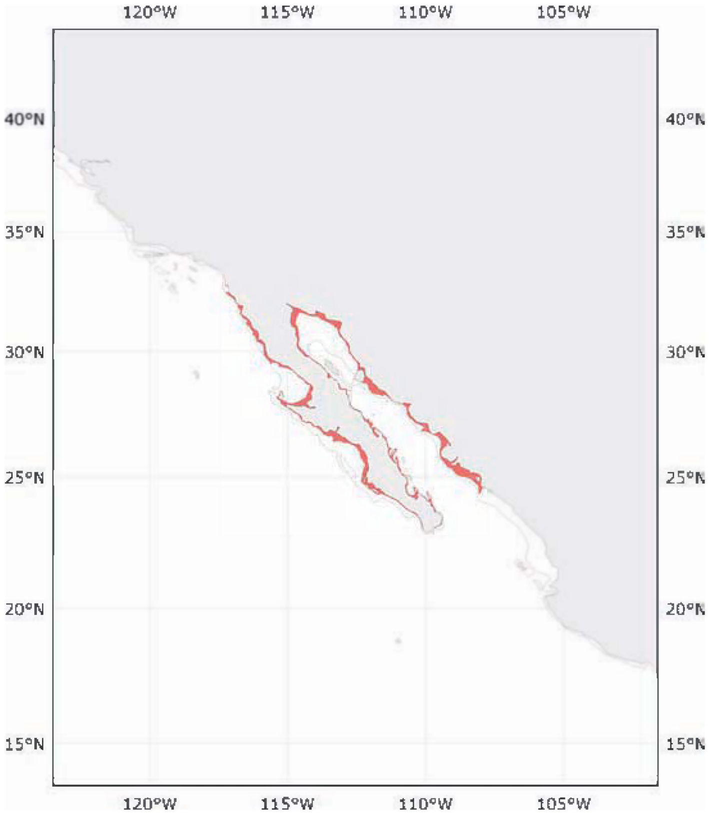


Fig. 126 ***Pickfordiateuthis vossi***

🟥 Known distribution

Sepioteuthis Blainville, 1824

Sepioteuthis Blainville, 1824, *Dictionnaire des Sciences Naturelles*, 32:1–394, Atlas 2, 118 plates. [175].

Type Species: *Sepioteuthis sepioidea* (Blainville), 1823.

Diagnostic Features: Mantle broad, relatively stout, tapered to a blunt posterior end. Tentacular **clubs expanded**, with suckers in 4 series. Arm sucker rings with pointed teeth around entire margin. **Hectocotylus without crest**; sucker stalks elongated along modified portion of arm to form papillae on both dorsal and ventral series; proximal suckers unmodified. Posterior mantle not elongated into tail-like structure. **Fins extend nearly full length of mantle** (except in very young squid). **Eggs longer than 5 mm**, laid in single, straight series in egg strand; strands, attached at bases, form masses. Spermatophore cement body short. Photophores absent.

Size: Medium- to large-sized squid; maximum reported mantle length 422 mm (male specimen).

Geographical Distribution: Widely distributed in the ropical and subtropical waters of the western Atlantic (from Cape Canaveral to to northeastern Bazil) and Indo-West Pacific Ocean, all around Australia and down to Tasmania. Recorded also in the Mediterranean Sea.

Habitat and Biology: Mostly inhabitants of coastal waters and bays, common in coastal environments on sea grass beds, coral reefs and sandy bottoms.

Remarks: Currently, the genus comprises 3 species: ***Sepioteuthis australis***, ***S. lessoniana*** and ***S. sepioidea*** (Vecchione *et al*, 2005). A fourth species, ***S. loliginiformis*** was described from near Mohila, Red Sea by Rüppell and Leuckart (1828), but there are not adequate observations to confirm it to be a different species from ***S. lessoniana*** (see also Adam 1938, 1939b, 1959).

Literature: Adam (1939b, 1959), Vecchione *et al.* (2005), Vecchione (2008j).

Sepioteuthis sepioidea (Blainville, 1823)

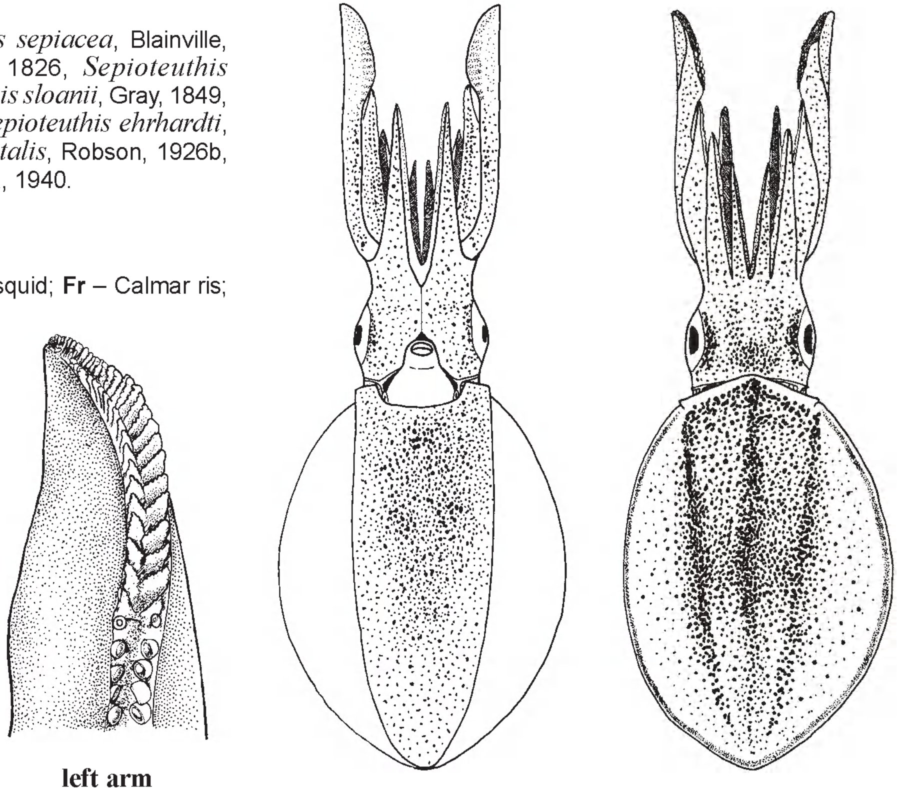
Fig. 127; Plate VI, 30–31

Loligo sepioidea Blainville, 1823, *Journal de Physique de Chimie et d'Histoire Naturelle*, 96:116–135. [133]. [Type locality: Martinique, Caribbean Sea, tropical western Atlantic Ocean].

Frequent Synonyms: *Sepioteuthis sepiacea*, Blainville, 1824, *Sepia affinis*, D'Orbigny, 1826, *Sepioteuthis biangulata*, Rang, 1837, *Sepioteuthis sloanii*, Gray, 1849, *Sepioteuthis ovata*, Gabb, 1868, *Sepioteuthis ehrhardti*, Pfeffer, 1884, *Sepioteuthis occidentalis*, Robson, 1926b, *Sepia officinalis jurujubai*, Oliveira, 1940.

Misidentifications: *Sepia* sp.

FAO Names: En – Caribbean reef squid; **Fr** – Calmar ris; **Sp** – Calamar de arrecife.



left arm IVhectocotylus

ventral view

dorsal view

Fig. 127 ***Sepioteuthis sepioidea***

Diagnostic Features: Mantle widest at anterior opening; **fins elliptical to weakly rhomboidal**, their **width about 65% of mantle length**; buccal lappets without suckers; modified portion of **hectocotylized** (left ventral) **arm** occupies **distal fourth of arm length** and is characterized by a sudden reduction in size of 1 or 2 pairs of suckers, the complete absence of suckers in both series from the remaining distal portion of the arm, and the increase in size of the pedicels into large, fleshy papillae. **Colour**: quite varied in life from translucent with irredescent sheen, through greenish brown to deep reddish brown, depending on location and behavioural situation; may show "eye-spots", bands, or stripes on mantle, these sometimes outlined in white.

Size: Medium-sized squid; maximum reported size 200 mm mantle length.

Geographical Distribution: Tropical western Atlantic Ocean from Cape Canaveral, Florida, Bermuda and the Bahama Islands, Florida Keys, through the Caribbean Islands, Campeche, Yucatan and Venezuela to Farol de Barra Beach, northeastern Brazil (13°00'S, 38°31'W, Bahia) (Fig. 128).

Fig. 128 ***Sepioteuthis sepioidea***

🟥 Known distribution

Habitat and Biology: A truly tropical species that is limited in distribution by the distribution of coral reefs, primarily, and turtle-grass flats (*Thalassia testudinum*). Accordingly, factors such as temperature, salinity, water depth and turbity that affect turtle grass and coral reef distribution are limiting factors for the Caribbean reef squid, as well. It occurs at depths of 0 to 20 m, mostly 3 to 7 m. As shallow coral reefs are absent from most of the Gulf of Mexico, ***S. sepioidea*** also appears to be excluded from the Gulf. It occurs in schools of 4 to 50 individuals of about equal size that cruise around the reefs or about the reef flats, or grass beds behind the reefs. Males mature earlier and at smaller sizes than females; the hectocotylus is developed on males at 30 mm mantle length, and between 70 and 85 mm mantle length specimens are ready to mate and fertilize females; the smallest mature females measure 110 mm mantle length and at 140 mm 50% of the studied population is mature. Eggs are very yolky and large, about 5 to 6 mm long; only 3 to 4 eggs are laid in each large, gelatinous capsule, several of which are attached together at their bases; these small clusters are laid under rocks or in conch shells (*Strombus gigas*), mainly on turtle grass beds and coralline formations; breeding apparently occurs year-round. Embryo survival rate and development is strictly related to salinity and temperature. The species feeds on fishes and shrimps. In aquaria, newly hatched juveniles start feeding almost immediately, (i.e. after 10 to 15 h), on mysid shrimps.

Interest to Fisheries: Presently ***Sepiotethis sepioidea*** is not fished commercially, but it often is a bycatch of other target fisheries. However, the other species of ***Sepioteuthis*** in the Indo-Pacific are fished extensively and are of excellent quality for eating. Therefore, this species has a potential interest to future fishing activity. In Bermuda, accidentally caught squid are used for bait.

Local names: USA: Tropical squid; VENEZUELA: Chopo.

Remarks: ***Sepioteuthis sepioidea*** is the only Western Hemisphere species of an otherwise Indo-west Pacific genus. A single record from the waters off Woods Hole, Massachussets (41°32'N, 70°41'W; Mercer, 1970b), conspicuously far from the normal northern distribution limit of the species, was explained as an example of transportation by the Gulf Stream. A single record from southeastern Brazil waters off Buzios (23°47'S; 45°10'W) also exists (Begossi and Duarte, 1988); the specimen was associated with a rocky and sandy substrate, at about 5 to 6 m deep, in March 1987. However, the species was not reported in the Brazilian waters afterwards, till the recent observations off northeastern Brazil (Nunes de Anchieta *et al*., 2007).

The Caribbean reef squid exibits complex patterns of true and false displays and "anti-displays", disruptive colorations (camouflaging techniques) and deimatic behaviours, during social (including sexual) interactions among individuals of the same species and/or during encounters between the squids and potential predators (Moynihan and Rodaniche, 1982; Hanlon and Messenger, 1996). On the coastal reefs of northeastern Brazil, Nunes de Anchovieta *et al*. (2007) reported frequent associations of small groups of juvenile reef fish with large shoals of reef squid. Since no foraging activity was observed, these aggregations were explained as an efficient technique employed by juvenile fish to obtain protection against occasional visual-oriented predators and to increase survivorship.

Literature: Voss (1956), Roper (1978), Moynihan and Rodaniche (1982), Roper *et al*. (1984), Robaina and Voglar (1986), Voglar and Robaina (1987), Hanlon and Messenger (1996), Nunes De Anchieta *et al*. (2007), Vecchione, (2008j).

Sepioteuthis australis Quoy and Gaimard, 1832

Fig 129; Plate V, 27

Sepioteuthis australis Quoy and Gaimard, 1832, *Zoologie*, 2(1): 1–320, Atlas of 93 plates (1833) [77, pl 4 fig 1]. [Type locality: New Holland, Australia, probably Port Western].

Frequent Synonyms: None.

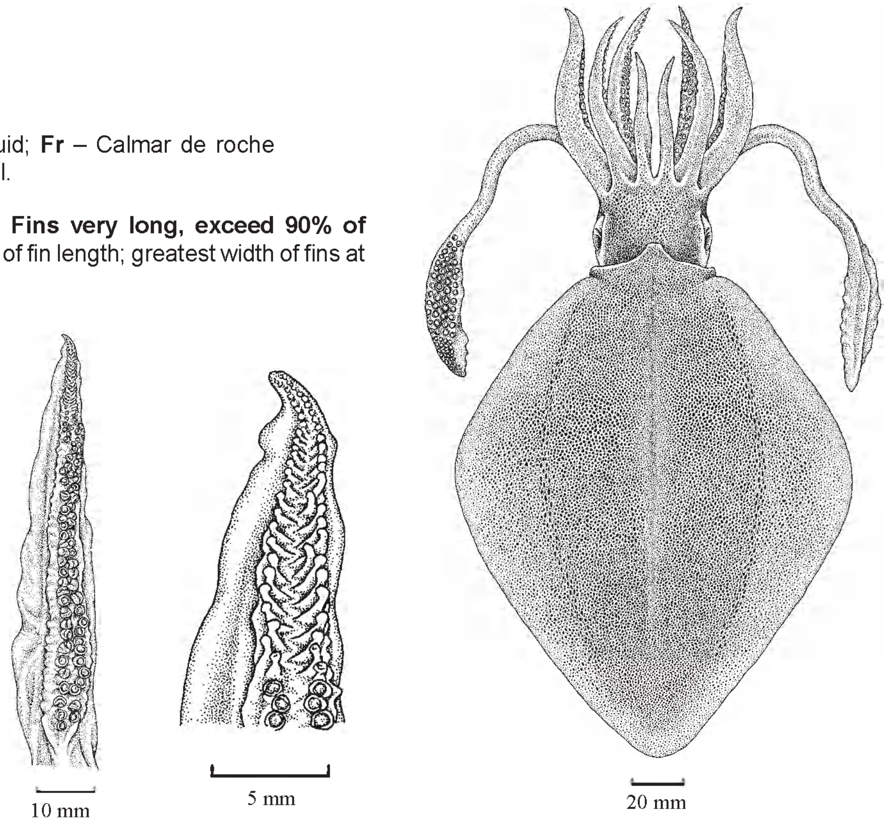
Misidentifications: None.

FAO Names: En – Southern reef squid; **Fr** – Calmar de roche austral; **Sp** – Calamar roquero austral.

Diagnostic Features: Mantle robust. **Fins very long, exceed 90% of mantle length**, fin width less than 50% of fin length; greatest width of fins at about midpoint. Tentacular **clubs long, not greatly expanded**; suckers moderate sized with 22 to 27 sharp teeth around the rings of the largest suckers. Arm III sucker rings with 25 to 30 sharp teeth. A narrow white to blue line occurs along the base of the fins where they attach to the body. General appearance closely resembles ***Sepioteuthis lessoniana***, but lateral margins of fins are weakly angular.

Size: Maximum mantle length 394 mm; maximum weight about 4 kg.

Geographical Distribution: Southwestern Pacific Ocean: Australia and northern New Zealand; from Dampier in Western Australia to Moreton Bay in Queensland, including Tasmania (Fig. 130).



hectocotylus **hectocotylus tip** **dorsal view**

Fig. 129 ***Sepioteuthis australis***

Habitat and Biology: For most of its distribution ***S. australis*** inhabits coastal waters and bays, usually in depths of less than 70 m, and it is commonly found in depths from the surface to 10 m. In South Australia, offshore nursery and inshore spawning grounds have been identified, with small (<30 mm ML) and large (>150 mm ML) individuals found predominately in shallow, inshore waters, while medium sized animals are more abundant offshore. The distribution and abundance patterns of adult squids in the Gulf St Vincent (South Australia) were found to be highly variable, but they conform to a systematic, seasonal pattern consistent year to year; abundance typically increases for 6 months, peaks and declines for the remainder of the year, with the peak timing varying among regions, following an anti-clockwise direction around the Gulf. Males attain larger sizes than females and trawl data indicate a 1.01:1.0 sex ratio. However, jig data show a markedly higher proportion of

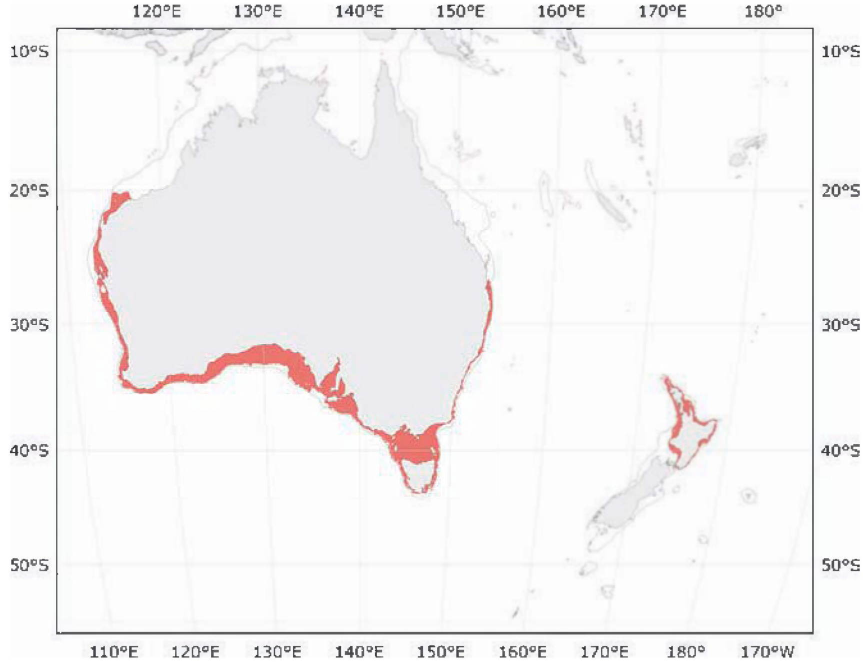


Fig. 130 ***Sepioteuthis australis***

🟥 Known distribution

males in the catches, indicating that this fishery is selective for males and that jig fishing throughout the spawning season can potentially modify the process of sexual selection and the mating behaviours of the individuals within the spawning population, highlighting the need for closures over this crucial period.

The smallest observed mature male measured 88 mm mantle length and the smallest mature female 117 mm mantle length, while size at 50% maturity is about 150 and 160 mm for males and females, respectively. Mature individuals occurr year-round indicating that spawning, also, extends throught the year. Spawning involves complex body patterns and various mating types. Reproductive behaviour may differ among different populations. Eggs are laid in white, finger-like strands, approximately 60 to 70 mm long, each strand containing between 3 and 9 eggs. Since females may store sperm from more than one male, individual egg strands may display considerable genetic diversity through multiple paternities. Clusters of egg strands are attached to macroalgae and seagrass, in sheltered, shallow, inshore areas. Egg mass size varies considerably, ranging from solitary egg strands attached at the end of seagrass blades to large masses containing up to 1 912 strands. Most egg masses contain < 300 egg strands.

Embryonic development takes 61 days at 13°C and 31 days at 20°C. Hatching rates decline significantly with increasing temperature. Embryo mortality rates range between 2 to 25% and are highly variable, both spatially and temporally, depending on egg-mass size, the substrate upon which the mass is attached, the location of the embryo within the mass, and the degree of biofouling. While relatively unaffected by natural temperature fluctuations, embryos may be damaged by sudden salinity changes, like those caused by heavy rainfall and subsequent runoff of freshwater in coastal areas. Also, embryos located deeper within the egg mass suffer higher rates of mortality and abnormal development than those located around the periphery. Embryos hatch at night, reducing the risk of predation by visual predators. Tasmanian ***S. australis*** hatchlings range in size from 4.3 to 7.3 mm mantle length, slightly larger than those from South Australia (mean 4.75 mm ML). Once hatched, paralarvae are photopositive and actively swim to the surface. Observations on South Australia paralarvae indicate that they remain planktonic on the spawning grounds until approximately 8 mm mantle length, after which they become benthic. Small paralarvae (~7 mm mantle length) have been observed to feed on mysid shrimp and other zooplankton associated with low relief seagrass beds. Although their dietary requirements are unknown, mysid shrimp and crab zoea have been successfully used to rear hatchlings in captivity. Initial hatchling size may, by itself, explain the high variability in size in animals of the same age. Growth is rapid, and the life span is approximately one year; males grow faster and attain larger sizes than females. Water temperature significantly affects growth rates, with individuals hatched in warmer seasons reaching a final size that could surpass that of earlier-hatched therefore older individuals. The effect of temperature is not limited to initial growth stages, but continues to influence growth patterns throughout the adult life cycle. These seasonal differences in growth translate into substantial variations in size-at-age. The dynamic nature of oceanographic conditions in some areas of its distributional range (i.e. Tasmania waters) may result in high variability in both the population structure and stock-recruitment relationship. Also, significant differences in growth occur between genetic types, with the hybrids always growing faster (at least 60% larger at 150 days old) than the 2 parental taxa, a phenomenon commonly referred to as hybrid vigour. Spatial differences in growth also exist, e.g. individuals from Western Australia usually grow faster than those from South Australia and New Zealand. ***Sepioteuthis australis*** is a key component of the marine ecosystem as a primary consumer of crustaceans and fishes and as a food source for a variety of predatory species.

Interest to Fisheries: ***Sepioteuthis australis*** is the object of fisheries throughout its distributional range, where it is taken by commercial trawlers as well as by jigging and recreational fishing activities. The South Australian fishery is the most productive and more extensively studied and documented. It began to develop in the early to mid 1970s when squids were taken as a byproduct of the net sector of the marine scalefish and prawn fisheries. Catch and effort in the late 1970s increased, and by 1979/80 total catch had increased four–fold to 193 tonnes, with an estimated value of AUD 540 000. The fishery has continued to expand, and ***S. australis*** has become South Australia's third most valuable Marine Scalefish (MSF) species behind King George whiting (*Sillaginodes punctata*) and snapper (*Pagrus auratus*). Also, the average price of the southern reef squid has continuously increased to approximately A$3 per kg and, despite lower catches in 2002/03, the total value peaked that year at an estimated A$3.0 million. Jigging dominates the fishery and it is permitted in most State waters, with the exception of several aquatic reserves. In New Zealand, relatively low quantities are caught by trawl.

Even though most of the catch is landed by the hand jig and haul net sectors, gill nets and dab nets also are used. Conventional 5 to 6 m fibreglass or aluminium vessels with high-powered motors (>60 hp) are typically used by both the commercial and recreational sectors. Recreational fishers also fish from jetties, breakwaters and other shore-based platforms. Prawn trawlers operating in deeper waters (>10 m) of South Australia's Gulf of St Vincent, Spencer Gulf and Far West Coast continue to take incidental catches of calamary, although the magnitude of this catch is unknown. Currently, no harvest controls exist on the commercial catch of the southern reef squid. High market value, relatively low set-up costs, and open access to all fishers with a Marine Scalefish, or rock lobster licence, suggest that there is considerable latent effort and potential for the fishery to expand rapidly. Since fishing effort for this species focuses on the spawning aggregations, in 1992 the fisheries management agency raised concerns about the increasing popularity of calamary fishing by both recreational and commercial fishers and the potential vulnerability of the spawning stocks (Marine Scalefish White Paper, 1992). Also, the illegal sale of squids has been reported. These influences resulted in the implementation of recreational bag and boat limits in 1995 (i.e. 15 per bag/45 per boat per day). Currently, generic control measures such as spatial and temporal closures and gear restrictions apply to the net sector; also, netting is forbidden in all metropolitan waters and in waters less than 5 metres deep, as well as in numerous bays and marine protected areas. To date, no specific regulations apply to the commercial fishery. The spatial segregations of squid populations in South Australian waters, with juveniles and subadults distributed offshore and adults and spawning individuals aggregated inshore, enables quantification of offshore squid catch rates. This is accomplished by fishery-independent trawl surveys that target prawn and provide a feasible method to forecast inshore recruitment to the fishery.

Local Names: AUSTRALIA: Southern calamary.

Remarks: Allozyme electophoresis identified three different calamary 'genetic-types' from southern Australian and northern New Zealand waters (Triantafillos and Adams, 2001) that were categorized as 'peripheral', 'central' or 'hybrid' types. The 'peripheral' types were almost exclusively found around the southwestern and southeastern limits of the distributional range (i.e. Perth and Albany on the western coast and Newcastle, New South Wales on the eastern coast), whereas the 'central' type dominated in the gulf waters and the southern Australia Bight. Where these two forms overlap, a third, 'hybrid' form is found. Preliminary morphological and reproductive data support the hypothesis of the existence of two taxa of ***Sepioteuthis australis*** in South Australian waters, while mitochondrial DNA sequence data are inconclusive.

Observations on spawning individuals in protected areas with acoustic telemetry (Pecl *et al*., 2007), demonstrate that animals spawn over several months, traveling hundreds of kilometers within the spawning areas during this period, without leaving the protected areas. Consequently, closures of critical spawning regions during periods of reproductive activity may protect spawners and enable undisturbed egg-laying.

Literature: Roper *et al*. (1984) Triantafillos and Adams (2001), Steer *et al*. (2005, 2006, 2007), Pecl and Moltschaniwskyj (2006), Hibberd and Pecl (2007), Moltschaniwskyj and Pecl (2007), Pecl *et al*. (2007), Vecchione (2008j).

Sepioteuthis lessoniana Ferussac *in* Lesson, 1831

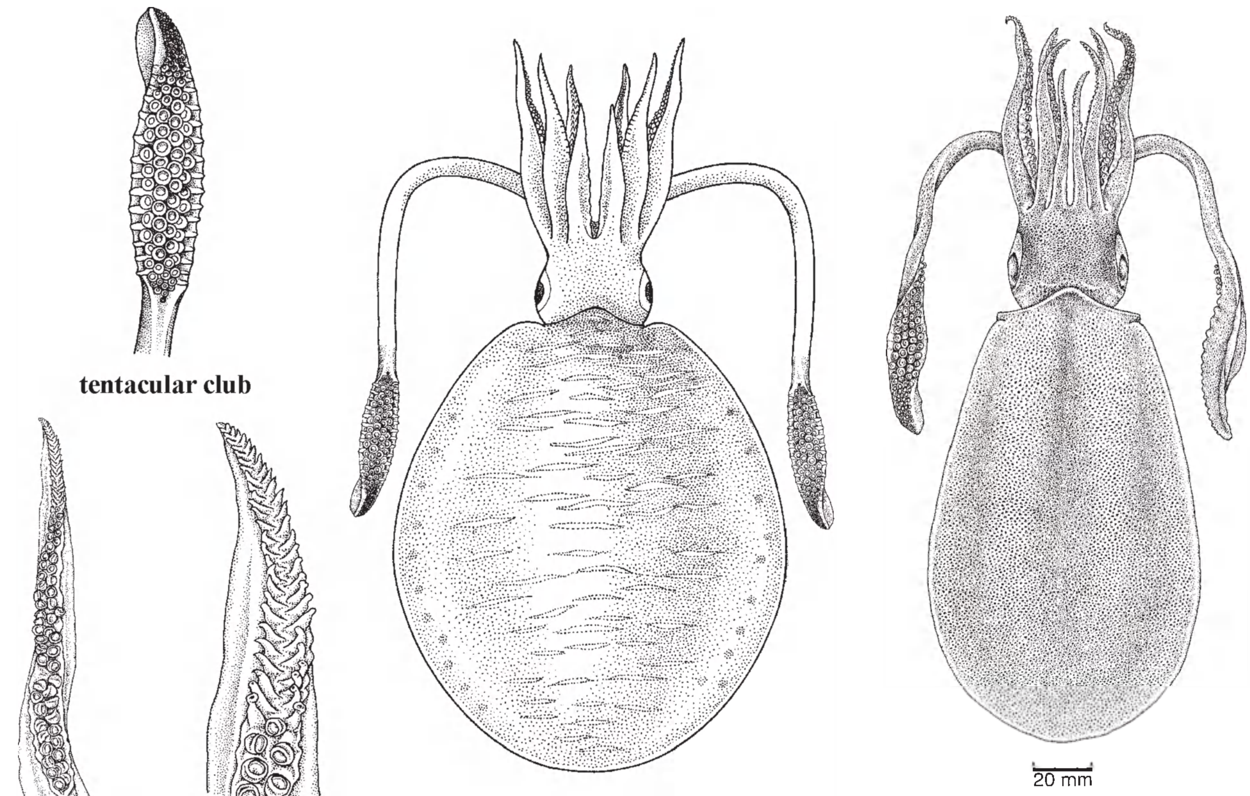
Fig. 131; Plate V, 28–29

Sepioteuthis lessoniana Ferussac, 1831, *in* Lesson, 1830–1831, *Zoologie*, 2(1): 471 pp. [241, pl 11]. [Type locality: not designated].

Frequent Synonyms: *Sepioteuthis hemprichii* Ehrenberg, 1831, *Sepioteuthis mauritiana* Quoy and Gaimard, 1832, *Sepioteuthis guinensi* Quoy and Gaimard, 1832, *Sepioteuthis lunulata* Quoy and Gaimard, 1832, *Sepioteuthis doreiensis* Quoy *in* Ferussac and D'Orbigny, 1835, *Sepioteuthis sinensis* D'Orbigny *in* Ferussac and D'Orbigny, 1848, *Sepioteuthis arctipinnis* Gould, 1852, *Sepioteuthis brevis* Owen, 1881, *Sepioteuthis neoguinaica* Pfeffer, 1884, *Sepioteuthis indica* Goodrich, 1896, *Sepioteuthis sieboldi* Joubin, 1898, *Sepioteuthis malayana* Wülker, 1913, *Sepioteuthis krempfi* Robson, 1928.

Misidentifications: None.

FAO Names En – Bigfin reef squid; **Fr** – Calmar tonnelet; **Sp** – Calamar manopla.



hectocotylus **hectocotylus tip** **dorsal view (Indo-Pacific form)** **dorsal view (Northeastern Australian form)**

Fig. 131 *Sepioteuthis lessoniana*

Diagnostic Features: Mantle long, robust, **width about 40% of length. Fins very large, broadly oval in outline, fin length over 90% up to nearly 100% of mantle length**, their **width up to 75% of mantle length**; the greatest width occurs posterior to the midpoint of the fins. Tentacular **clubs long, expanded**; median manal suckers enlarged, rings with 14 to 23 sharp teeth. Arm sucker rings with 18 to 29 sharp, triangular teeth. Tentacles long, robust. Left ventral arm hectocotylized along distal one-third to one-fourth of arm where the 2 series of suckers are transformed into long, conical, fleshy papillae with a minute sucker with smooth chitinous ring on each tip; long, fleshy papillae connected by low folded ridge that extends along arm between the series of papillae; papillae on dorsal series thicker and longer than those on ventral series.

Size: Medium to large-sized squid; maximum reported mantle length 422 mm in males; females smaller, 382 mm mantle length; commonly 200 to 300 mm mantle length. Weight to about 2 kg.

Geographical Distribution: One of the most widely distributed loliginid squids of the Indo-West Pacific region. It occurs from Japan to northern Australia and New Zealand and from Hawaii to the east African coast, north into the Red Sea and south to southern Mozambique and Madagascar. Records from the eastern Mediterranean (Fig. 132).

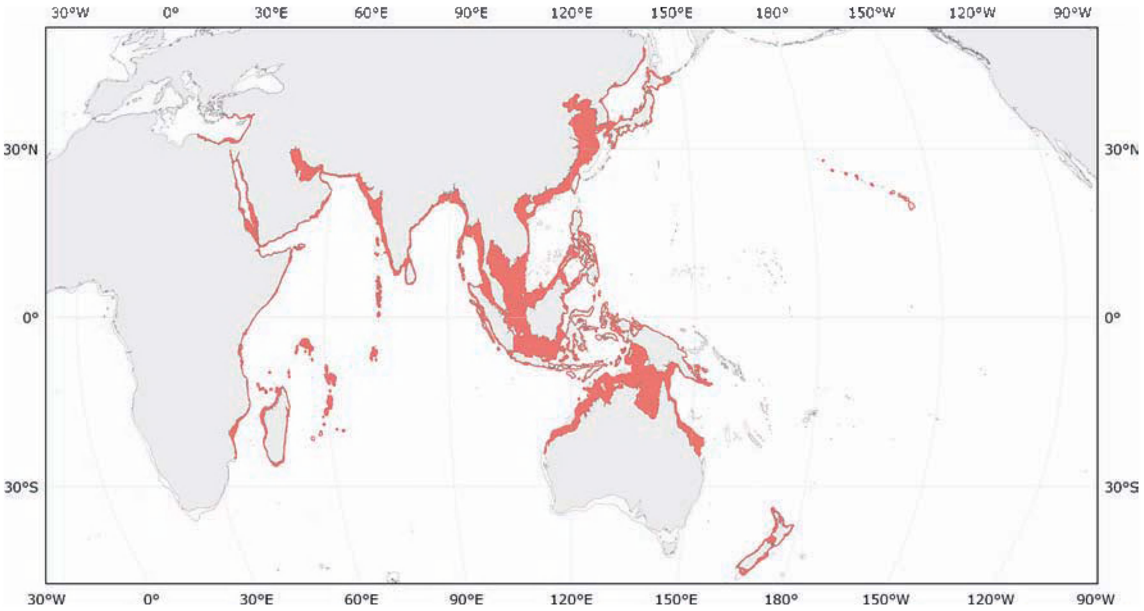


Fig. 132 ***Sepioteuthis lessoniana***

🟥 Known distribution

Habitat and Biology: ***Sepioteuthis lessoniana*** occurs from the surface to about 100 m depth throughout its area of distribution. Rather common in coastal environments on sea grass beds, coral reefs and sandy bottoms, it consistently migrates inshore after winter to start mating and spawning in spring. During mating, squid form close pairs, and paired males exhibit characteristic agonistic colour patterns against other intruding males. The spawning season depends on the hydrographic conditions and can extend to all year-round. Spawning occurs from January to June off southern India and from mid-June to late August and September in the cooler southern Japanese waters. Several peaks of 2 to 3 months during the year are reported for the Andaman Sea and the Gulf of Thailand populations.

Significant spatial and temporal variation occurs in growth rates and maturity of the equatorial, tropical and subtropical Indo-Pacific populations. In the “hot”, shallow, equatorial waters of the Gulf of Thailand, ***S. lessoniana*** grow faster and mature earlier, at a much smaller size, than ***S. lessoniana*** that inhabit the “cool” subtropical waters of southern Australia. The tropical population off Townsville, northeastern Australia, show an intermediate situation between the 2 extremes, as well as an alternation of generations that depends on the season of hatching.

Flexible reproductive strategies exist in this species and it is able to spawn multiple batches of eggs at discrete times throughout the adult life span. While field observations of spawned-out females show a consistent degeneration of the tissues of the whole body and confirm that egg-laying is the final event of the life cycle, the spawning phase itself may be quite prolonged (as also indicated by rearing observations). Eggs are embedded in milky white, soft, gelatinous, slender, finger-like capsules, each of which contains up to 13 eggs in a row. These capsules are attached in clusters to the substrate. Hatchlings are planktonic and range in size between 4.5 and 6.5 mm mantle length. The number of eggs in a single capsule, the mode of capsule attachment to the substrate, the spawning season and hatchling chromatophore number and arrangement, all are elements that supported the existence of a complex of populations in Japanese waters, and of different morphs in other areas, e.g. Thai waters and Western Australian waters. This was supported also by genetic studies. The taxonomic status of these populations, however, remains unresolved (see Remarks).

While length frequency analyses and field observations indicated a life span of 1 to 3 years, subsequent rearing experiments and field studies indicate a considerably shorter life cycle; females may reach sexual maturity and spawn at ages of 110 to 115 days, at mantle lengths between 105 and 145 mm. Direct ageing techniques (i.e. statolith reading and analysis) used on field-captured animals reveal that ***S. lessoniana*** of tropical Australian waters grow at an even faster growth rate. Individuals reach maturity and complete the whole life cycle in less than 100 days, at a size of about 180 to 200 mm mantle length.

Such a rapid growth rate is one of the characteristics that makes ***S. lessoniana*** especially suitable to laboratory experiments and to aquaculture projects. The life cycle in captivity is completed in 4 to 6 months with adult weights between 0.4 and 2.2 kg; feeding rate is high. A variety of prey items, e.g. live fishes and crustaceans, is eaten, and late juveniles and adults also can be trained to accept and ingest prepared food pellets. Crowding in captivity can be a problem during the crucial juvenile phase, but it is tolerated afterwards; the incidence of disease and cannibalism is low; reproduction is easily achieved in captivity. All these biological characteristics make ***S. lessoniana*** promising for aquaculture projects focused on the needs of biomedical research as well as on human food production. Successful cephalopod mass-culture experiments in Thailand on 3 cephalopod species, including ***S. lessoniana***, have led to the production and release of a consistent amount of cephalopod paralarvae (about 2 million each year since 1990) to enhance natural stocks. Furthermore, ***S. lessoniana*** has been cultured through several successive generations in a large-scale, experimental culture system in Thailand. Marketable size is attained about four months after hatching, so the production of three crops annually is possible.

In the natural environment this species preys primarily on prawns and fishes, occasionally on stomatopods and crabs. Cannibalism is not very common.

Interest to Fisheries: ***Sepioteuthis lessoniana*** is of commercial interest throughout its distributional range, and it is marketed mostly fresh but also dried. Over it's entire range it is captured throughout the year with a variety of gears, including lure-hooks, set nets, spears, beach seines, purse seines, jigs and even traps (which they enter to spawn, attracted by the clusters of eggs placed in the traps by the fishermen) in inshore waters, and by trawlers on the continental shelf. Most squids in Japanese waters are caught by directed trawl fishery and also as a trawl bycatch. A directed purse seine fishery for ***S. lessoniana*** occurs from May to September around Hong Kong, where squid jigging also is efficiently practiced. The bigfin reef squid is one of the several loliginid species caught in the waters of the South China Sea, and it probably represents one of the main components of the captures in Indonesian waters, as evidenced by local studies. It also is one of the cephalopod species that supports a small domestic fishery in northern Australian waters. This species is highly abundant in the Gulf of Thailand and the Andaman Sea, where it represents one of the most important commercial species for the cephalopod fishery. It is caught in smaller quantities all along the east coast of India, and it supports a fishing industry in the Madras state. ***Sepioteuthis lessoniana*** accounts for around 7% of Indian east coast cephalopod landings, all from Palk Bay and the Gulf of Mannar. The species is reported as moderately abundant in Sri Lankan waters but rather scarce on the west coast of India. Very poor information is available for the remaining part of the Arabian Sea and the eastern African waters, although significant local fishery production is likely to occur.

Local Names: AUSTRALIA: Oval squid; CHINA: Daai mei yau yue; INDIA: Kanava; JAPAN: Aoriika, Akaika, Bashouika, Izuika, Kuaika, Kutsuika, Mizuika, Moika, Shiroika.

Remarks: Both morphological and molecular evidence indicate that ***S. lessoniana*** may be a complex of cryptic species, and a number of "types" are morphologically distinct, even in hatchlings. In Japan, local populations around the coast of Okinawa were long classified by the fisherman into three groups, based on their general appearance and meat quality and therefore market price (Okutani, 1984). Segawa *et al*., (1993a) suggested the existence of 2 different populations based on the difference between the egg capsules and the way these are laid. Subsequent isozyme analysis confirmed the existence of 3 reproductively isolated groups: Akaika (Red squid), Shiroika (White squid) and Kuaika (Quacking squid) (Izuka *et al*., 1994), which show different distributional patterns (Izuka *et al*., 1996a). In spite of their spatial segregation, it was impossible to separate the 3 populations morphologically until Izuka *et al*. (1996b) described different chromatophore patterns on the ventral side of funnel in the 3 "forms". Now, significant differences, mainly associated with the size, number and configuration of chromatophores on hatchlings, (Jivaluk *et al*., 2005) are recognized for the Thai type and the 3 Japanese forms. Okutani (2005) reports 3 different forms in his recent monograph on the cuttlefishes and squids of the world: 1) ***Sepioteuthis lessoniana*** *sensu stricto*, widely distributed throughout the Indo-Pacific, including the southern waters off Japan; 2) ***Sepioteuthis lessoniana*** form "Akaika", distributed in the Japanese waters south of Shikoku and the Nansei-Shoto Islands; 3) ***Sepioteuthis lessoniana*** form "Kwaika", in Japanese waters from the Ogasawara and the Nansei-Shoto Islands. Also, genetic evidence indicates that ***Sepioteuthis lessoniana*** from the northwestern waters off Australia may be a species complex (Triantafillos and Adams, 2005). Based on the above-mentioned observations, further studies need to be carried out to better understand the systematics of the Australasian and the Indo-Pacific forms of this valuable and important species. The complete mitochondrial genome of ***Sepioteuthis lessoniana*** has been determined (Akasaki *et al*., 2006).

Initial studies on the development of statoliths in embryos and hatchlings reared under different regimes of temperature, salinity and photoperiod indicate a variable number of growth increments under different environmental conditions; this result indicates the necessity to verify the hypothesis of daily growth increments being reflected in the rings of statoliths (Chung and Lu, 2005) in this species.

Literature: Okutani (1984), Roper *et al*. (1984), Segawa *et al*. (1993a), Dunning (1998d), Salman (2002), Okutani (2005), Jivaluk, *et al*. (2005), Nabhitabhata *et al*. (2005), Triantafillos and Adams (2005), Jereb and Roper (2006), Vecchione (2008j).

Uroteuthis Rehder, 1945

Uroteuthis Rehder, 1945, *Proceedings of the Biological Society of Washington*, 58:21–26, 1 plate. [21].

Type Species: *Uroteuthis bartschi* Rehder, 1945.

Diagnostic Features: Tentacular **clubs expanded**, with suckers in four series. Proximal margin of arm sucker rings with semi-crescent plate; distal margin with square teeth. Hectocotylus with two rows of papillae. Spermatophore cement body short. Eggs small. **Pair of photophores on ventral surface of ink sac**.

Size: Medium-sized squid; mantle length up to 200 mm.

Geographical Distribution: Indo-West Pacific Ocean.

Remarks: The pair of photophores on the ventral surface of the ink sac in all ***Uroteuthis*** species is perhaps the strongest indication of a close relationship among species to be found in this family. This relationship is further supported by similarities in the hectocotylus and arm-sucker dentition. These characters led Natsukari (1984a) to establish the genus ***Photololigo*** for the Indo-West Pacific species with photophores, formerly assigned either to ***Loligo*** or ***Doryteuthis***. However, ***Uroteuthis bartschi*** also has similar photophores, a similar hectocotylus and arm suckers, and an Indo-West Pacific distribution. The elongation of the posterior mantle, which was given generic status in the description of ***Uroteuthis***, is the extreme example in a cline of mantle elongation, similar to that found in the eastern Atlantic where ***Alloteuthis*** is the extreme example. This elongation is so extreme in ***Uroteuthis*** as to cause a discontinuity in the cline, which warrants separate taxonomic status, but the sole recognized species in this taxon possesses all of the generic characters of ***Photololigo***. Thus, it should be included in the genus that Natsukari described. However, nomenclatural priority belongs to ***Uroteuthis*** as the name of the genus, rather than the more descriptive ***Photololigo***. Aside from the photophores, ***Uroteuthis*** and ***Alloteuthis*** can be separated based upon position of the fins - lateral versus terminal, respectively - and tentacular ring dentition. Therefore, elongation of the posterior mantle in these 2 taxa appears to be analogous, not homologous (from Vecchione *et al*., 1998b, Vecchione, 2008k). Following the general consensus reached in Phuket in 2003, 15 nominal species, divided into 3 subgenera and 3 species with undetermined subgenus, are presently included in ***Uroteuthis*** (Vecchione *et al*., 2005); however, this generic and subgeneric arrangement is controversial. Yeatman (1993) and Yeatman and Benzie (1994) presented evidence that some species of ***Uroteuthis*** (***Photololigo***) actually are species complexes.

Since the type species of the formerly monotypic genus belongs to the subgenus ***Uroteuthis***, the subgenus ***Uroteuthis*** is treated first in this work.

Literature: Vecchione *et al*. (1998b), Vecchione *et al*. (2005), Vecchione (2008k).

Key to the subgenera of *Uroteuthis*

1a. Tail-like elongation of posterior mantle extends beyond fins . . . . ***Uroteuthis (Uroteuthis)***
1b. Elongation of posterior mantle variable but not tail-like, fins extend along sides to posterior mantle tip . . . . **→ 2**

2a. Modified portion of hectocotylus less than entire arm, proximal portion not modified . . . ***Uroteuthis (Photololigo)***
2b. Hectocotylus modified along entire arm . . . . ***Uroteuthis (Aestuariolus)***

Subgenus *Uroteuthis* Rehder, 1945

Uroteuthis Rehder, 1945, *Proceedings of the Biological Society of Washington*, 58:21–26, 1 plate. [21].

Type Species: *Uroteuthis bartschi* Rehder, 1945.

Uroteuthis (Uroteuthis) bartschi Rehder, 1945

Uroteuthis bartschi Rehder, 1945, *Proceedings of the Biological Society of Washington*, 58:21–26, 1 pl. [22, pl. 3]. [Type locality: Jolo Harbour, Jolo Island, Philippine Islands, western Pacific Ocean].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Bartsch's squid; **Fr** – Calmar tépo; **Sp** – Calamarete.

Diagnostic Features: Mantle very narrow, elongate, with **very long, pointed tail**; **more pronounced in males**. Fins rhomboidal, their lateral angles rounded, posterior borders concave, generally fins extend the entire length of tail (occasionally only as a minute membrane). Head relatively small, narrow. **Arm suckers with broad, plate-like teeth in the distal margin, smooth proximally**. Large medial tentacular club suckers with long, square-tipped teeth. **Left ventral arm hectocotylized in distal half** by abrupt transformation of suckers into long, stout papillae.

Size: Medium-sized squid; maximum mantle length 200 mm.

Geographical Distribution: Western Pacific Ocean: in Philippine and Indonesian waters (Fig. 134).

Habitat and Biology: Upper and lower limit of depth distribution undetermined.

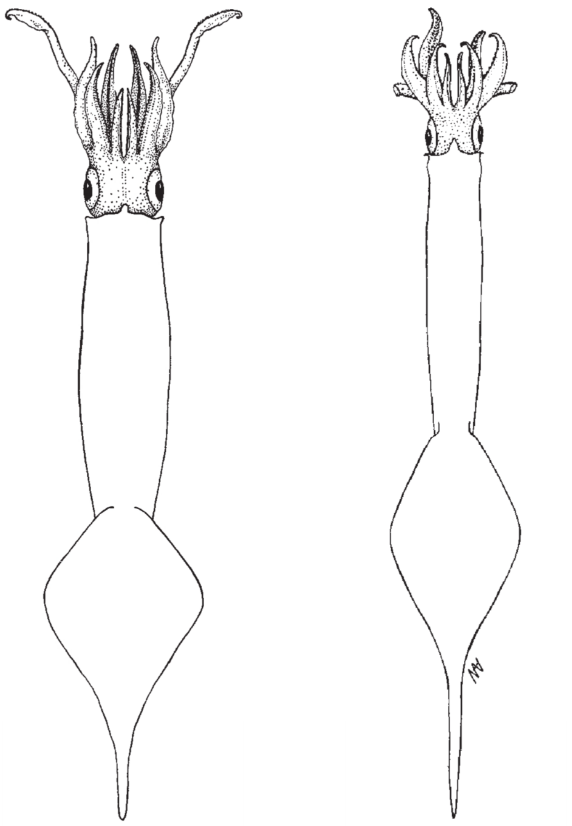
Interest to Fisheries: Taken as bycatch in local trawl fisheries. Utilized mostly fresh.

Local Names: None available.

Remarks: None.

Literature: Roper *et al.* (1984), Dunning (1998d).

Fig. 133



dorsal view of female dorsal view of male

Fig. 133 *Uroteuthis (Uroteuthis) bartschi*

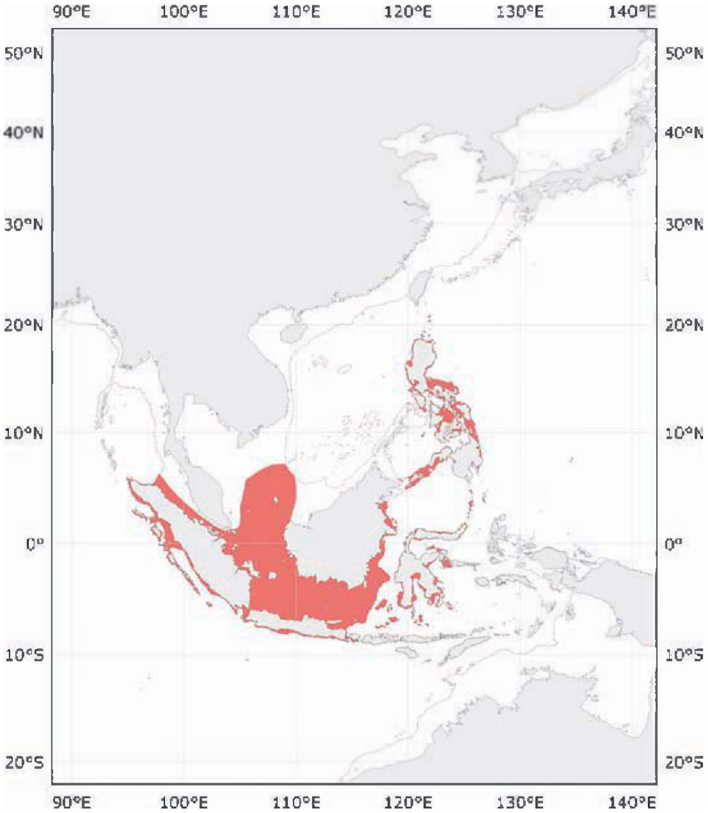


Fig. 134 *Uroteuthis (Uroteuthis) bartschi*

🟥 Known distribution

Subgenus ***Aestuariolus*** Alexeyev, 1992

Aestuariolus Alexeyev, 1992, *Zoologicheskij Zhurnal*, 71(11):12–23, 2 figures. [21].

Type Species: *Aestuariolus noctiluca* (Lu, Roper, and Tait, 1985).

Uroteuthis (Aestuariolus) noctiluca (Lu, Roper, and Tait, 1985) **Fig. 135**

Loliolus noctiluca Lu, Roper, and Tait, 1985, *Proceedings of the Royal Society of Victoria*, 97(2): 59–85. [59, figs 1–6]. [Type locality: North Port Phillip Bay, Australia].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Luminous bay squid; **Fr** – Calmar lumineux; **Sp** – Calamar luminoso.

Diagnostic Features: Mantle cylindrical; mantle width about 28 to 30% mantle length. **Fins roundish**. Arms short; arm sucker rings with 4 to 7 teeth. Tentacles relatively short, robust, **clubs large, broadly expanded; medial manal suckers 3 to 6 times** the diameter of marginal manal suckers; large manal-sucker rings smooth. **Left ventral arm of males hectocotylized along the entire length**; suckers modified into conspicuous elongate interconnected papillae with minute apical suckers.

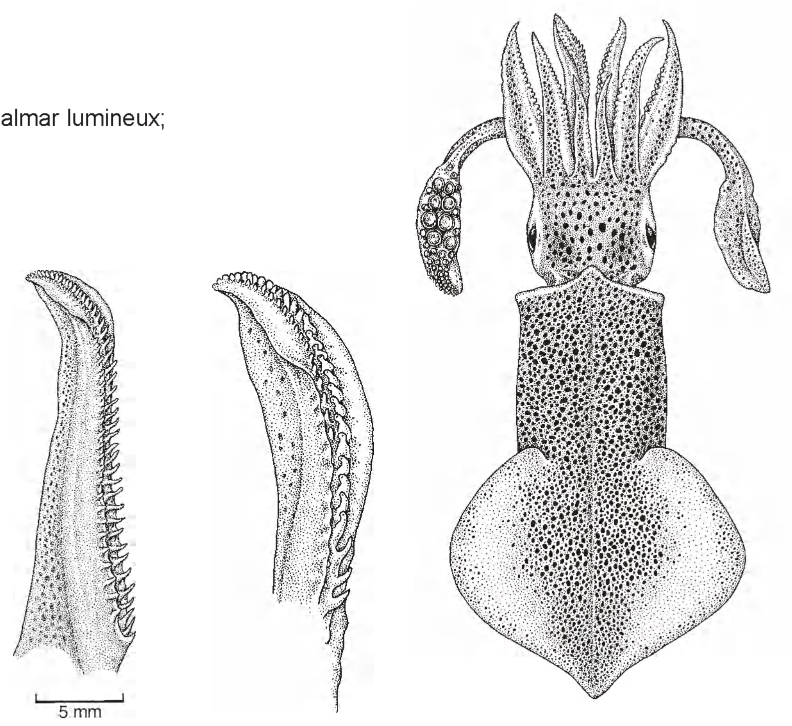
Size: Small-sized squid; maximum reported mantle length 90 mm.

Geographical Distribution: Australian waters from the Gulf of Carpentaria, along the eastern Australian coast, south to Tasmania (Fig. 136).

Habitat and Biology: This species occurs in shallow coastal habitats on sandy bottoms with seagrass beds, to depths of about 50 m. It can enter estuarine water with bottom-water salinities as low as 24 PSU, surface salinities as low as 17 PSU and a temperature of approximately 11°C. A short-lived species, it can complete its life cycle in northern Australian waters in less than 4 months; here, winter-caught individuals show faster growth than summer- or autumn-caught individuals. Also, females grow faster than males during winter. A comparison between tropical North Queensland and the temperate New South Wales populations indicates that temperate individuals live longer and have slower growth rates than tropical forms. Females grow larger than males.

Interest to Fisheries: Caught incidentally in inshore prawn trawls along the northeastern Australian coast.

Local names: AUSTRALIA: Bottle squid.



hectocotylus hectocotylus tip dorsal view

Fig. 135 *Uroteuthis (Aestuariolus) noctiluca*

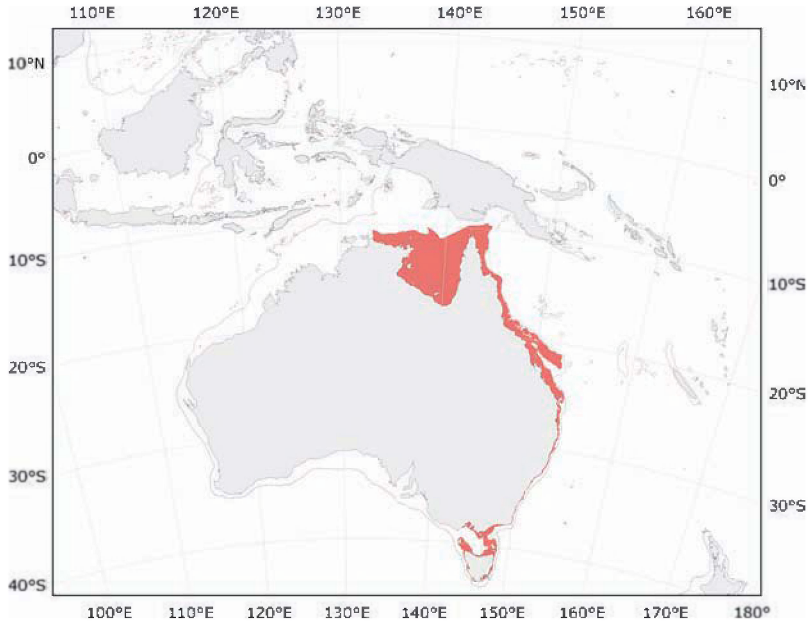


Fig. 136 *Uroteuthis (Aestuariolus) noctiluca*

🟥 Known distribution

Remarks: This species may be confused with juveniles of other, larger, more commercially important species from which it can be separated by fin shape and, in freshly caught specimens, by the presence of yellow and pink chromatophores on the fin margins and mantle. Two forms exist on the eastern Australian coast, with males differing by the sucker rings on right ventral arms. However, no difference in females is known. The luminous bay squid appears to be the ecological equivalent to ***Lolliguncula brevis***. Similar in body size and shape, they both inhabit shallow inshore waters and are highly tolerant of salinity and temperature variations, an unusual characteristic among cephalopods.

Literature: Lu *et al*. (1985), Dunning (1998d), Okutani (2005).

Subgenus ***Photololigo*** Natsukari, 1984

Photololigo Natsukari, 1984a, *Venus, Japanese Journal of Malacology*, 43: 229–239. [230].

Type Species: *Photololigo edulis* Hoyle, 1885.

Uroteuthis (Photololigo) edulis (Hoyle, 1885) **Fig. 137; Plate VI, 33**

Loligo edulis Hoyle, 1885a, *Annals and Magazine of Natural History*, Series 5 (16):181–203. [186]. [Type locality: purchased in market, Yokohama, Japan].

Frequent Synonyms: *Doryteuthis kensaki* Wakiya and Ishikawa, 1921, Okutani, 1973, *Loligo budo* Wakiya and Ishikawa, 1921, Okada, 1927a, Roper *et al*., 1984, Nesis, 1982, Okutani *et al*., 1987, *Loligo chinensis*, Sasaki, 1914, Wakiya and Ishikawa, 1921, non Gray, 1849, *Loligo edulis*, Hoyle, 1885, as form *grandipes* and *nagasakiensis*, Sasaki, 1929, *Loligo kensaki* Wakiya and Ishikawa, 1921, *Loligo singhalensis*, Adam, 1954 (fide Korzun and Alekseyev, 1991), non Ortmann, 1891.

Misidentifications: *Uroteuthis sibogae*, *Uroteuthis (Photololigo) chinensis*.

FAO Names: En – Swordtip squid; **Fr** – Calmar épée; **Sp** – Calamar espada.

Diagnostic Features: Mantle moderately stout, elongate, slender in mature males. **Fins rhombic, attain 70% of mantle length** in adults, anterior margin slightly convex, posterior margin gently concave, lateral angles rounded; fins slightly longer than wide in adults, width 60% of mantle length (usually slightly larger in females). Gladius long, moderately narrow, about 6 to 7 times longer than wide; vanes distinctly curved laterally; free rachis length about 20% of gladius length. Arms moderately long, 25 to 45% of mantle length. Arm formula variable: 3>4>2>1 or 4>3>2>1. **Suckers on arms II and III of mature males noticeably enlarged** as a secondary sexual character (Brakoniecki, 1986). Arm sucker rings with up to 12 (more often 6 to 8) long, slender, square-cut (bluntly-pointed) teeth on the distal margin; the proximal margin smooth or only irregularly denticulate with inconspicuous teeth. Tentacles moderately long, slender; tentacular clubs expanded, lanceolate; about 16 medial manal suckers slightly larger than the marginal suckers, approximately equal in diameter to largest arm suckers, with 30 to 40 sharp conical teeth, 20 to 30 small teeth interspersed between 10 large teeth. **More than 50% of left ventral arm** (up to 65 to 80%, Jereb and Roper 2006), **hectocotylized** by enlargement of at least 50 pairs of sucker stalks into swollen papillae, each with a minute rudimentary sucker on the tip; papillae slightly larger in ventral series. **Mature males have a cutaneous ridge on their ventral mantle surface**.

Size: Medium to large sized squid; maximum mantle length 502 mm for males, 410 mm for females; common size in commercial catches between 150 and 250 mm.

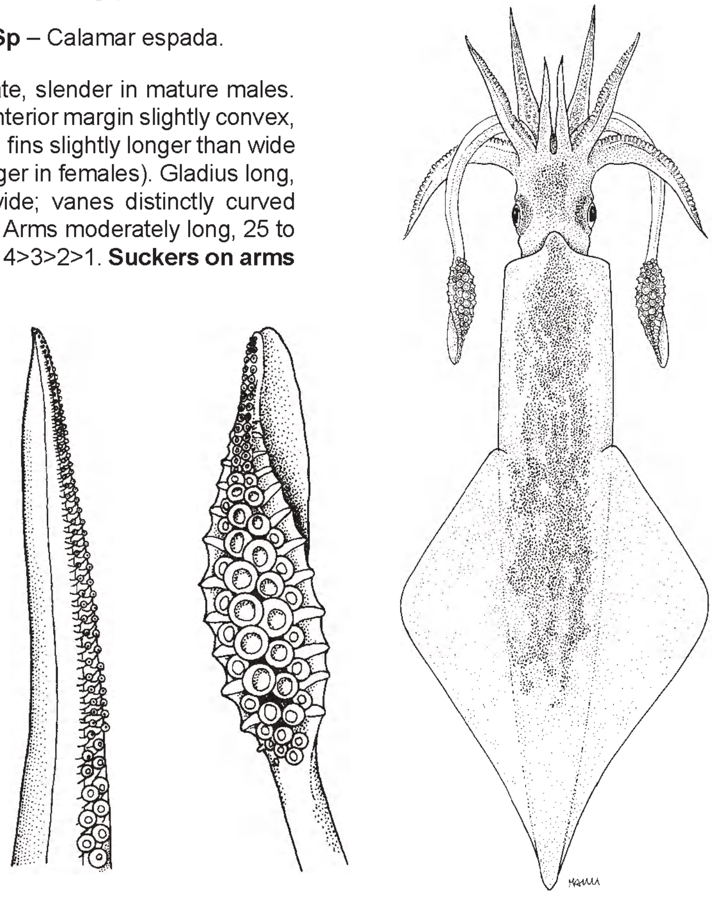

hectocotylus **tentacular club** **dorsal view**

Fig. 137 ***Uroteuthis (Photololigo) edulis***

Geographical Distribution: An Indo-Pacific species, ***Uroteuthis edulis*** is common and relatively abundant in the western Pacific, from its northern waters (East China Sea, Japan Sea) to tropical seas (Indonesia, Java Sea, Malaysia, Thailand), south to northern Australia. The distribution of ***U. edulis*** also extends throughout the Indian Ocean, from its southeastern waters, i.e. the Andaman Sea, Thailand, and the southeastern Bay of Bengal, to the Arabian Sea, including the Gulf of Aden, the Gulf of Oman, and the Persian Gulf, the Red Sea, and southward to Mozambique (East African coast, Saya de Malha Bank) (Fig. 138).

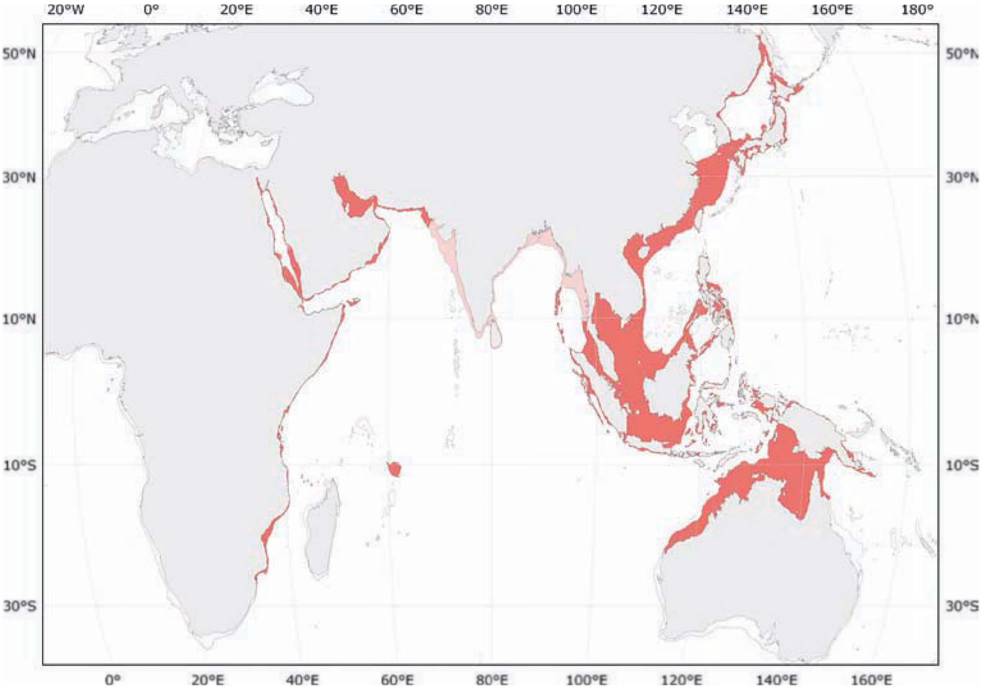


Fig. 138 ***Uroteuthis (Photololigo) edulis***

🟥 Known distribution ▨ Probable presence

Habitat and Biology: ***Uroteuthis edulis*** inhabits continental shelf waters in Japan and winters inshore in shallow water. Although reported as one of the most oceanic species of the Japanese loliginids, it does not occur in the waters beyond the continental shelf.

The spawning season extends throughout the year, with 3 main peaks in spring, summer and autumn. Spawning and feeding migrations occur in the western region of the Japan Sea. The size at which individuals become sexually mature is very variable, depending on the season and locality. Most specimens of both sexes reach full maturity by 150 to 200 mm mantle length. The smallest size recorded for full maturity was 52 and 59 mm mantle length for males and females, respectively, while some specimens were not sexually mature at a size larger than 300 mm mantle length. Spawning occurs from 30 m down to 100 m, on sandy bottoms in coastal waters where warm oceanic currents inflow. Data from northern Australia support an extended spawning season for the species and show that in the Gulf of Carpentaria it reaches sexual maturity at smaller sizes (70 to 80 mm mantle length) than in the northern waters of the western Pacific. On the northwestern side of the Indian Ocean it also reaches sexual maturity at a small size, 70 to 80 mm mantle length or even smaller, 50 to 60 mm mantle length. The spawning period extends from autumn to spring or even to the beginning of summer.

Juveniles feed preferentially on crustaceans, while adults are mainly piscivorous. The life span is about one year. Length-weight relationships obtained for the species in different seasons and locations of the northwestern Pacific indicate a highly variable growth depending on season and area.

Interest to Fisheries: ***Uroteuthis edulis*** has excellent flesh quality, and it is exploited throughout its distributional range. One of the principal commercial squid species of the Japanese market, it constitutes one of the most important resources for the coastal fisheries of Kyushu and the southwestern Japan Sea. It is caught throughout the year by jig, set net, bottom trawl and other gears. This species is very abundant in the Yellow and East China Seas, and in the northern waters of Taiwan (Province of China), where, together with ***U. chinensis***, it is believed to account for the majority of the Chinese squid catch; it is vigorously exploited by the Hong Kong fishery and it is believed also to be rather abundant in the South China Sea. Fished also in Malaysian waters, it is not mentioned, however, among the squid resources of Thai waters in the Gulf of Thailand. It is one of the main species of the Philippine and Indonesian fisheries and constitutes one of the most important commercial cephalopod species in northern Australian waters. Highly abundant in the Andaman Sea, where it represents one of the main Thai squid resources, it is not mentioned among the cephalopod resources of India. Its apparent absence from Indian waters probably is a matter of misidentification rather than of disjunct distribution. The presence of this species in the western Indian Ocean (i.e. Arabian Sea, Red Sea, East African waters) is confirmed; however, its potential to the fishery there is still unknown. This species is sold at high prices both fresh and frozen, processed into a dried product and also used for sashimi in Japan.

Local Names: CHINA: Tor yau yue; JAPAN: Gotouika, Kensakiika, Mawashikko (juveniles), Mehikariika.

Remarks: ***Uroteuthis edulis*** is characterized by a marked polymorphism, both by locality and by season. The existence of such a variety of "forms", the taxonomic relationships of which still are not clear, makes the confident identification of the species and the assessment of populations (stocks) difficult. After the original description by Hoyle (1885a), who referred to 1 male specimen from the Yokohama Fish Market (Japan), the condition of maturity of which was not specified, the species was repeatedly redescribed by subsequent authors (see Jereb and Roper, 2006 for a review). While there is still no general consensus on the status of the species complex, at least 3 different seasonal 'forms' are indicated for the Indian Ocean and the northwestern Pacific: form ***'budo'***, form ***'edulis'*** and form ***'kensaki'*** (Nesis, 1982, 1987, Natsukari and Tashiro, 1991, Natsukari *et al*., 1986, 1988, Okutani, 2005). While form "***budo***" is characterized by very large clubs, long arms and large suckers in comparison with the typical ***U. edulis***, the 2 other forms differ essentially in the structure of the hectocotylized arm: a) 7 or 8 pairs of normal suckers at the base of the arm, no small suckers on the papillae of the modified portion (form "***edulis***"), versus b) 20 to 27 pairs of normal suckers and rudimentary suckers on the papillae of the modified portion (form "***kensaki***"). Also, fin length in adults differ: they occupy up to 50 % of the mantle length in form "***edulis***", while they reach up to 70% of the mantle length in form "***kensaki***" (Okutani, 2005).

In Australian waters, four different species of ***Uroteuthis (Photololigo)*** from the northern area were identified using allozymes (Yeatman and Benzie, 1994). Two of these species fit the gross morphology of ***U. edulis*** from Japan, while the other 2 share the distinguishing features of ***U. chinensis***. However, no major population genetic structuring was evident in any of the species over the geographical range sampled. It was suggested that depth constraints, or factors associated with depth, may act as effective barriers to gene flow and, therefore, provide mechanisms for allopatric differentiation in this genus. All these observations support the opinion that widely distributed loliginid species, such as ***U. edulis***, may in fact represent a series of morphologically similar sibling species; also, they underline the need for more detailed observations, information and clarification on ***U. edulis*** throughout the Indian Ocean, especially because of its well-documented importance as a fisheries resource in the western Pacific (Jereb and Roper, 2006).

Literature: Voss (1973), Chikuni (1983), Roper *et al*. (1984), Natsukari and Tashiro (1991), Okutani (2005), Jereb and Roper (2006).

Uroteuthis (Photololigo) abulati (Adam, 1955)

Fig. 139

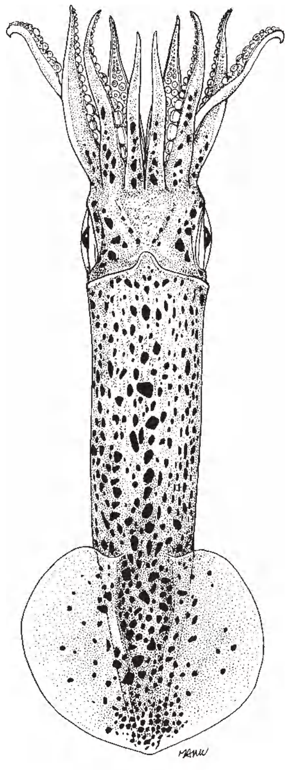
Loligo abulati Adam, 1955, *Annales de l'Institut Océanographique*, 30:185–194, 1 pl. [185, pl 50 fig 1]. [Type locality: Ile Abulat, Saudi Arabia, Red Sea].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Red Sea squid; **Fr** – Calmar de la Mer Rouge; **Sp** – Calamar del Mar Rojo.

Diagnostic Features: Mantle slender, mantle width about 25% mantle length. Fin length and width both up to 40% mantle length. **Fourth to sixth suckers on arms II enlarged; sixth and seventh suckers on arms III enlarged**. Chitinuous sucker rings with 5 to 7 quadrangular teeth on distal margin, proximal margin smooth. Hectocotylized arm with 6 pairs of proximal suckers, followed by biserial papillae to distal end. Chitinous rings of tentacular suckers with about 20 sharp teeth.



dorsal view

Fig. 139 ***Uroteuthis (Photololigo) abulati***

Geographical Distribution: Red Sea (Fig. 140).

Remarks: After a general consensus was reached in Phuket in 2003 by worldwide experts on the loliginid family re-organization (Vecchione *et al*., 2005), the status of this species was questioned (Roeleveld, pers. comm.) on the basis of new studies which suggest ***Uroteuthis abulati*** is closely related to ***Afrololigo mercatoris***. However, this species is too poorly known at present to enable a determination of specific status; therefore, the species is retained herein as it was designated by Vecchione *et al*. (2005).

Literature: Adam (1955) Okutani (2005), Vecchione *et al*. (2005).

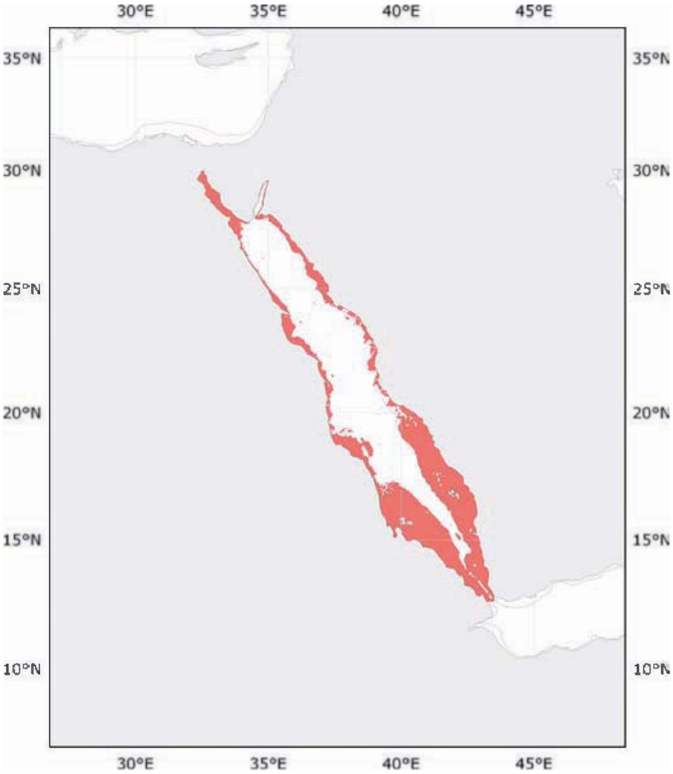


Fig. 140 ***Uroteuthis (Photololigo) abulati***

🟥 Known distribution

Uroteuthis (Photololigo) arabica (Ehrenberg, 1831)

Pteroteuthis arabica Ehrenberg, 1831, *in* C.G. Ehrenberg, 1828–1845. *Symbolae Physicae, seu Icones et descriptiones Corporum Naturalium novorum aut minus cognitorum... P.C. Hemprich et C.G. Ehrenberg... Pars Zoologica*, [4]: 6, unnumbered pages. Berlin. [Type locality: Red Sea].

Frequent Synonyms: None.

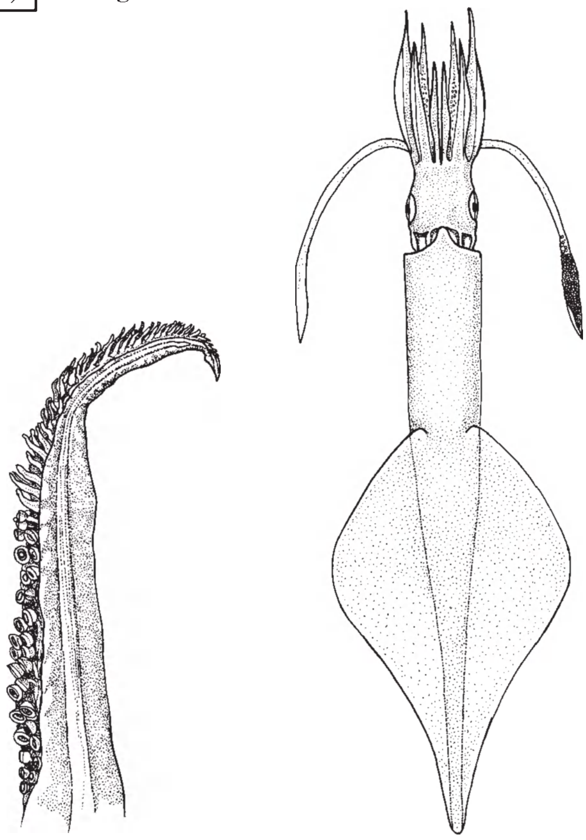
Misidentifications: None.

FAO Names: En – Needle squid; **Fr** – Calmar aiguille; **Sp** – Calamar aguja.

Diagnostic Features: Mantle long, narrow. **Mantle width about 20% mantle length (minimum 12%)**. Fin length commonly 60 to 65% mantle length. Fin width in adults 33 to 50% mantle length. Edges of gladius thickened, almost straight. **Club sucker rings with 20 to 40 teeth alternating in size between large and small**. Arm sucker rings with 18 to 24 blunt teeth distributed all around the ring. Hectocotylized arm with 15 proximal pairs of normal suckers followed by fine, dense biserial papillae distally.

Size: Medium-sized squid, mantyle length up to 270 mm.

Fig. 141



hectocotylus **dorsal view**

Fig. 141 ***Uroteuthis (Photololigo) arabica***

Geographical Distribution: Gulf of Aden, Red Sea, Mozambique (Fig. 142).

Habitat and Biology: None available.

Interest to Fisheries: Currently, no data available.

Local names: None available.

Remarks: None.

Literature: Ehrenberg, 1831, Okutani, 2005.

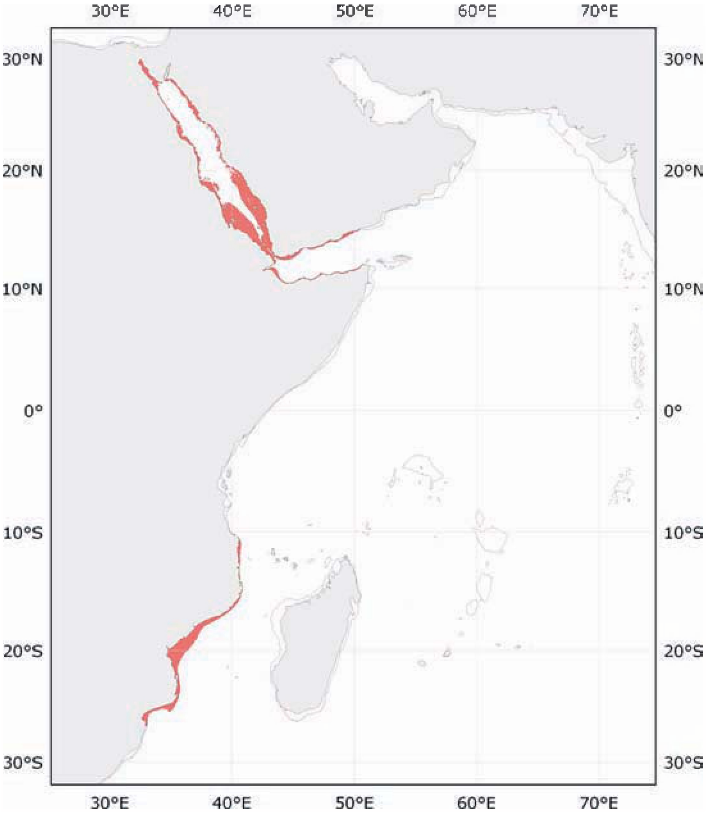


Fig. 142 ***Uroteuthis (Photololigo) arabica***

🟥 Known distribution

Uroteuthis (Photololigo) bengalensis (Jothinayagam, 1987)

Loligo bengalensis Jothinayagam, 1987, *Zoological Survey of India, Technical Monograph*, 15:1–85 [48, text; fig 17, pl 3]. [Type locality: Bay of Bengal].

Frequent Synonyms: None.

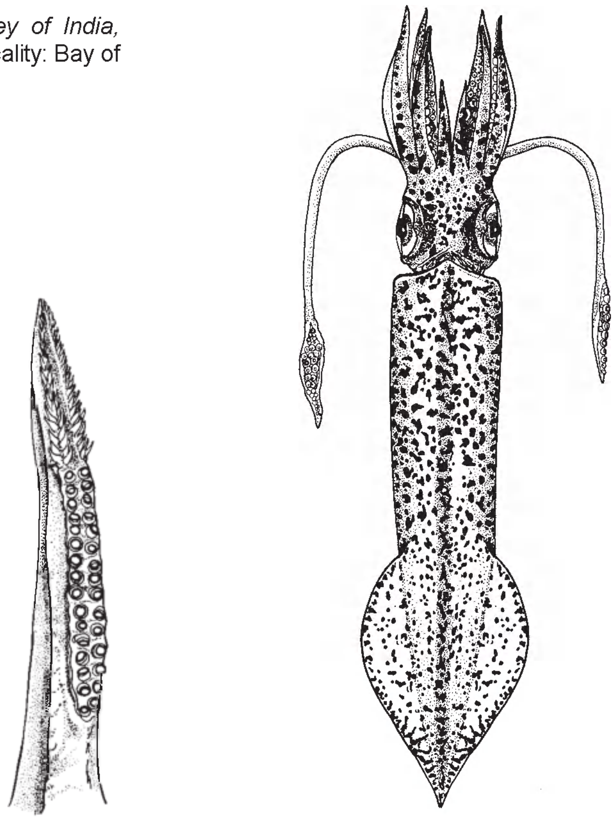
Misidentifications: *Uroteuthis chinensis*, *Uroteuthis singhalensis*.

FAO Names: En – Bengal squid; **Fr** – Calmar du Bengala; **Sp** – Calamar del Bengala.

Diagnostic Features: Mantle narrow, slender, pointed at posterior end; mantle width about 23% mantle length. Vane of galdius broadest at anterior area; **vane without thickened edges**. **Fins short and narrow; fin angle very low (about 30°)**. Tentacle long, club narrow. **Large and small teeth alternate along distal portion** of tentacular club sucker rings, whereas along proximal portion teeth are small and subequal. Male left IV arm hectocotylized: 15 to 16 pairs of normal suckers in proximal two-thirds, sucker pedicels swollen and transformed into biserial papillae in the distal third.

Size: Medium-sized squid; mantle length to 150 mm.

Fig. 143



hectocotylus **dorsal view**

Fig. 143 ***Uroteuthis (Photololigo) bengalensis***

Geographical Distribution: Bay of Bengal (Fig. 144).

Habitat and Biology: No data available.

Interest to Fisheries: Currently unknown.

Local Names: None available.

Remarks: This species is separable from other sympatric squids, in particular from ***Uroteuthis singhalensis***, by the different shape and size of the fins, by sucker teeth configuration and by the gladius vane devoid of thickened edges (Jothinayagam, 1987).

Literature: Jothinayagam, 1987, Okutani, 2005.

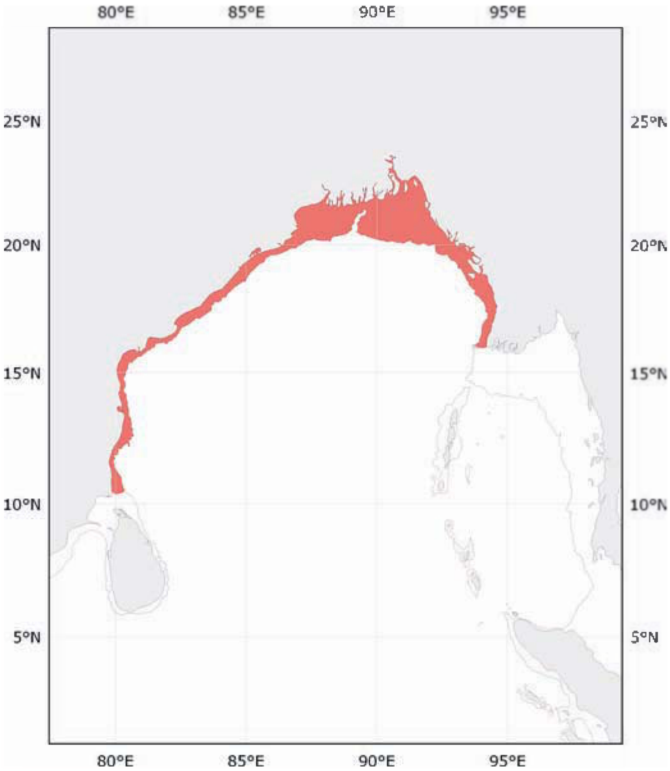


Fig. 144 ***Uroteuthis (Photololigo) bengalensis***

🟥 Known distribution

Uroteuthis (Photololigo) chinensis Gray, 1849

Fig. 145

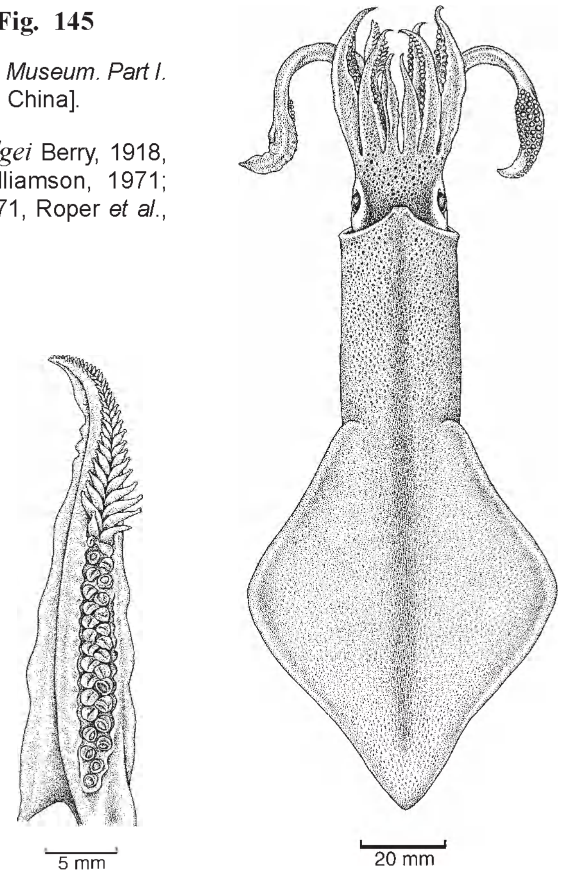
Loligo chinensis Gray, 1849, *Catalogue of the Mollusca in the British Museum. Part I. Cephalopoda Artepedia*, 164 pp. [74]. [Type locality: Canton market, China].

Frequent Synonyms: *Loligo indica* Hoyle, 1886; *Loligo etheridgei* Berry, 1918, Adam, 1954; *Loligo formosana* Sasaki, 1929, Voss and Williamson, 1971; *Doryteuthis singhalensis*, Voss, 1963a, Voss and Williamson, 1971, Roper *et al*., 1984, Silas, 1986; *Loligo singhalensis*, Okutani, 1980.

Misidentifications: None.

FAO Names: En – Mitre squid; **Fr** – Calmar mitre; **Sp** – Calamar mitrado.

Diagnostic Features: Mantle elongate, slender, bluntly pointed posteriorly. Mantle width about 20 to 30% of mantle length, widest in its anterior part. A cutaneous ridge may be present or absent on the ventral surface of mantle in adult males. Fins rhombic, long, over two-thirds of mantle length. Gladius rather narrow: gladius width 6 to 8% of gladius length. Edges of gladius arched, not thickened. **About 12 medial manal suckers of tentacular clubs enlarged to one and a half times the diameter of the lateral suckers and 2 times the largest arm sucker**; large rings with 20 to 30 sharp, separate teeth **very unequal in size: 6 to 12 larger ones usually interspersed with 1 to 4 smaller ones**. Larger sucker rings of lateral arms with 10 to 18 sharp teeth distally, smooth or with a few plate-like teeth proximally; left ventral arm hectocotylized at distal one-third to one-half (hectocotylized arm index, HcLI, up to 70%) by modification of more than 30 suckers and stalks in each series into slender, conical papillae that are larger in the ventral series. **A secondary sexual modification of enlarged proximal suckers on arms II and III in mature males**.



hectocotylus tip **dorsal view**

Fig. 145 ***Uroteuthis (Photololigo) chinensis***

Size: Large-sized species; maximum reported size 490 mm mantle length for males, 310 mm for females (as ***Doryteuthis singhalensis***); commonly to 200 mm mantle length.

Geographical Distribution: An Indo-Pacific species, extending from the western Pacific (Japan, South China Sea, Hong Kong, Philippines, Indonesia, northern, western and eastern Australian waters), to the Indian Ocean (Andaman Sea, Thailand and the Bay of Bengal) (Fig. 146).

Habitat and Biology: The biology of the species still is poorly known, and most basic biological information is lacking. Found from approximately 15 to 170 m depth, like many other congeneric species, ***U. chinensis*** is positively phototactic and forms large aggregations at certain periods of the year. Spawning occurs throughout the year, but peaks are observed in spring and autumn (February to May-June and August to November). Fecundity varies from 3 000 to 11 000 eggs. Mantle length at 50% maturity is 160 and 140 mm mantle length for males and females, respectively. Age analyses suggest that maturity is governed more by individual size than by age. This is one of the largest loliginid species of the Indo-Pacific region. It feeds on a variety of fishes and crustaceans.

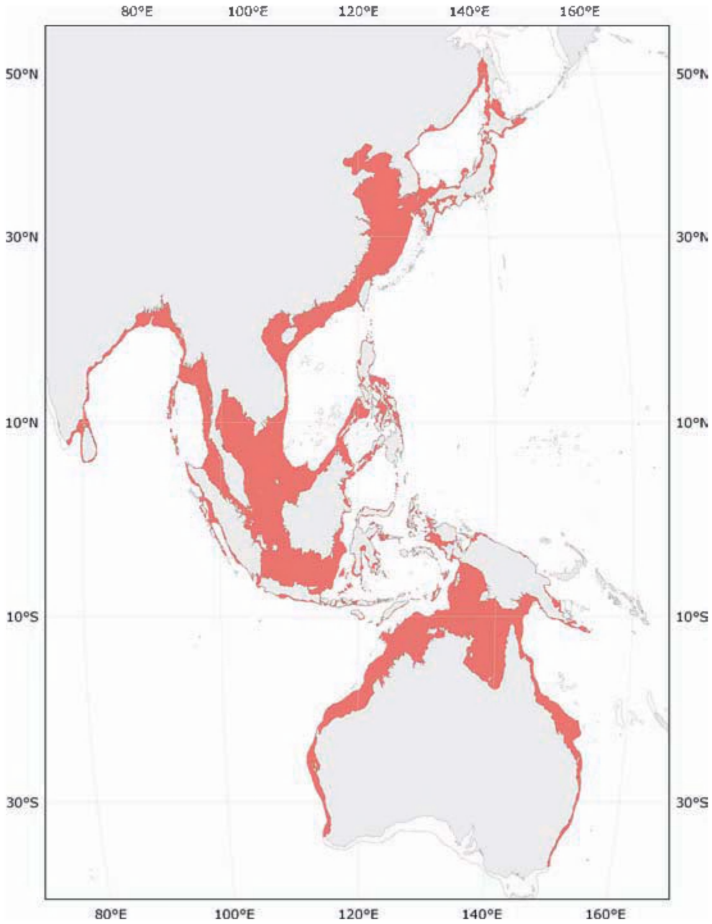


Fig. 146 ***Uroteuthis (Photololigo) chinensis***

🟥 Known distribution

Interest to Fisheries: ***Uroteuthis (Photololigo) chinensis*** is a target species or a welcome bycatch of numerous commercial and small-scale fisheries throughout its range. It is reported to be exploited currently in the Yellow Sea and the East and South China Seas, and it probably constitutes, together with ***U. edulis***, the majority of the Chinese squid catch. It is extensively exploited by the Hong Kong fishery and Taiwanese trawlers. Of occasional commercial relevance in Japanese waters, ***U. chinensis*** is likely to represent a small part of the squid catch around the Philippine Islands, as well, and it constitutes about half of the trawl catch of squid in the South China Sea. It is also likely to constitute a substantial portion of the catch in the Malaysian waters, where it is reported as the dominant squid species for some local fisheries. It is probably well represented in the Indonesian fisheries (Arafura Sea, Java Sea), and is one of the most important commercial cephalopod species in Northern Australian waters, where it is taken also by Taiwanese trawlers, along with ***U. singhalensis***. It is one of the major squid species in the Gulf of Thailand, where it is taken in waters between 15 and 30 m depth and amounts to between 15 and 40% of the trawl catch. Concurrently with the decrease of finfish catches in that area, squids have become an increasingly important resource since the mid-1960s and early 1970s and even during recent problems with overfishing, loliginid squid still are abundant in Thai waters. Catches also occur in other countries that border the Bay of Bengal (Thai coasts, Andaman Sea), and ***U. chinensis*** it is reported among the commercially exploited squid species of India and Sri Lanka. This species is captured with a variety of gears, various bottom trawls, purse seines, dip-, and cast nets, hook-and-line, scoop nets, and bamboo stake nets, sometimes involving light attraction with torches and lamps. Usually it is marketed dried, but also it is sold fresh or frozen, processed into cleaned “hoods” and rings.

Local Names: CHINA: Tor yau yue; JAPAN: Hirakensakiika.

Remarks: Following its original description, this species has been redescribed several times under different names, as summarized by Natsukari and Okutani (1975), who also give a redescription of the type-specimen, along with a taxonomic review. The long-term confusion inherent in the convoluted regional loliginid nomenclature makes it very difficult to assess the true importance of ***U. chinensis*** *sensu stricto* to the fisheries, and it seems probable that it is under-reported, at least in the westernmost areas of its range. For example, it is assumed to be present in the Arabian Sea (Chikuni 1983, Siraimeetan 1990, as ***Doryteuthis singhalensis***), but it is not clear to what extent these records are due to confusion in the loliginid nomenclature. As is the case with other congeners, it is now acknowledged that specific investigations are needed to clarify a potential species complex among squids currently considered to be ***U. chinensis*** throughout the tropical Indian and western Pacific Ocean (e. g. Yeatman and Benzie, 1994). Recent studies indicate that extracts from ink of ***U. chinensis*** show potent antitumor activity and low toxicity (Su *et al*., 2005).

Literature: Voss (1963a), Natsukari and Okutani (1975), Natsukari (1984a), Natsukari and Tashiro (1991), Chotiyaputta (1993a, b), Jackson (1993), Chantawong and Suksawat (1997), Dunning (1998d), Jereb and Roper (2006).

Uroteuthis (Photololigo) duvaucelii (Orbigny, 1835)

Fig. 147

Loligo duvaucelii D'Orbigny, 1835 *In* Ferussac and D'Orbigny, 1834–1848, *Histoire Naturelle Generale et Particuliere Cephalopodes Acetabuliferes Vivants et Fossiles*, 361 pp, Atlas of 144 Plates. [318, Calamar pls 14, 20]. [Type locality: India].

Frequent Synonyms: *Loligo indica* Pfeffer, 1884, Goodrich, 1896, Massy, 1916; *Loligo galatheae* Hoyle, 1885a; *Loligo oshimai* Sasaki, 1929; *Loligo sumatrensis*, Brock, 1887.

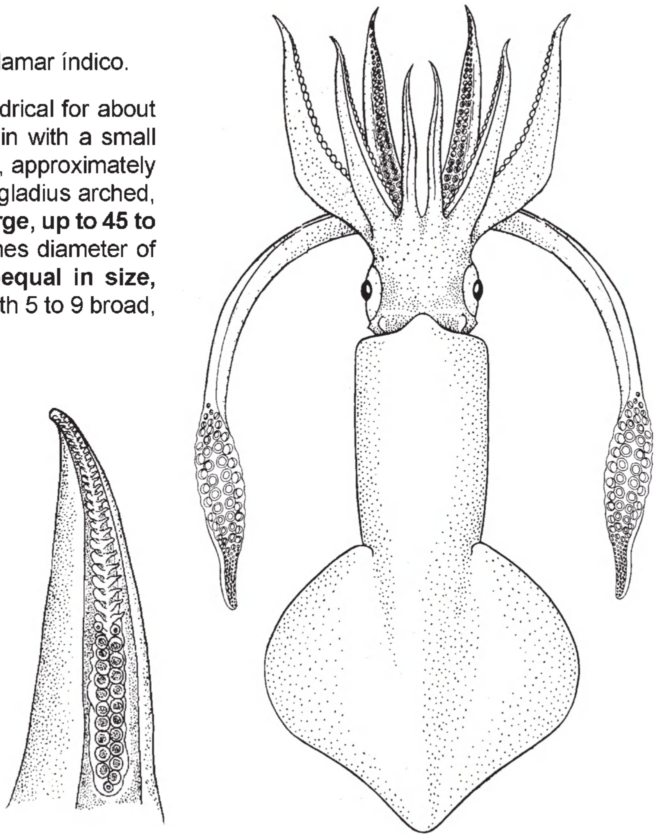
Misidentifications: None.

FAO Names: En – Indian squid; **Fr** – Calmar indien; **Sp** – Calamar índico.

Diagnostic Features: Mantle moderately long, slender, cylindrical for about half its length; it tapers gently into a blunt tip. Anterior margin with a small rounded lobe in the dorsal midline. Fins gently rhombic, broad, approximately 50% of mantle length (up to 60% of mantle length). Edges of gladius arched, not thickened. Tentacles long; **tentacular clubs expanded, large, up to 45 to 50% of mantle length**; large median manal suckers, (<2 times diameter of marginal suckers), **with 14 to 22 short, sharp teeth, subequal in size, regularly spaced around the entire margin.** Arm suckers with 5 to 9 broad, large, square teeth on the distal margin in females and up to 18 teeth around the entire ring in males. Left ventral arm of male hectocotylized for more than half its length (up to 75%), with two series of large papillae, some with minute suckers on tips; ventral series of papillae larger, turned outward, comb-like.

Size: Medium-sized species; maximum reported size 320 mm mantle length from Thai waters and 330 mm mantle length along the west coast of India, for males; commonly to 150 mm mantle length. Maximum weight 1.5 kg.

Geographical Distribution: An Indo-West Pacific species, ***Uroteuthis duvaucelii*** extends its distribution throughout the Indian Ocean, from the South African coasts (Kei River, South Africa; Mozambique), the Red Sea and the Arabian Sea, eastward to the Bay of Bengal, Sri Lanka and the Andaman Sea. A common Malaysian squid (Sumatra, Malaysia, Thailand), ***U. duvaucelii*** also is very abundant in Philippine waters and moderately abundant in the South China Sea, having been recorded in the West Pacific north to Formosa Island and the Taiwan Strait and south to the Java and Arafura Seas (Fig. 148).



hectocotylus **dorsal view**

Fig. 147 ***Uroteuthis (Photololigo) duvaucelii***

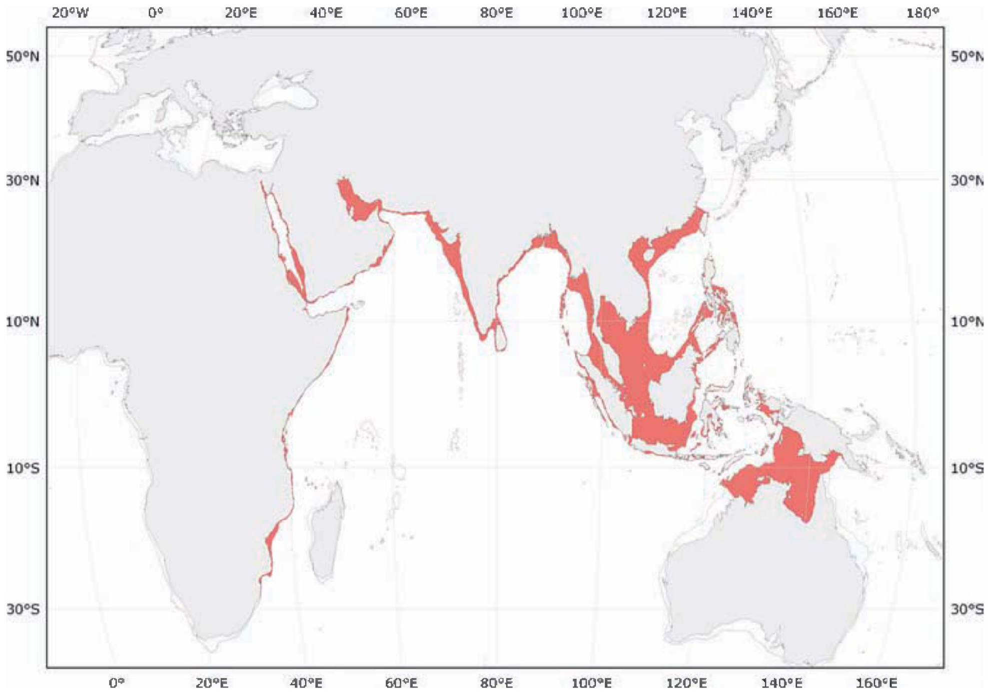


Fig. 148 ***Uroteuthis (Photololigo) duvaucelii***

🟥 Known distribution

Habitat and Biology: Considerable attention has been paid to the biology of this species, due to its importance in the fisheries in Indian (both west and east coasts) and Thai waters. ***Uroteuthis duvaucelii*** occurs at depths between 30 and 170 m, and it forms large aggregations during the spawning season.

The spawning period appears to be prolonged, almost year-round, with peaks in different months, principally in spring and autumn. Spawning aggregations occur in the post-monsoon months along the west coasts of India, and spawning seems to be dependent on the southwest and northeast monsoons in the western part of the Gulf of Thailand. Size at 50% maturity ranges between 90 and 130 mm mantle length for females and 70 to 150 mm mantle length for males. Observations on growth after sexual maturity is reached support an extended reproductive phase within the life cycle, i.e. not a strictly semelparous reproduction, as it is the case in other squid. Egg mops (masses) consist of many egg capsules, each of which, in turn, contains 125 to 290 eggs. Eggs are about 2 mm long and 1.75 mm wide and very yolky. Eggs take between 7 and 10 days to develop at a temperature range between 28° to 32°C. Hatchlings are about 1 to 1.8 mm mantle length and are planktonic.

Growth is allometric; females grow faster than males and are heavier at the same length; however, males ultimately attain a greater size and age. Maximum reported size is 330 mm mantle length from Indian waters. According to statolith-based age analysis, the life cycle of the species is one year, which is shorter than estimates obtained by length frequency analysis.

The Indian squid feeds on crustaceans, fishes and squids, and it is preyed upon by a variety of predators, including fishes and marine mammals. Cannibalism is common.

Interest to Fisheries: ***Uroteuthis duvaucelii*** is exploited throughout its distributional range, mainly by artisanal fisheries. It is caught by various fishing gears, such as otter trawl, pair trawl, night-light luring, push net, hook and line. One of the most common species among the Indo-Pacific loliginids, it was considered the most promising species for the Indian dried squid industry, and it probably constitutes, along with ***U. chinensis***, the main fraction (up to 90%) of the squid catches of Thailand. It is known to be fairly important for the fisheries of the eastern Arabian Sea, as well as off the Gujarat (northwest coastal India) and Karnataka coasts (northeast coastal India). Cuttlefishes constitute the dominant species group for all capture techniques in the Indian cephalopod fisheries, but ***U. duvaucelii*** represents up to 68% of the catches off central west India. It also constitutes a significant fraction of the total cephalopod production off southern India, where it is caught by shore seine, boat seine, and hook-and-line. The Indian squid is important for all the main eastern Indian landing places (i.e. Waltair, Kakinada, Madras, Mandapam, Vishakhapatnam), where it constitutes the most abundantly caught squid species. It also represents the most commonly landed species along the Andaman Sea coast of Thailand, where it can contribute up to 45% of the squid landed. ***Uroteuthis duvaucelii*** is one of the main commercial squid species for the Philippine fishery, and it is reported among the 5 major squid species known in the Malaysian area, as well as among the most common squid species caught in the Java Sea. It is abundant in the South China Sea, and it is reported among the commercial squid species of the Hong Kong fishery. However, very little information is known about the abundance and landings of this species in the Yellow and East China Seas. This species probably is exploited above its optimum level in Indian waters and increase in cod end mesh size and reduction in the fishing effort have been suggested as management measures to sustain the fishery.

Local Names: CHINA: Chin sui yau yue, Yau jai; INDIA: Narsinga, Narasingha, Bondas, Koonthal, Oosikanava, Kumutimuna, Samudra shasha.

Remarks: ***Uroteuthis duvuacelii*** is another loliginid species that exhibits polymorphism and possibly is a species complex, which is not surprising considering its wide distributional range. Different forms are recognized in the commercial fishery: a very slender form and a chubby/stout form occur in the eastern Indo-Pacific region (Okutani, 2005), and a large form and small form are reported from the Gulf of Aden and the Arabian Sea (Nesis, 1982, 1987). First attempts to culture the Indian squid were made from eggs collected in the field (Prinngennies *et al*., 2000), and the species currently is hatched and reared in a large-scale cephalopod culture system in Thailand, in research aimed to determine the feasibility of commercial culture (Nabhitabhata *et al*., 2005).

Literature: Voss (1963a), Chikuni (1983), Roper *et al*. (1984), Silas (1986), Kripa *et al*. (1996), Mohamed (1996), Chotiaputta (1997), Dunning (1998d), Okutani, (2005), Jereb and Roper (2006).

Uroteuthis (Photololigo) machelae Roeleveld and Augustine, 2005

Uroteuthis (Photololigo) machelae Roeleveld and Augustine, 2005, *Phuket Marine Biological Center Research Bulletin*, (66): 97–107, 10 figs [98]. [Type locality: 19°49'S, 36°5'E, off Beira, Mozambique, western South Indian Ocean].

Frequent Synonyms: *Loligo (Doryteuthis) pickfordae* Nesis, 1982: 146, fig. 38 E-K; 1987:155, fig. 38 H-J, non Adam, 1954.

Misidentifications: None.

FAO Names: En – Mozambique squid; **Fr** – Calmar du Mozambique; **Sp** – Calamar del Mozambique.

Fig. 149

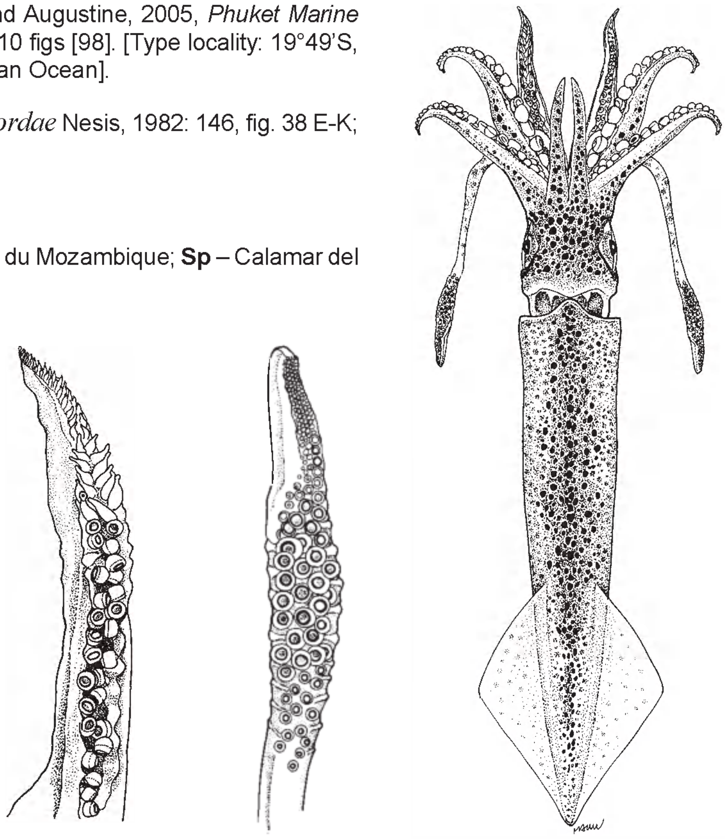

hectocotylus tentacular club dorsal view

Fig. 149 *Uroteuthis (Photololigo) machelae*

Diagnostic Features: Suckers on arms II to III greatly enlarged in males, much larger than median manus suckers on clubs; **arm sucker rings of both sexes with** wide, rough teeth distally and laterally, **proximal edge smooth**; arm length index 19 to 41% mantle length; left arm IV hectocotylized with 13 to 16 pairs of proximal suckers, 35 to 65% arm length modified distally, proximal papillae elongate conical; fin length 39 to 46% mantle length; **club length 18 to 28% mantle length, 26 to 36% tentacle length**.

Size: Small-sized squids; maximum reported mantle length 110 mm.

Geographical Distribution: Mozambique and western Madagascar, Seychelles, Saya de Malha Bank (Fig. 150).

Habitat and Biology: Specimens have been captured with bottom trawls at depths of 54 to 200 m. Smallest mature males measure 61 mm mantle length, smallest females 83 mm mantle length.

Interest to Fisheries: None.

Local Names: None.

Remarks: Specimens were originally identified as ***Uroteuthis pickfordi***, the species described by Adam (1954), from 2 small specimens (mantle length less than 100 mm) collected in Indonesian waters off Flores Islands, and subsequently reported by Nesis (1982, 1987) from the Mozambique waters (Roeleveld and Augustine, 2005). However, ***U. machelae*** differs from ***U. pickfordi*** by having shorter fins, longer arms, hectocotylized arm modified over shorter section, with more proximal suckers; also, its tentacles and clubs are longer in relation to mantle length, and clubs are shorter in relation to tentacle length. ***Uroteuthis machelae*** also differs in having smooth proximal edges on the arm sucker rings in both sexes, while in ***U. pickfordi*** the arm sucker rings are toothed all around the whole edge. It seems that the specimens mentioned by Nesis (1982, 1987) from Mozambique, the Seychelles and the Saya de Malha Bank (Western Indian Ocean) may belong to ***U. macheale*** rather than to ***U. pickfordi***.

Literature: Roeleveld and Augustine, 2005.

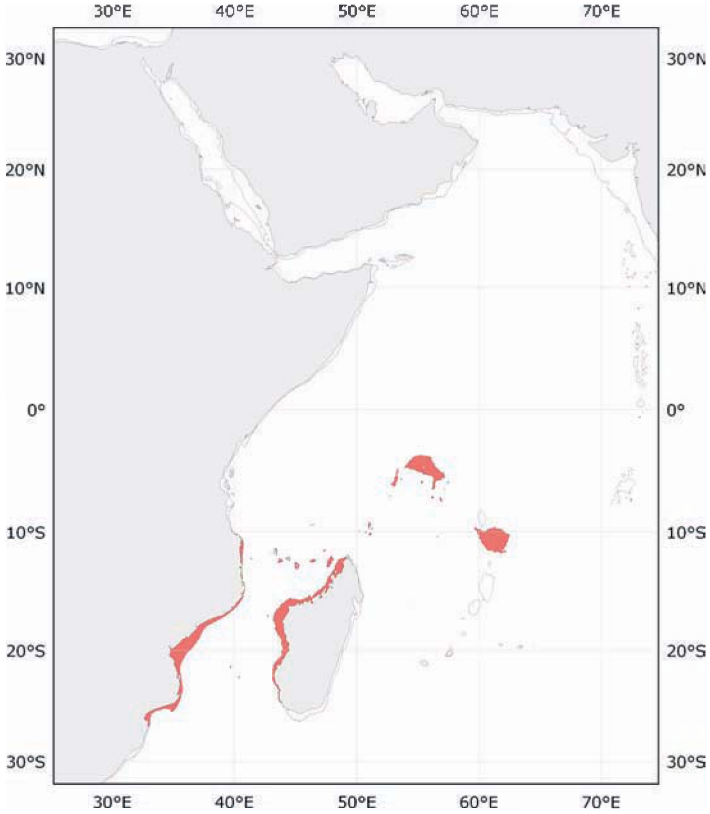


Fig. 150 ***Uroteuthis (Photololigo) machelae***

🟥 Known distribution

Uroteuthis (Photololigo) robsoni Alexeyev, 1992

Fig. 151

Uroteuthis robsoni Alexeyev, 1992, *Zoologicheskij Zhurnal, Moscow*, 71(11): 12–23, 2 figs [13, fig. 1]. [Type locality: 19°45'S, 36°22'E, off Mozambique, western South Indian Ocean].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Robson's squid; **Fr** – Calmar de Robson; **Sp** – Calamar de Robson.

Diagnostic Features: Mantle slender, elongate; mantle width about 20% mantle length. **Fleshy midventral ridge present**. Fins rhombic, elongate; fin length 60% of mantle length, fin width 50% mantle length. **Arm sucker rings with about 20 sharp, triangular teeth**. Hectocotylized arm modified on its distal one-third (modified section 33 to 37% arm length). T**entacular club-sucker rings similar in size, with irregularly alternating large and sharp teeth**. Gladius vane lateral margins not thickened.

Size: Medium-sized squid, mantle length to 240 mm.

Geographical Distribution: Western Indian Ocean: coastal Mozambique (Fig. 152).

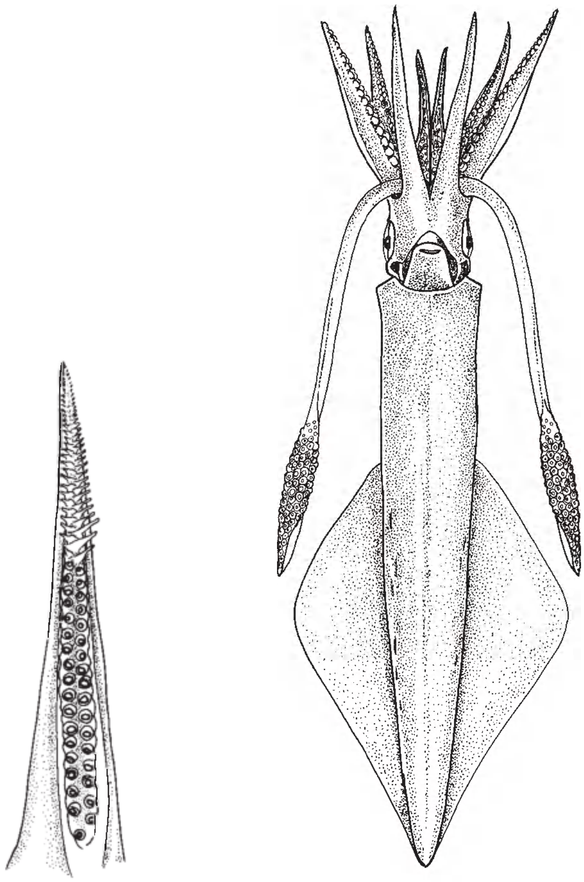
Habitat and Biology: No data available.

Interest to Fisheries: Currently, unknown.

Local names: None available.

Remarks: This species resembles ***Uroteuthis arabica*** and ***U. chinensis***; however, in males the shorter modified portion of the hectocotylus (32 to 37% instead of 40 to 50% of the arm length) is distinctive.

Literature: Alexeyev, 1992, Roeleveld, 1998, Okutani, 2005.



hectocotylus **dorsal view**

Fig. 151 ***Uroteuthis (Photololigo) robsoni***

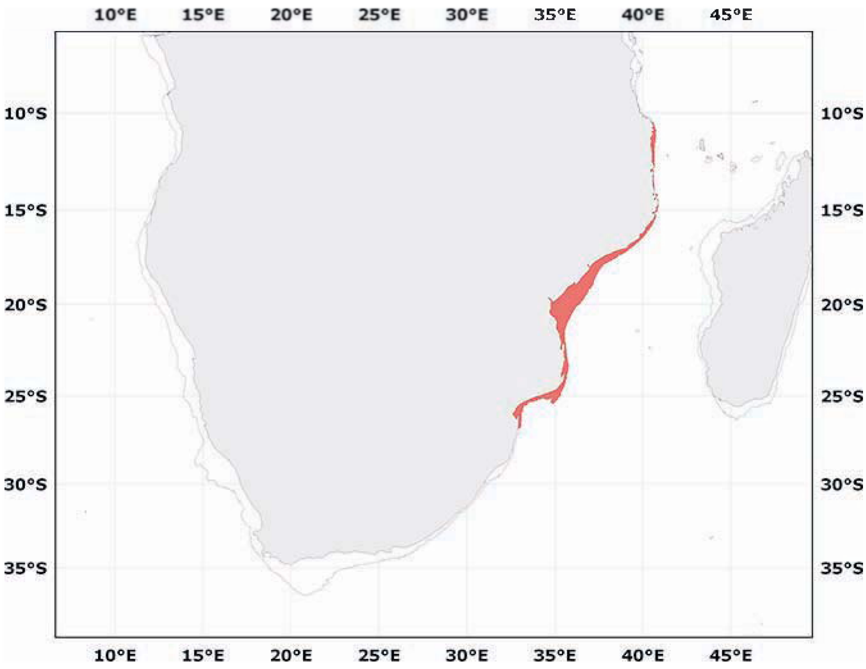


Fig. 152 ***Uroteuthis (Photololigo) robsoni***

🟥 Known distribution

Uroteuthis (Photololigo) sibogae (Adam, 1954)

Fig. 153

Doryteuthis sibogae Adam, 1954, *Siboga Expedition, Monographie*, 55(c):123–193, 40 figs, 4 pls. [146, text-figs 16, 18, pl. 1]. [Type locality: off southeast coasts of Soemba, Indonesia, eastern Indian Ocean].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Siboga squid; **Fr** – Calmar siboga; **Sp** – Calamar siboga.

Diagnostic Features: Mantle very long, slender; width one-fifth to one-seventh of length. Fins narrow, relatively short, length <50% of mantle length. Edges of gladius straight, thickened. Tentacles short, slender, clubs short; **medial suckers on manus slightly enlarged, the largest with 15 to 20 conical, sharp, teeth around entire ring; teeth subequal in size**. The largest suckers from the clubs and ventrolateral arms are about equal in size. Arms relatively very short; **arm-sucker rings smooth proximally, with 7 to 9 plate-like, truncate (squared) teeth distally**, the central 1 or 2 narrowest; left ventral arm hectocotylized for 30 to 45% of its length with the distal suckers and stalks modified into cone-shaped fleshy papillae, those in the ventral series the longest.

Size: Maximum mantle length 160 mm.

Geographical Distribution: Indian Ocean: southern African waters, India, Thailand, Andaman Sea; Western Pacific Ocean: eastern Indonesia and South China Sea (Fig. 154).

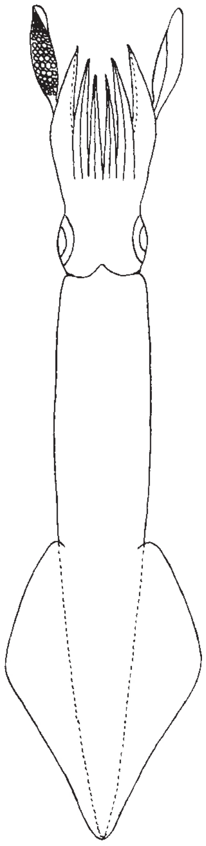
Habitat and Biology: The depth range of this species is undetermined. Sexually mature squids occur during August off the Pescadores Islands. The biology of this species is very poorly known.

Interest to Fisheries: This species is fished commercially in India and Thailand, and it is taken as bycatch in the fisheries for larger squids in Taiwan (Province of China).

Local Names: INDIA: Olaikanava, Soochikanava.

Remarks: ***Uroteuthis sibogae*** was synonymized with ***Uroteuthis singhalensis*** by Korzun and Alexeyev (1991) and, as such, it is not mentioned in the species listed by Okutani (1995, 2005) for the western Pacific. However, no general consensus on this synonymy was reached in the Phuket CIAC meeting (Vecchione *et al*., 2005); therefore, for the sake of consistency, we list it here, until the species status is resolved.

Literature: Adam (1954), Roper *et al*. (1984), Nesis (1982, 1987), Korzun and Alexeyev (1991), Nateewathana (1992), Roeleveld (1998), Narasimham (2005), Vecchione *et al*. (2005).



dorsal view

Fig. 153 ***Uroteuthis (Photololigo) sibogae***

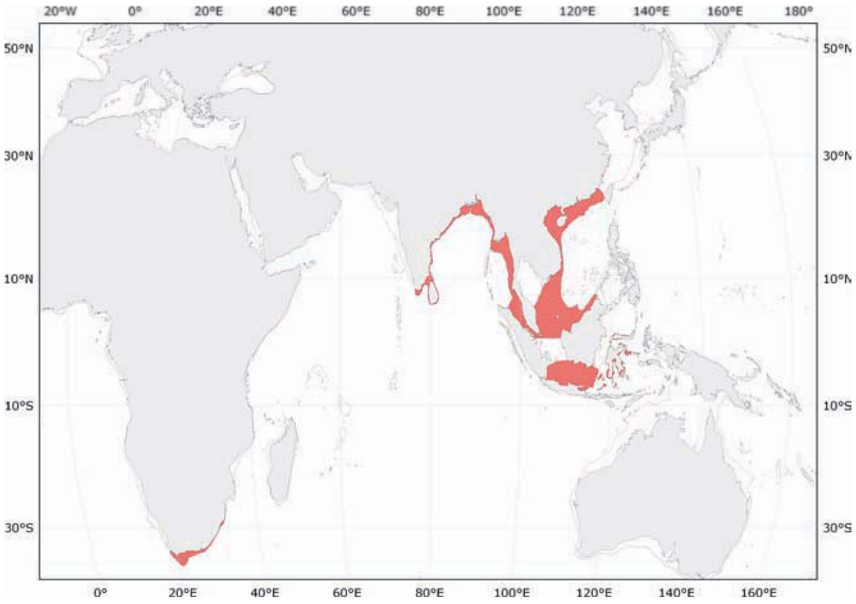


Fig. 154 ***Uroteuthis (Photololigo) sibogae***

🟥 Known distribution

Uroteuthis (Photololigo) singhalensis (Ortmann, 1891)

Fig. 155

Loligo singhalensis Ortmann, 1891, *Zoologische Jahrbücher (Systematisches)*, 5: 669–678. [676, pl 46 fig. 3a-d]. [Type locality: Sri Lanka, Indian Ocean].

Frequent Synonyms: non *Doryteuthis singhalensis* Adam, 1939b, 1954, (= *Loligo edulis*), non *Doryteuthis singhalensis* Voss, 1963a, Voss and Williamson, 1971, Roper *et al.*, 1984, Silas *et al.*, 1986a, (= *Loligo chinensis*), *Doryteuthis* sp. Silas *et al.*, 1982, Mohan and Rayudu, 1986; *Loligo singhalensis* var. *beryllae* Robson, 1928, *Doryteuthis sibogae* Adam, 1954, Natsukari, 1976, Silas *et al.*, 1985, Silas 1986a; *Loligo sibogae* Natsukari, 1976, Nesis, 1982, 1987, Roper *et al.*, 1984, Alekseyev, 1989, non *Loligo singhalensis* Okutani, 1980, Nesis, 1982, 1987, Alekseyev, 1989 (= *Uroteuthis (Photololigo) chinensis*), *Photololigo sibogae* Natsukari, 1984a, Dunning, 1998d, non *Photololigo singhalensis* Natsukari, 1984a (= *L. chinensis*).

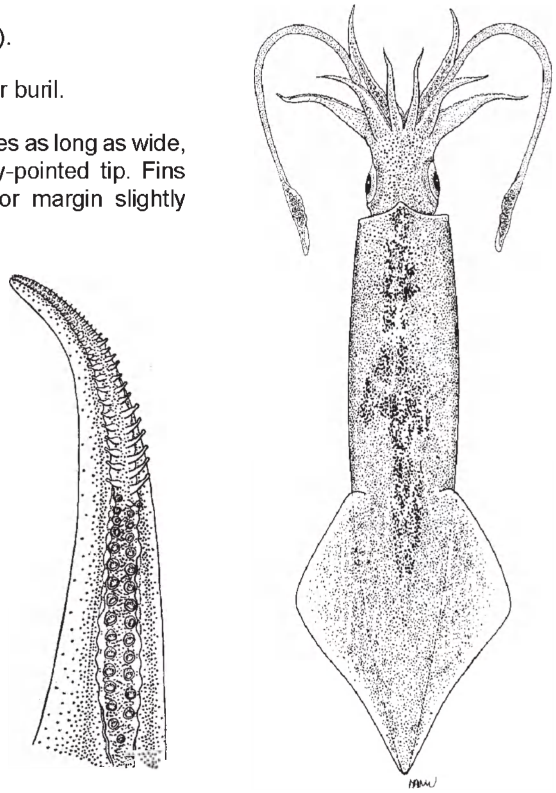
Misidentifications: *Uroteuthis (Photololigo) chinensis* (Gray, 1849).

FAO Names: En – Long barrel squid; **Fr** – Calmar baril; **Sp** – Calamar buril.

Diagnostic Features: Mantle long, slender, cylindrical, about 4 to 7 times as long as wide, widest at the midpoint of its length; tapers posteriorly into a sharply-pointed tip. Fins narrow, rhombic in outline, anterior margin slightly convex, posterior margin slightly concave; relatively short in young specimens, up to 50 to 60% of mantle length in adults. Gladius narrow, widest in anterior one-third, with thickened, nearly straight vane margins. Tentacular clubs short, slightly expanded; **suckers in medial series** of manus only about 25% larger than those on lateral series; **with 15 to 25 conical, sharply-pointed teeth around the entire margin**, occasionally interposed with small, almost inconspicuous, pointed teeth. Arms relatively short; sucker rings **with 6 (5) to 11 long, wide, squared, plate-like teeth distally, smooth proximally**. Left ventral arm hectocotylized over 45 to 50% of total arm length with slender, uniform, cone-shaped, pointed, fleshy papillae, devoid of minute suckers on tips; papillae on ventral series only slightly longer than papillae on dorsal series.

Size: Large-sized squid; maximum mantle length 500 mm in males, 310 mm in females; weight about 1 kg in males, 800 g in females.

Geographical Distribution: An Indo-Pacific species, widely distributed in the western Pacific from the South China Sea and Singapore (Indonesian waters) north to Formosa Island, into the Indian Ocean from the Andaman Sea, Thailand and the Bay of Bengal, westward to the Arabian Sea and the eastern African coasts (Somalia, Seychelles, Mozambique, Madagascar and South Africa east coast) (Fig. 156).



hectocotylus

dorsal view

Fig. 155 ***Uroteuthis (Photololigo) singhalensis***

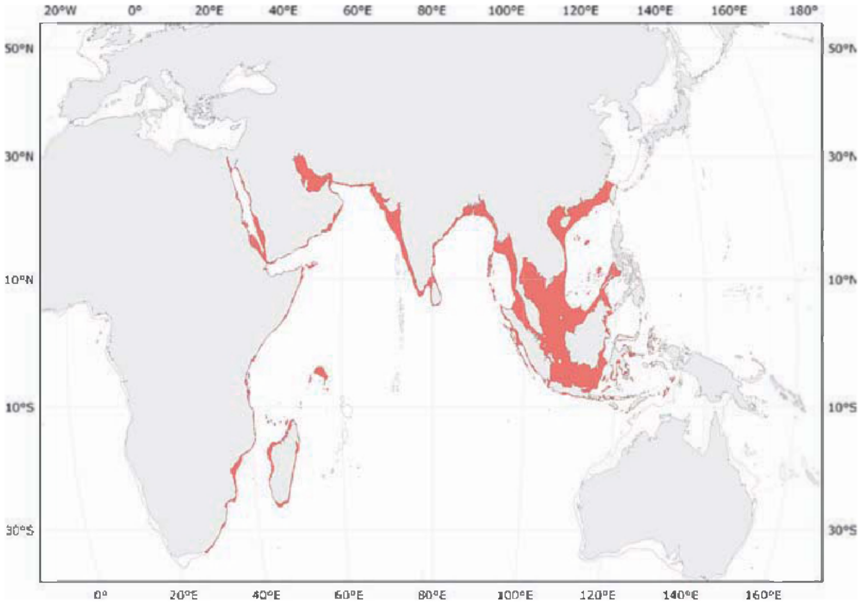


Fig. 156 ***Uroteuthis (Photololigo) singhalensis***

🟥 Known distribution

Habitat and Biology: This species usually occurs at depths from 30 to 120 m, but extends to bottom depths of 220 m. The biology of ***Uroteuthis singhalensis*** is still poorly known. Data from the southwest coast of India indicate that males in this area attain sexual maturity at a size range of 70 to 170 mm mantle length (50% mature at 97 mm mantle length), and females mature at a size range of 70 to 130 mm mantle length (50% mature at 84 mm mantle length). All males and females are fully mature at a size of 170 and 130 mm, respectively. Mature specimens of both sexes occur from October to April, suggesting a protracted spawning season. They aggregate in large schools in summer, probably for a peak of mating and spawning. Juveniles are caught along the coast from January/February to June (in some years). Data from the southeastern slope of the Mascarene submarine ridge, western Indian Ocean, indicate that the species is represented there by 2 sympatric groups that differ slightly in the size at first maturity. Males of the first group, which is widespread over the distributional area, reach sexual maturity at a size range of 80 to 210 mm mantle length and females at a size range of 100 to 170 mm mantle length. The second group occurs only in the northern part of the area, where males and females become mature at a size of 100 to 230 mm mantle length and 110 to 170 mm mantle length, respectively.

Uroteuthis singhalensis is positively phototactic, a feature that is utilized in the fishery by attracting it to artificial light for capture. Based on seasonal abundance data, some migrations are possible.

Interest to Fisheries: Reported mainly as a bycatch in the Indonesian and South China Sea finfish fisheries, ***U. singhalensis*** is the third most important squid trawled in Hong Kong waters after ***Uroteuthis edulis*** and ***U. chinensis***, and it is likely to be rather important to the fisheries in the Indian Ocean waters, even though the extent of its contribution is difficult to assess, because of taxonomic confusion (see Remarks). For example, the long barrel squid is listed among the major species of loliginid squid that occur in the Indo-Pacific region, with small catches recorded from the China Sea to the eastern Arabian Sea, but it is not clear to what extent this pattern refers to different species. Included among the important species for the commercial squid fishery of Thailand, ***U. singhalensis*** seems consistently present in the Andaman Sea, where it is one of the target species of a light-attraction fishery in Phuket and Phang-Nga provinces. Among the important species for the Indian fishery, it is reported on both coasts of India, and it is particularly important for the local fisheries off the southwestern coast. It also contributes to the small local pelagic fishery in Sri Lankan waters and probably is important in the northern part of the Bay of Bengal. However, it is not clear to what extent this species comprises the second most important squid resource of India, in general, and off the northwestern coast, in particular, because of potential misidentification. It is taken by jigs, purse seines, and dip-nets using light attraction together with ***Photololigo chinensis*** and other large loliginids.

Local Names: CHINA: Cheung woo chak, Cheung yau tung.

Remarks: The systematic position of this species has been the object of several discussions and various contradictions during the past (see Jereb and Roper, 2006 and Okutani, 2005 for reviews) and the nomenclature applied to it varies greatly. Consensus exists among several scientists that ***Doryteuthis sibogae*** Adam, 1954 is a junior synonym of ***Loligo singhalensis*** Ortmann, 1891 (e.g. Okutani, 2005). In spite of recent efforts to clarify the nomenclature, many references, mainly those that report fishery statistics, remain doubtful, and their validation requires knowledge about species-specific characters. The subgeneric status of this species is unsettled. The first major revision of Loliginidae, placed the species in the genus ***Uroteuthis***, within the subgenus ***Photololigo*** (i.e. ***Uroteuthis (Photololigo) singhalensis***) (Vecchione *et al.* 1998). This was not modified during the last major meeting os scientific esperts held in Phuket (Vechione *et al.* 2005). However, during that meeting, molecular data against this placement were discussed and the proposal to establish a new subgenus for the species was made, but this recommendation has not yet been accomplished. Clearly, further studies are required to claify the problematic systematics of the ***Uroteuthis (Photololigo)*** species (complicated as it is by both sexual dimorphism and ontogenetic variation), and the status of ***U. singhalensis*** in particular..

Literature: Voss (1963a), Okutani (1970, 1980), Roper *et al.* (1984), Nesis (1982, 1985, 1987), Silas *et al.* (1985), Alekseyev (1991), Korzun and Alexeyev (1991), Nateewathana (1992), Chotiyaputta (1993a), Chantawong (1994), Okutani (2005), Jereb and Roper (2006), Vecchione (2008k).

Uroteuthis (Photololigo) vossi (Nesis, 1982)

Fig. 157

Loligo vossi Nesis, 1982, *Moscow, Light and Food Industry Publishing House*, 385 p. [144]. [Type locality: Dumaran Island, Philippine Islands, South China Sea].

Frequent Synonyms: *Loligo* sp. A Voss (1963a).

Misidentifications: None.

FAO Names: En – Voss' squid; **Fr** – Calmar de Voss; **Sp** – Calamar de Voss.

Diagnostic Features: Mantle slender; mantle width up to 20% of mantle length; fin length up to 60% of mantle length, fin width up to 50% of mantle length. Edges of gladius arched, not thickened. **Medial manal suckers 2 to 3 times the diameter of the lateral suckers**; **large sucker rings with 15 to 20 sharp, equally spaced teeth**; 2 to 4 distal teeth occasionally fused together. Teeth of club sucker rings subequal in size, somewhat larger distally. Arm suckers with 7 to 11 teeth on distal margin of rings.

Size: To 136 mm mantle length in males.

Geographical Distribution: Philippine Islands, Sri Lanka to the Arabian Sea (Fig. 158).

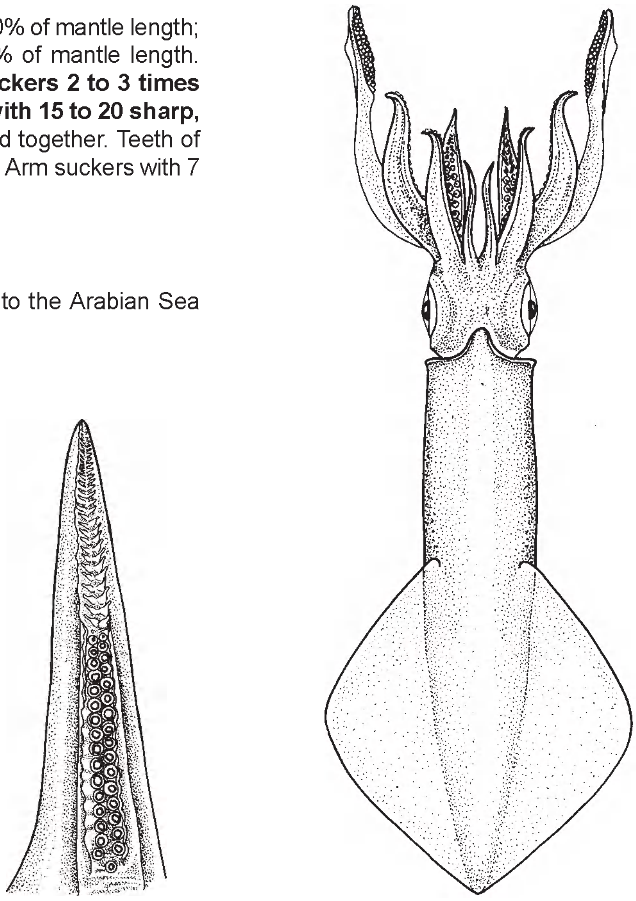
Habitat and Biology: No data available.

Interest to Fisheries: Currently unknown.

Local Names: None available.

Remarks: Nesis (1982) published this name for *Loligo* sp. A of Voss (1963a).

Literature: Voss (1963a), Nesis (1982), Okutani (2005), Vecchione (2008k).



hectocotylus **dorsal view**

Fig. 157 ***Uroteuthis (Photololigo) vossi***

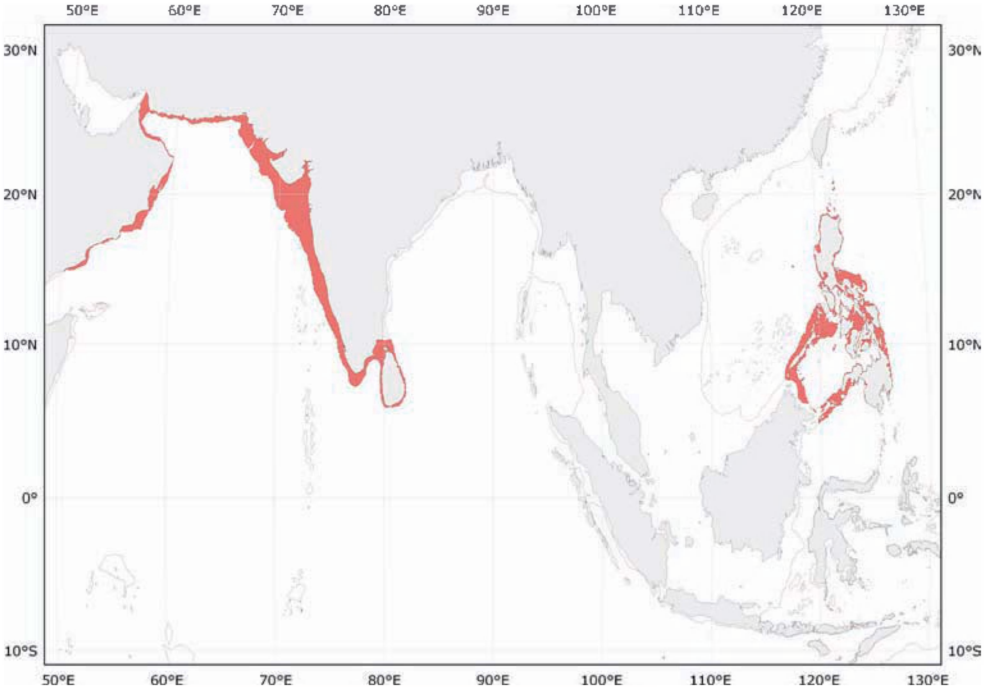


Fig. 158 ***Uroteuthis (Photololigo) vossi***

🟥 Known distribution

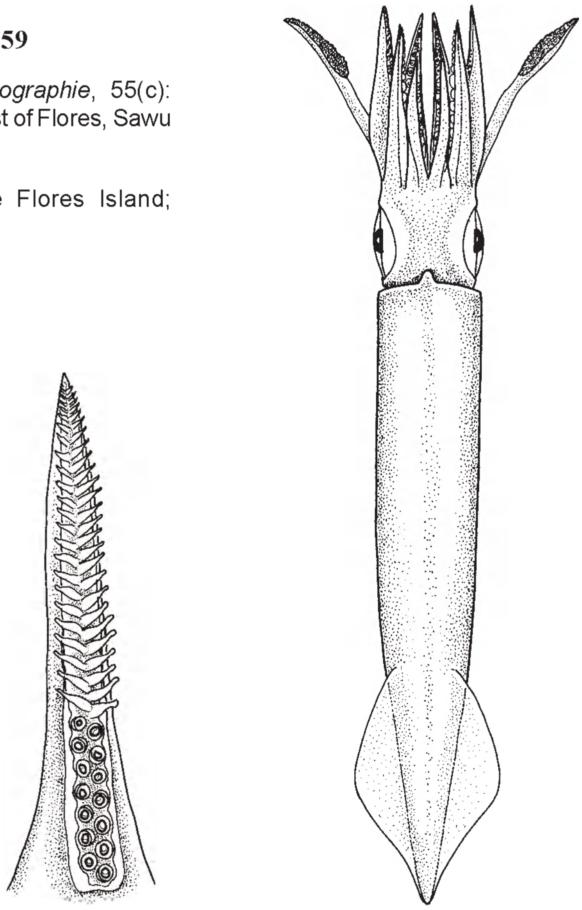
Subgenus undetermind

Uroteuthis pickfordi (Adam, 1954)

Fig. 159

Doryteuthis pickfordi Adam, 1954, *Siboga-Expeditie, Monographie*, 55(c): 123–193. [149, text-figs 19–21, pl 1]. [Type locality: southern coast of Flores, Sawu Sea, Indonesia].

FAO Names: En – Flores Island squid; **Fr** – Calmar de Flores Island; **Sp** – Calamar de Flores Island.



hectocotylus **dorsal view**

Fig. 159 ***Uroteuthis pickfordi***

Diagnostic Features: Fin length <50% mantle length. **Edges of gladius** straight, **thickened**. **Teeth of club sucker rings subequal in size**. Arm sucker rings with wide teeth around entire ring. Large suckers of lateral arms much larger than club suckers.

Size: Small-sized squid, 110 to 140 mm mantle length.

Geographical Distribution: Flores Island, Indonesia (Fig. 160).

Remarks: ***Uroteuthis pickfordi*** was described by Adam (1954), from two small specimens (less than 100 mm mantle length) collected in Indonesian waters off Flores Islands; subsequently, the species has been reported from Mozambique waters by Nesis (1982, 1987). However, it is possible that the specimens mentioned by Nesis (1982, 1987) from Mozambique, the Seychelles and the Saya de Malha Bank (Western Indian Ocean) belong to ***Uroteuthis machelae*** rather than to ***U. pickfordi*** (Roeleveld and Augustine, 2005). The 2 species differ by fin length, hectocotylized arm configuration, tentacular club length and arm sucker rings dentition (see remarks in ***Uroteuthis machelae***). Confusion about the name of the species exists (i.e. ***pickfordae*** versus ***pickfordi***). Usually a species named after a female should end in "ae" rather than "i" (art 31.1.2, ICZN, 1999). However, Adam's original description ended in "i". According to art 32 (ICZN, 1999) original spelling is correct unless it is in one of the categories listed in 32.5 as "spellings that must be corrected". In our opinion, this is not the case and the change in ending is an unjustified emendation. According to 33.2.3.1 (ICZN, 1999) an unjustified emedation in prevailing usage is considered to be a justified emendation. However, since the specific name "***pickfordi***" is in prevailing usage and it is the original designation, this is the name used in this Catalogue.

Literature: Adam (1954), Nesis (1982, 1987), Roeleveld (1998), Okutani (2005), Roeleveld and Augustine (2005).

Fig. 160 ***Uroteuthis pickfordi***

🟥 Known distribution

Uroteuthis reesi (Voss, 1962)

Fig. 161

Doryteuthis reesi Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 169–176. [173]. [Type Locality: off Port Maricaban, southern Luzon, Philippine Islands].

FAO Names: En – Rees' squid; **Fr** – Calmar de Rees; **Sp** – Calamar de Rees.

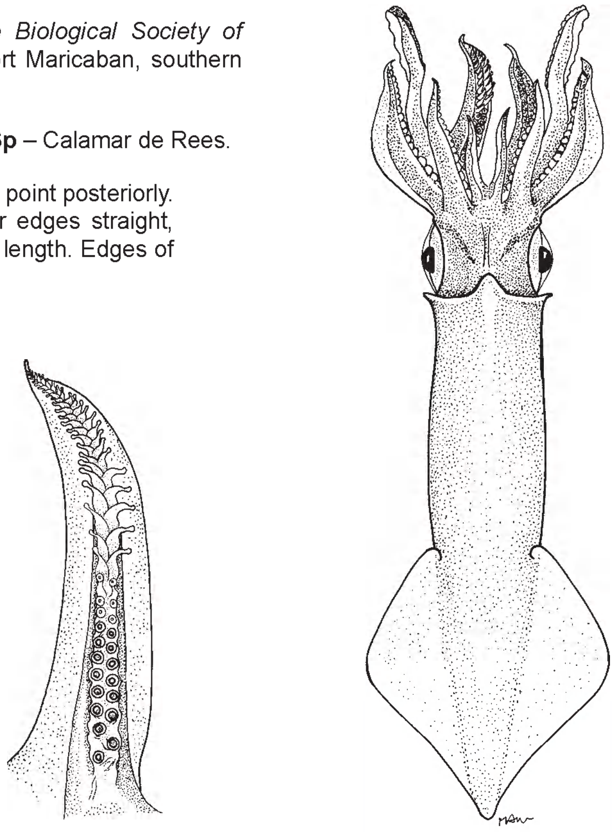
Diagnostic Features: Mantle long, slender, with a sharp point posteriorly. Fins small, fin length <50 % of mantle length, anterior edges straight, posterior edges concave; fin width about 45% of mantle length. Edges of gladius straight, thickened. Tentacles short, only a little longer than the longest arm. **Club suckers quadriserial, the largest ones with 11 to 12 sharp, slender teeth subequal in size**, on rings. Arms short, about 25% mantle length; arm suckers approximately equal in size to manal club suckers; **arm sucker rings with 7 to 9 wide teeth distally**. **Both arms IV modifieded in males:** left arm longer than right, biserial row of papillae with small ringless suckers on the tip occupy more than distal half of the arm; on right arm eighth to sixteenth suckers abruptly reduced, followed by only pedicels distally.

Size: Maximum reported size 72 mm mantle length for males, 63 mm mantle length for females.

Geographical Distribution: Philippine Islands (Fig. 162).

Remarks: Males of this small loliginid may easily be distinguished from those of the other small species in the Indo-Malayan region by the hectocotylization of both ventral arms.

Literature: Voss (1962a), Voss (1963a), Okutani (2005).



hectocotylus

dorsal view

Fig. 161 *Uroteuthis reesi*

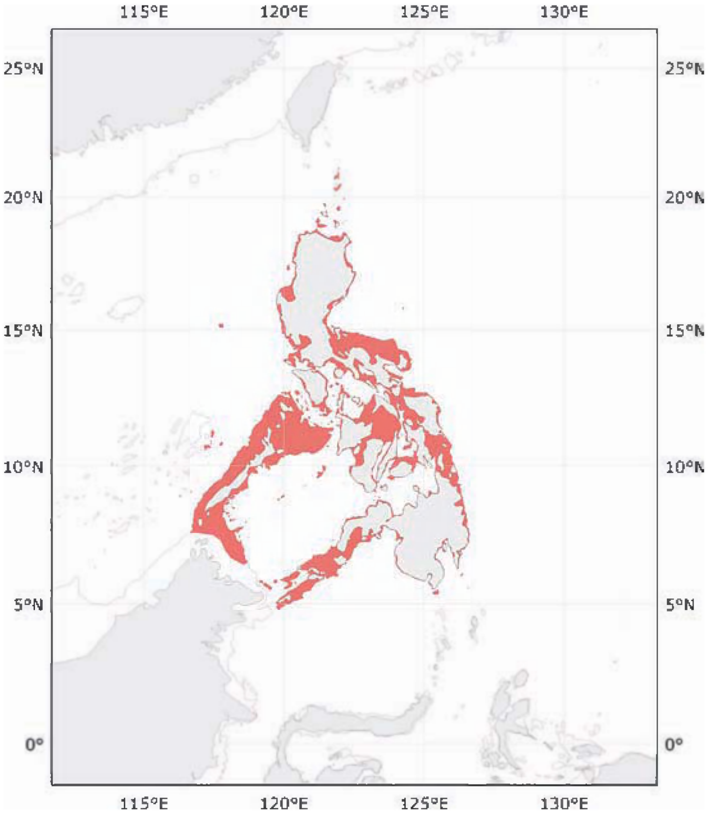


Fig. 162 *Uroteuthis reesi*

🟥 Known distribution

Oegopsid Squids

Diagnostic Features: **No corneal membrane** covers the eyes, which are exposed directly to seawater. Head **without tentacle pocket**, except in Bathyteuthidae and Chtenopterygidae. **No suckers** on the **buccal lappets**, except in Bathyteuthidae and Chtenopterygidae. Funnel without lateral adductor muscles. Arms and clubs with suckers **and/or hooks** in some species. Tentacular club usually **with carpal-locking** apparatus. Shell a gladius, that extends the full length of the mantle. Female **gonoducts paired**. **Accessory** nidamental glands **absent**.

Size: From very small-sized (dwarf) squids, e.g. some ***Abralia*** and ***Abraliopsis*** species (Enoploteuthidae; maximum recorded size 20 mm ML), to the gigantic ***Architeuthis*** (Architeuthidae), ***Mesonychoteuthis*** (Cranchiidae), ***Moroteuthis*** and ***Onychoteuthis*** (Onychoteuthidae) squids, for which mantle lengths of over 2 m are not unusual.

Geographical Distribution: Oegopsid squids are widely distributed in all oceans and seas of the world.

Habitat and Biology: Oegopsid squids inhabit virtually all depths and areas of the oceans, from the surface and midwater layers, down to bathyal depths (4 000 to 5 000 m). Many species undergo significant diel vertical migrations, wherein they occur in deep waters during the day, then ascend toward surface waters at night (0 to 200 m). Some nerito-oceanic species are found in association with sea-mounts and submarine ridges, but most species are pelagic. Some oegopsids are very muscular and powerful squids, remarkable hunters, even capable, though rarely, of attacking divers (i.e. ***Dosidicus gigas***); on the contrary, many members of the Cranchiidae (also known as glass squid) are transparent, small to medium-sized squids, that spend much of their lives in partially sunlit epipelagic waters, where their transparency provides camouflage. Many oegopsid species bear photophores and bioluminescence occurs almost universally in mesopelagic squids. Spawning often extends throughout the year, but peaks, seasonal spawning seasons, do occur as well. Most oegopsid squids lay eggs in pelagic, floating, neutrally buoyant egg masses, but ***Brachioteuthis*** species are know to spawn individual eggs into the plankton, and some members of the family Enoploteuthidae are known to produce long, gelatinous strings with eggs embedded in a single series. In many species of the family Gonatidae, maturing and spawning females undergo a rapid degradation of body tissues into a gelatinous consistency, tentacles are lost and locomotion is reduced; females of species in this family hold the egg masses in their arms while the embryos develop. In some oegopsid squids the paralarvae are very characteristic and differ substantially from adults, such as the chiroteuthid *doratopsis* stage, characterized by an elongate, chambered neck, and the ommastrephid *Rhynchoteuthion*, characterized by the fusion of the tentacles into a trunk-like proboscis.

Interest to Fisheries: Members of the oegopsid squids support the major cephalopod fisheries around the world. FAO’s Fishery Yearbook (FAO, 2009) reports over 3 200 000 tonnes of oegopsid squids caught in 2007, i.e. about 68.4% of the total squid catch for that year. Also, oegopsid squids undoubtedly constitute the major component of the non-identified-squid fraction reported for the same year, over 658 000 tonnes (FAO, 2009). Among oegopsids, squids of the family Ommastrephidae are the main contributors to the fisheries, totalling about 98% of the total oegopsid catch in 2007; fluctuations in the catches occur yearly, but ***Dosidicus gigas*** (eastern Pacific Ocean), ***Illex argentinus*** (southwest Atlantic Ocean) and ***Todarodes pacificus*** (northwest Pacific) together accounted for about 95% of the total ommastrephid squid catch in 2007 (i.e. about 64% of total loliginid and oegopsid squid catch for that year (FAO, 2009).

Remarks: Currently, 26 families are recognized in the oegopsid squids with over 70 genera and well over 250 species recognized. However, many of these species still are poorly known or undescribed, especially within those families of unknown or no interest to fisheries, due to their inaccessibility, or unsuitable flesh consistency, or size. A total of 72 genera and 247 species are treated in this work.

Literature: Naef (1916, 1923), Roper *et al.* (1984), Nesis (1982/1987), Sweeney and Roper (1998), Norman (2000), Young and Vecchione (2004), Okutani (2005).

2.3 Family ANCISTROCHEIRIDAE Pfeffer, 1912

by Clyde F.E. Roper and Patrizia Jereb

Ancistrocheiridae Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2F(a): 1–815 [174].

Type Genus: *Ancistrocheirus* Gray, 1849.

FAO Names: **En** – Sharpear enope squid; **Fr** – Encornet cachalot; **Sp** – Enoploluria rómbica.

Diagnostic Features: Buccal crown with 8 supports. Buccal connectives attach to dorsal margins of arms IV. No secondary buccal connectives attach to ventral margins of arms I and II. Gladius with pointed conus and elongate cone field; long, pointed rostrum present. **Hooks present on all arms**; **tentacular clubs with 2 series of hooks on manus**; **suckers absent**. Photophores present on ventral surface of fins, mantle, funnel, head, arms, and tentacles. Photophores absent from viscera and eyeballs. Nidamental glands present; oviducal glands normal. Oviducts unpaired. **Fins very large, slightly subterminal**, without posterior lobes. **Posterior end of mantle elongate, forms tail**. Head and tail with fleshy, gelatinous tissue; vesicles absent. Nuchal folds present. Tentacles not modified near bases; stalk “ligament” and vein leave tentacle at base and in membrane. Ink sac not embedded in digestive gland.

Remarks: The currently recognized family Ancistrocheiridae formerly was included as a subfamily in the family Enoploteuthidae, ever since Pfeffer (1912) formalized his concept of Enoploteuthidae into 4 subfamilies. The family was considered by Roper *et al.* (1969b) to be comprised of 3 subfamilies (Enoploteuthinae, Ancistrocheirinae, Pyroteuthinae), all of which were elevated to familial status by Clarke (1988b). This classification was thoroughly analyzed and reconfirmed by Young *et al.* (1998a) and Young and Harman (1998). The Ancistrocheiridae is a monotypic family, with ***Ancistrocheirus lesueurii*** (d'Orbigny, 1842) the sole recognized species at this time.

Literature: Roper *et al.* (1969b), Clarke (1988b), Young *et al.* (1998b), Young and Harman (1998), Sweeney and Young (2003a), Vecchione and Young (2008a).

Ancistrocheirus Gray, 1849

Ancistrocheirus Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia,* 164 pp. [49].

Type Species: *Ancistrocheirus lesueurii* (d'Orbigny, 1842).

Frequent Synonyms: *Thelidioteuthis* Pfeffer, 1900.

Ancistrocheirus lesueurii (d'Orbigny, 1842)

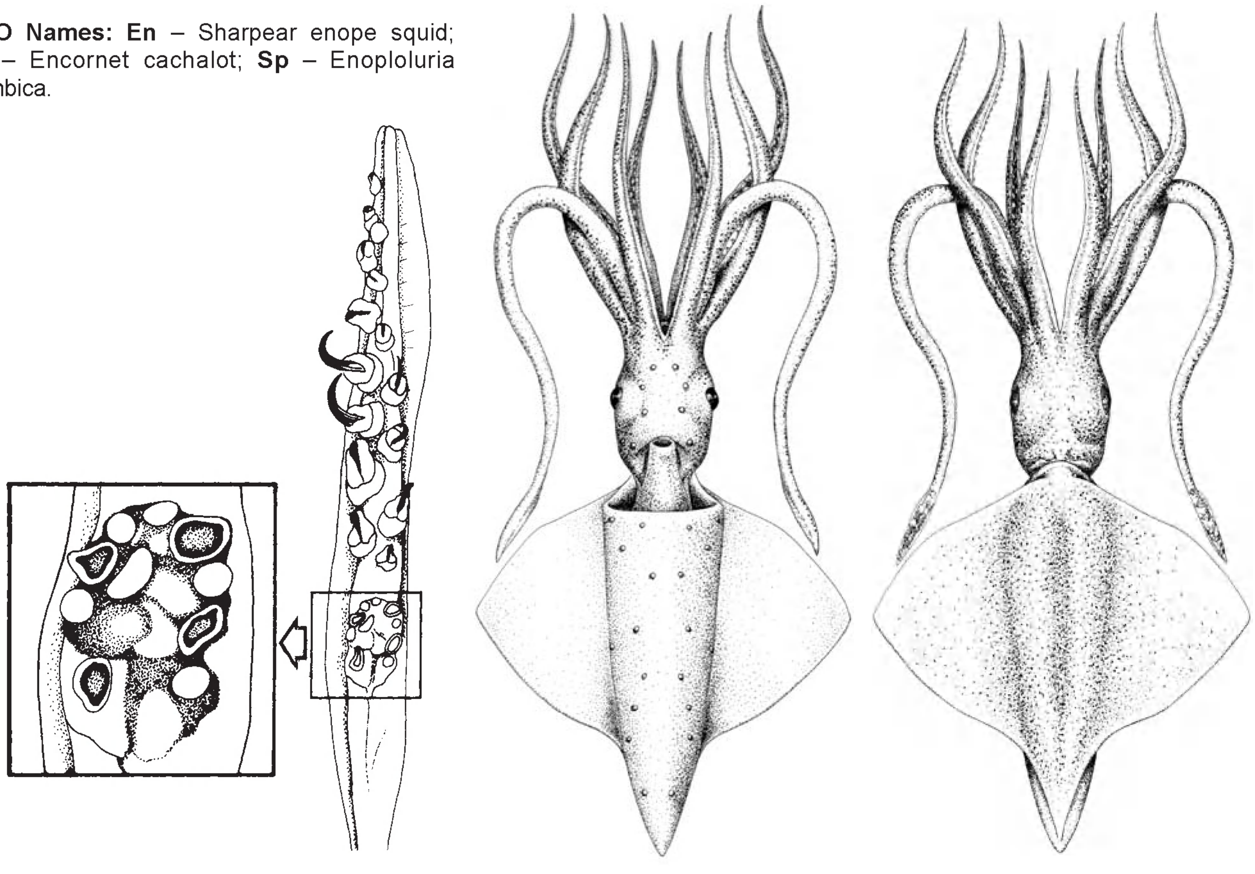
Fig. 163

Enoploteuthis lesueurii d'Orbigny, 1842, *in* Férussac and d'Orbigny, 1834–1848, Voyage dans l'Amérique Méridionale, 5(3): 1–758 [339, pl.14]. [Type locality: not designated].

Frequent Synonyms: *Onychoteuthis lesueurii* d'Orbigny, 1842; *Thelidioteuthis alessandrinii* (Verany, 1847); *Abralia megalops* Verrill, 1882b; *Enoploteuthis pallida* Pfeffer, 1884; *Enoploteuthis polyonyx* Troschel, 1857.

Misidentifications: As *Thelidioteuthis alessandrinii* (Verany, 1851).

FAO Names: En – Sharpear enope squid; **Fr** – Encornet cachalot; **Sp** – Enoploluria rómbica.


tentacular club

ventral view

dorsal view

Fig. 163 ***Ancistrocheirus lesueurii***

Diagnostic Features: Same as for family, plus as follows: mantle long, broad, conical, thick-walled. **Fins thick, rhomboidal, long (70 to 80% of mantle length)**; **broad (80% of mantle length)**.Tentacles robust with 12 photophores along the aboral side of the stalk; clubs narrow, unexpanded, with a distinct carpal cluster; **manus with 2 tranvserse series of sharp hooks, the 7 or 8 of the ventral series being larger than the 8 of the dorsal series**. Arms robust, with 2 series of hooks; small, stalked suckers may be present on arm tips. Buccal-membrane connectives attach dorsally to armas IV. Nuchal folds present, prominent. **Ventral surface of mantle studded with 20 to 24 relatively large, separated photophores** arranged in transverse rows; ventral surface of head with 8 to 10 similarly arranged photophores; large photophores on funnel, bases of dorsolateral arms and tentacular stalks. Numerous very small photophores on ventral surface of fins, mantle, funnel, head and ventral arms. No photophores on eyeballs or viscera.

Size: The maximum mantle length reaches 410 mm. Gravid females attain 3 kg.

Geographical Distribution: Worldwide in tropical, subtropical and temperate open ocean waters (about 40°N to 30°S); includes the entire Mediterranean Sea (Fig. 164).

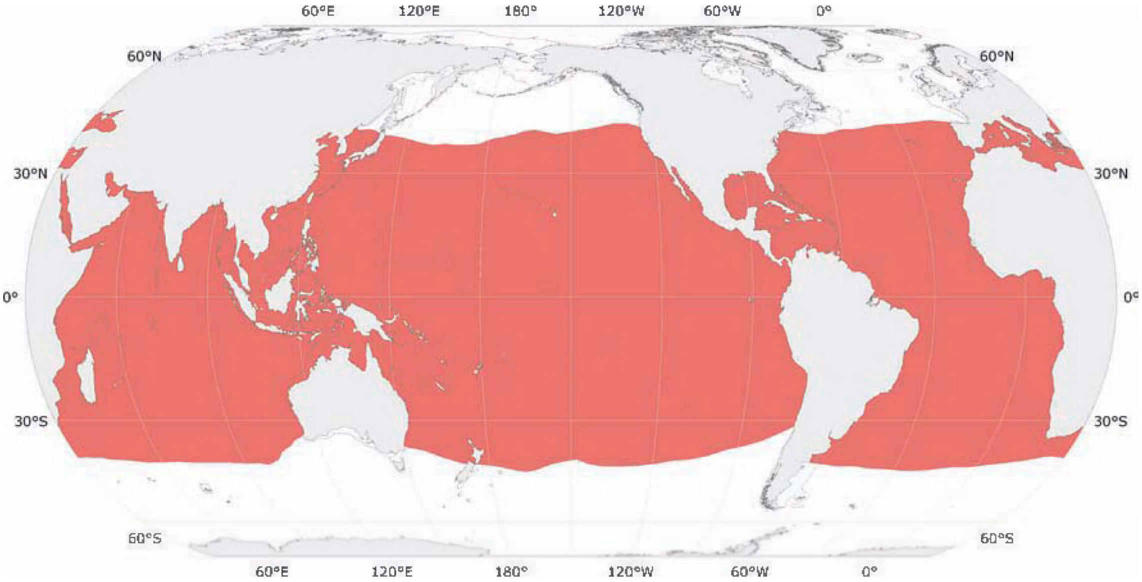


Fig. 164 ***Ancistrocheirus lesueurii***

🟥 Known distribution

Habitat and Biology: An oceanic species, *Ancistrocheirus lesueurii* is lower epipelagic to mesopelagic and bathyal, and it ranges in tropical and temperate waters of the 3 major oceans and the Mediterranean Sea. It undergoes diel vertical migration and consequently is able to regulate its bioluminescent counterillumination. As a nerito-oceanic species it can occur in association with seamounts and submarine ridges. Age and growth studies based on statolith analysis indicate a strong sexual dimorphism: males live about 1 year, females begin to mature at 1 year and spawn at about 1.5 years. Following ontogenetic descent into bathyal waters, at least to 680 m, growth rate decreases to lowest known values for squids. The relative fecundity is 200 000 to 800 000 ova, 2.6 to 1.91 mm diameter, of which 60 to 65% are spawned. Hatching occurs throughout the year; peaks November to March. Sexually mature males captured in southern African waters had nidamental glands in addition to the fully developed male reproductive system. Intersexual males were significantly larger than normal males. The species is preyed upon by swordfish, *Xiphias gladius*, lancetfish, tunas, blue shark, oceanic seabirds, Antarctic fulmar and odontocete cetaceans, e.g. sperm whales, pygmy and dwarf sperm whales, long-finned pilot whale.

Interest to Fisheries: This species is believed to have some fishery potential because of its size, but development of a fishery beyond subsistence levels awaits a better understanding of both geographic and vertical distribution, as well as knowledge about its biology and population structure and density.

Local Names: ITALY: Totano dei capodogli.

Remarks: Marked differences among the paralarvae from different oceans seem to suggest that more than 1 species of *Ancistrocheirus* exists (Young *et al*, 1992).

Literature: Roper *et al*. (1969b), Roper and Young (1975), Okutani (1976, 1995), Arkhipkin (1997a), Nesis (1999b), Hoving *et al*. (2006c).

2.4 Family ARCHITEUTHIDAE Pfeffer, 1900

by Clyde F.E. Roper and Patrizia Jereb

Architeuthidae Pfeffer, 1900, *Mitteilungen aus dem Naturhistorischen Museum Hamburg,* 17(2): 145–198 [152].

Type Genus: *Architeuthis* Steenstrup, 1857b.

FAO Names: En – Giant squids; **Fr** – Encornets monstres; **Sp** – Megalurias.

Diagnostic Features: The Architeuthidae is characterized by a **tetraserial armature on the long, narrow tentacular clubs**, with **conspicuously large suckers in the 2 medial series of the manus** and small suckers in the marginal series; a **distinct cluster of numerous, small, alternating suckers and knobs in 6 or 7 irregular transverse series at the proximal end (carpus)** of the club; **2 longitudinal series of transverse pairs of alternating suckers and pads extend along nearly the entire length of the extremely long tentacular stalks**, increasingly more widely spaced proximally; arms with very numerous suckers in 2 transverse series; a straight simple funnel-locking cartilage; buccal connectives that attach to the dorsal border of arms IV; (apparent) absence of photophores; presence of ink sac; absence of hooks on arms and tentacles; fins proportionally small, ovoid, without free anterior lobes, subterminal posteriorly.

Size: Giant squids; have been reported to total lengths of 18 m and mantle lengths 3 m (to 5 m – questionable record), but animals of this size seldom are recorded. Most specimens are in the range of 6 to 13 m total length. Weight to 500 kg, possibly greater.

Geographical Distribution: Worldwide oceanic in distribution, but the true extent of geographical and depth ranges is yet to be determined. Specimens are excluded from equatorial, tropical and high polar latitudes. One stranded specimen was reported for the first time from the far western Mediterranean Sea.

Remarks: Eight genera have been named, but all of them are synonyms of ***Architeuthis***; therefore the family Architeuthidae is monotypic. This family includes the largest of all cephalopods in total length. Specimens occasionally are found moribund at the surface of the ocean, but most records are from strandings, sperm whale stomachs and, increasingly, from deep-sea trawling activity, e.g. for orange roughy (*Hoplostethus atlanticus*).

Literature: Verrill (1879–1880), Roper and Young (1972), Nigmatullin (1976), Roper *et al*. (1984), Roper (1998a), Sweeney and Young (2003b).

Architeuthis Steenstrup, 1857

Plate VI, 32

Architeuthis Steenstrup, 1857b. *Forhandlinger ved de Skandinaviske Naturforskeres*, 7: 182–185 [183].

Type Species: *Architeuthis dux* Steenstrup, 1857.

Frequent Synonyms: *Architeuthis (Architeuthis)* Steenstrup, 1857b; *Architeuthis* Steenstrup, *in* Harting, 1860; *Megaloteuthis* Kent, 1874; *Dinoteuthis* More, 1875; *Mouchezis* Velain, 1877; *Megateuthis* Hilgendorf, 1880; *Plectoteuthis* Owen, 1881; *Steenstrupia* Kirk, 1882; *Dubioteuthis* Joubin, 1900.

FAO Names: En – Giant squid; **Fr** – Encornet monstre; **Sp** – Megaluria.

Diagnostic Features: Because the Architeuthidae is monotypic, the generic characters are the same as those of the family.

Geographical Distribution: As above.

Remarks: Numerous species have been named in the sole genus of the family, ***Architeuthis***, but most of the 21 nominal species are based on incomplete, damaged specimens and are so inadequately described and poorly understood that the systematics of the group is thoroughly confused. A complete list of species associated with the Architeuthidae is presented by Sweeney and Young (2003b). Currently, 3 species are considered valid by some authors, while others regard these 3 entities as subspecies of ***Architeuthis dux***. The diagnostic morphological features currently are little understood and the entities are distinguised geographically. Molecular and morphological studies indicate that these entities possibly represent a single species of worldwide distribution, precisely, ***A. dux*** (Carlini and Graves, 1999; Förch, 1998; Roeleveld, 2000). However, the resolution and breadth of the analyses were insufficient to provide conclusive evidence. Genetic studies are underway that will compare characteristics of ***Architeuthis*** specimens from all major localities throughout its geographical range. Because the species characters and the distributional ranges of the species currently are in flux and unresolved, the species will be treated together here; however, data on the type locality, FAO names and geographical concentration of records are reported individually.

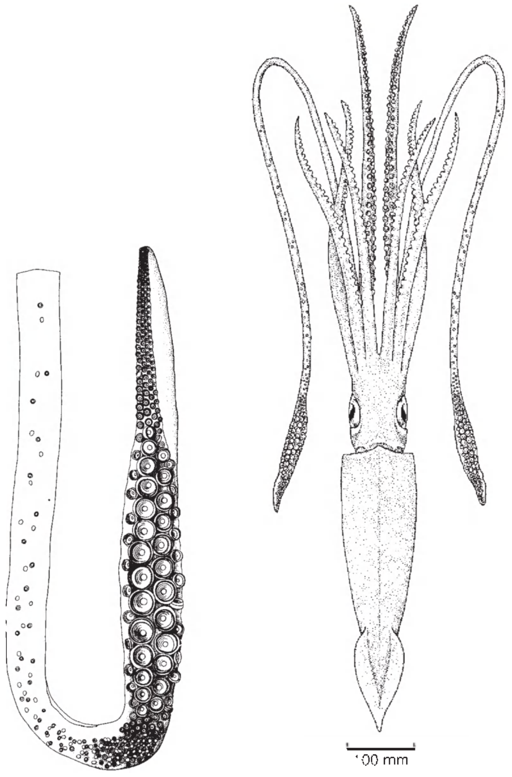
Architeuthis dux Steenstrup, 1857

Fig. 165

Architeuthis dux Steenstrup, 1857b, *Forhandlinger ved de Skandinaviske Naturforskeres*, 7: 182–185 [183]. [Type locality: 31°N 76°W, North Atlantic Ocean].

FAO Names: En – North Atlantic giant squid; **Fr** – Encornet monstre de l'Atlantique du Nord; **Sp** – Megaluria de l'Atlantico Norte.

Geographical Distribution: Concentrations of records are from the North Atlantic Ocean, especially Newfoundland, Norway, northern British Isles, northern Spanish waters and the oceanic islands of the Azores and Madeira. A number of records now exist from the lower Gulf of Mexico, through the Straits of Florida, Bahamian waters and Bermuda. Also recorded from the western Mediterranean Sea (Fig. 166).



tentacular club dorsal view

Fig. 165 ***Architeuthis dux***

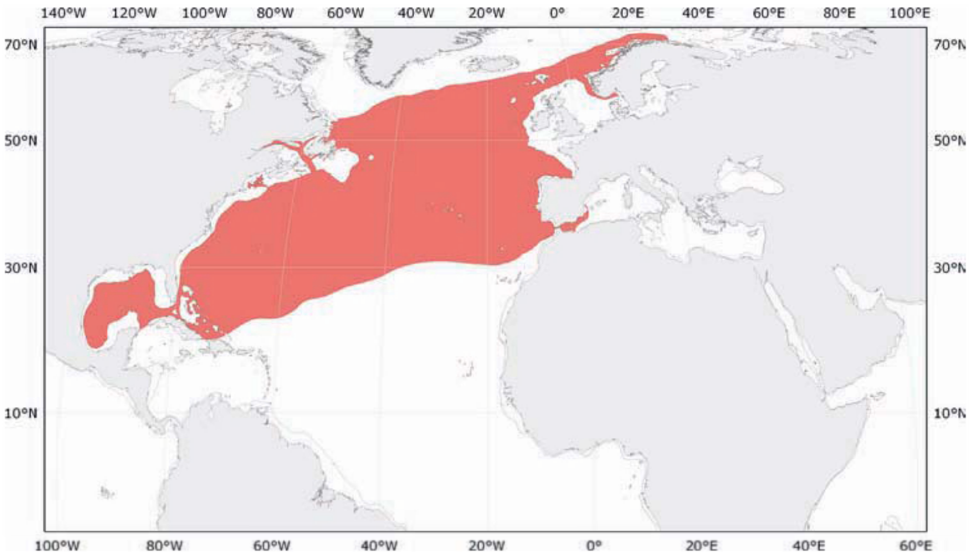


Fig. 166 ***Architeuthis dux***

🟥 Known distribution

Architeuthis martensii (Hilgendorf, 1880)

Megateuthis martensii Hilgendorf, 1880, *Sitzungsbericht Gesellschaft naturforschender Freunde, Berlin*, 4:65–67 [65]. [Type locality: Western North Pacific Ocean, Japan].

FAO Names: En – North Pacific giant squid; **Fr** – Encornet monstre de le Pacifique Nord; **Sp** – Megaluria del Pacífico Norte.

Geographical Distribution: Concentrations of records are from the North Pacific Ocean, especially around Japan and off northern California.

Architeuthis sanctipauli (Velain, 1877)

Mouchezis sanctipauli (Velain, 1877), *Archives de Zoologie Experimentale et Generale Southern Indian Ocean*, 6:1–143, [8]. [Type locality: 38°43'S, 77°32'E, St Paul Island, southern Indian Ocean, on the beach]

FAO Names: En – Southern Ocean giant squid; **Fr** – Encornet monstre de l'Océan Austral; **Sp** – Megaluria de l'Oceano Austral.

Geographical Distribution: Concentrations of records are from the southwestern Pacific around New Zealand, southern Australia and southern South America and circumglobal in the Southern Ocean, including the southern Indian Ocean.

Size: See family discussion. The maximum size of ***Architeuthis martensi*** appears to be smaller than that of the forms from other regions.

Habitat and Biology: The vertical distribution of ***Architeuthis*** remains difficult to assess precisely, but captures in deep-sea fishing nets and more accurate information on the foraging behaviour of its principal predator, sperm whales, indicate a range of about 200 to 800 m (perhaps to 1 000 m). The zone of maximum concentration appears to be about 400 to 600 m. These sources also indicate habitats associated with the bottom as well as in deep midwater layers well above very great bottom depths. A specimen of ***Architeuthis*** was photographed alive for the first time as it attacked a baited camera off Japan at 900 m. It became hooked on the baited jig and pulled the array up to 600 m before a tentacle broke and the squid escaped. ***Architeuthis*** may be a stronger predator than previously suspected, using vigorous attacks with its tentacles. Juveniles of the species have been reported from both the Atlantic and Pacific Oceans and from Japan. The morphology and temporal, geographic and bathymetric distribution of 17 paralarvae have been described from off New Zealand. Adults and preadults are reported from all major oceans, but verifying their actual habitat is difficult. As with other cephalopods the growth rate of ***Architeuthis*** is thought to be very rapid, and full adult sizes (up to perhaps 500 kg) may be attained in a maximum of 2 to 3 years based on statolyth analysis. However, isotopic analysis using delta super (18) Oxygen suggest a longer life span, perhaps to about 14 years. Analysis of stranded specimens on the northern coast of the Iberian Peninsula, Spain, shows a strong temporal and spatial relationship to geophysical prospecting utilizing high energy air gun (acoustic) arrays in near-by Bay of Biscay waters. Females produce very small eggs, 1.4 mm by 0.7 mm, in enormous numbers; 1 female examined had in excess of 5 kg of eggs in her ovary, numbering more than 1 million eggs. Other calculations suggest a fecundity of 10 million eggs. Males mature at smaller sizes than females; they produce hundreds of spermatophores (up to 500 mm long) that are stored in the large Needham's sac until mating occurs. The terminal end of Needham's sac, termed the penis, is extremely elongate and protrudes out of the mantle opening to the level of the anterior portion of the head. While mating has not been observed, spermatangia from extruded spermatophores have been noted embedded under the skin, into the subcutaneous tissue of the arms and head of females. Adults of ***Architeuthis*** are consistently preyed upon by sperm whales, subadults by adult sleeper sharks (*Somniosus* cf. *microcephalus*), while juveniles are subjected to predation by mesopelagic fishes such as lancetfishes, *Aphonopus carbo* and *Alepisaurus ferox*. Prey of ***Architeuthis*** consist of macrourid fishes (including *Macruronus novaezelandiae*, the blue grenadier), the blue whiting (*Micromesistius poutassou*), squids (including ***Architeuthis***, ***Nototodarus***) and orange roughy (*Hoplostethus atlanticus*). Analysis of tracers, heavy metals and stable isotopes suggests that ***Architeuthis*** is a very high level predator, feeding on high trophic level fishes and squids. Stable isotope and trace element analyses of ***Architeuthis*** beaks indicate aspects of its biology: ontogenetic change in diet early in life history, age of at least 2 years, and sedentary behaviour in adulthood, with gradual ontogenetic descent. Extremely unusual strandings of 9 specimens on the Iberian Peninsula (2001, 2003) have been linked to geophysical prospecting use of sonic explosion air guns, which caused acute tissue damage and death.

Interest to fisheries: While there is no interest in ***Architeuthis*** as a fishery commodity, many recorded specimens in the past 3 decades have been captured as bycatch in commercial fishery trawls. The principal fisheries involve deep-sea target species such as hoki, orange roughy and scampi, for example, where fishing depths are 400 to 1 000 m. Even if a predictable harvest were possible, which currently seems quite unlikely, the flesh of ***Architeuthis*** contains ammonium ions that help maintain buoyancy at the desired depth range but also render the musculature very bitter tasting to humans, thus inedible.

Local Names: GERMANY: Kraken, Karke.

Remarks: Recent records from the far western Mediterranean Sea, probably are in association with an increase of specimens reported in the Iberian Peninsula waters. A very small "market" exists for ***Architeuthis***, based on the desire of natural history museums, public marine aquaria and marine science centres to have on display a preserved representative of among the largest invertebrates ever to exist in the world. Such specimens with associated exhibition and educational materials and programmes provide marvelous opportunities to teach about the world's oceans and their deep-sea inhabitants and ecosystems. The extensive list of publications in the Appendix is provided because of the broad interest in ***Architeuthis***, the giant squid, even though it is not a target species for fisheries. Notations of "survey" and "review" indicate works of broader coverage, both geographically and in detail of morphology of particular specimens. "Locality" denotes a report of a specimen or specimens from a specific locality or region; these also may contain information on anatomy as well as measurements, but in general are less comprehensive than "review" or "survey" publications. Other notations are clearly topical.

Literature: Roper *et al*. (1984), Roeleveld and Lipinski (1991), Aldrich (1992), Förch (1998), Roper (1998a), Sweeney and Young (2003b), Guerra *et al*. (2004a, b, c), Hoving *et al*. (2004), Landman *et al*. (2004), Kubodera and Mori, (2005).

2.5. Family BATHYTEUTHIDAE Pfeffer, 1900

by Clyde F.E. Roper and Patrizia Jereb

Bathyteuthidae Pfeffer, 1900, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2): 145–198 [173].

Type Genus: *Bathyteuthis* Hoyle, 1885b.

FAO Names: En – Deepsea squids; **Fr** – Loutènes abyssales; **Sp** – Batilurias.

Diagnostic Features: The Bathyteuthidae is distinguished by the presence of a straight funnel-locking cartilage; **buccal connectives that attach to the dorsal borders of arms IV; minute suckers on the 7 buccal lappets**; **clubs small, unexpanded with many transverse series (6 to 8) of minute suckers, no carpal cluster**; **round or paddle-like subterminal, lobed fins** (i.e. posterior margins convex); mantle cylindrical, bluntly rounded posteriorly; head wider than mantle; eyes angled slightly anteriorly; suckers on the arms arranged in irregular transverse series (2 series proximally, increase to 4 series distally on arms I to III; 1 or 2 series only on IV); a uniform deep maroon colour over all surfaces. **A single, small, black-pigmented photophore is embedded at the base of each arm I to III** (this is clearly apparent in young specimens but may be obscure in adults).

Size: Small-sized squids; maximum mantle length 75 mm.

Geographical Distribution: Worldwide.

Habitat and Biology: ***Bathyteuthis abyssicola***, the most common species, is most abundant between 700 and 2 500 m. While most species of deepsea squids produce ammonium to achieve neutral boyancy, bathyteuthid squids, ***B. abyssicola*** and ***B. berryi***, instead concentrate high amounts of a low-density cation, as yet unidentified. This results in muscular tissue more comparable to shallow-living squids, which, in turn enables bathyteuthids to be much stronger swimmers than other deep-sea squids. Odontocete cetaceans are known predators. Photosensitive vesicles on the dorsal surface of the head appear to function to detect bioluminescent light from neighbouring organisms beyond the visual field.

Remarks: Bathyteuthidae formerly included a second genus ***Chtenopteryx***, because of several shared features. Roper (1969) considered the differences in other characters sufficiently strong as to warrant separate families for the 2 genera. A molecular study by Carlini and Graves (1999) confirmed a close relationship between the 2 families. The single genus, ***Bathyteuthis***, contains 3 species: ***B. abyssicola***, the most common species, that has been recorded from all major oceans; ***B. bacidifera*** and ***B. berryi***, rather more limited in distribution and infrequently captured.

Literature: Roper (1969), Young (1972a), Nesis (1982, 1987), Roper and Young (1975), Roper *et al*. (1984), Roper and Sweeney (1992a), Clarke and Young (1998), Miske (1998), Sweeney and Roper (1998), Roper (1998d), Carlini and Graves (1999), Sweeney and Young (2003c).

Bathyteuthis Hoyle, 1885

Bathyteuthis Hoyle, 1885b, *Report on the Scientific Results of the Voyage of H.M.S. Challenger*, 1(1): 269–274 [272].

Type Species: *Bathyteuthis abyssicola* Hoyle, 1885b.

Frequent Synonyms: *Benthoteuthis* Verrill, 1885.

Diagnostic Features: The family is monotypic so the generic characters are the same as those given for the Bathyteuthidae.

Key to the species of *Bathyteuthis* (adults and juveniles)

1a. Protective membranes on arms low to well developed, fleshy, with straight to gently scalloped borders; trabeculae not free, enlarged, or elongate . . . . **→ 2**

1b. Protective membranes reduced or absent; trabeculae free, elongate, finger-like; arm suckers numerous; sucker rings with 18 to 34 protuberances; gills long, broad . . . . ***Bathyteuthis bacidifera***

2a. Arm suckers relatively few, sucker rings with 8 to 18 protuberances; arms short, blunt; gills short, narrow . . . . ***Bathyteuthis abyssicola***

2b. Arm suckers extremely numerous; sucker rings with 10 to 14 protuberances; arms long, attenuate; gills long, broad . . . . ***Bathyteuthis berryi***

Bathyteuthis abyssicola Hoyle, 1885

Fig. 167

Bathyteuthis abyssicola Hoyle, 1885b, *Report on the Scientific Results of the Voyage of H.M.S. Challenger*, 1(1): 269–274 [272]. [Type locality: 46°16'S, 48°27'E, southwestern Indian Ocean].

Frequent Synonyms: *Benthoteuthis megalops* Verrill, 1885.

FAO Names: En – Bathyal deepsea squid; **Fr** – Loutène abyssale; **Sp** – Batiluria abisal.

Diagnostic Features: Mantle robust, bluntly rounded posteriorly. Fins round, small, separate, short; eyes orient slightly anteriorly. **Clubs unexpanded, short, with relatively few, small, coequal-sized suckers**. **Arms short, blunt with few** (about 100 on arms I to III) **small suckers**; **protective membranes present**, with straight or gently scalloped borders; **trabeculae not free, enlarged or elongate**; gills short, blunt, narrow; colour deep maroon.

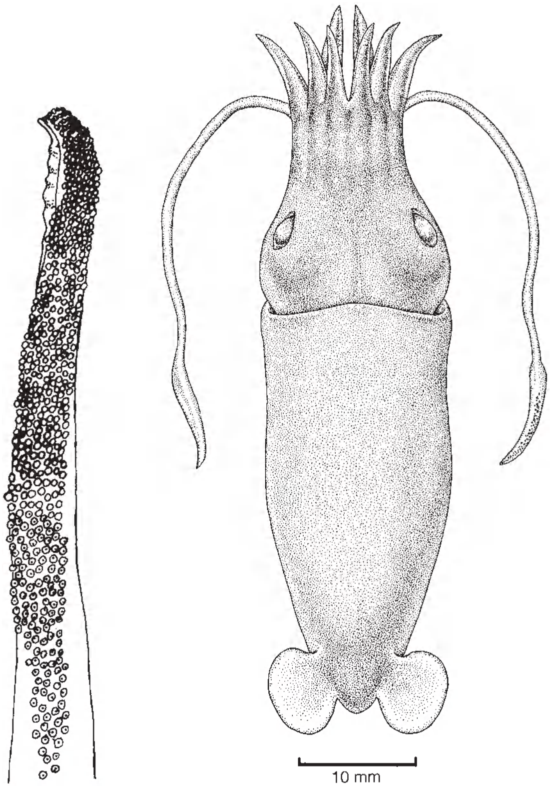
Size: The maximum mantle length is 75 mm.

Geographical Distribution: Circumglobal. Most abundant in the Southern Ocean and in highly productive waters of the eastern Pacific, Atlantic, and Indian oceans. Records from the Mediterranean Sea (Fig. 168).

Habitat and Biology: An oceanic species that occurs between about 100 and 4 200 m depth, but normally it is encountered between 700 and 2 000 m in the Southern Ocean where it carries out a deep vertical diurnal migration. Paralarvae and juveniles tend to live at shallower depths than the adults. The mantle length at first maturity is about 40 to 50 mm in females and 35 mm in males. Diel vertical migration of the population occurs in the eastern tropical-subtropical North Atlantic Ocean with the species concentrated between 100 and 1 000 m. Among predators of ***B. abyssicola*** are the melon-headed whale in Hawaiian waters.

Interest to Fisheries: Although the species is especially abundant in the Southern Ocean, it presently has no commercial value.

Literature: Roper (1968, 1969), Clarke and Lu (1975), Vecchione *et al*. (2001), Seibel *et al*. (2004).



tentacular club

dorsal view

Fig. 167 *Bathyteuthis abyssicola*

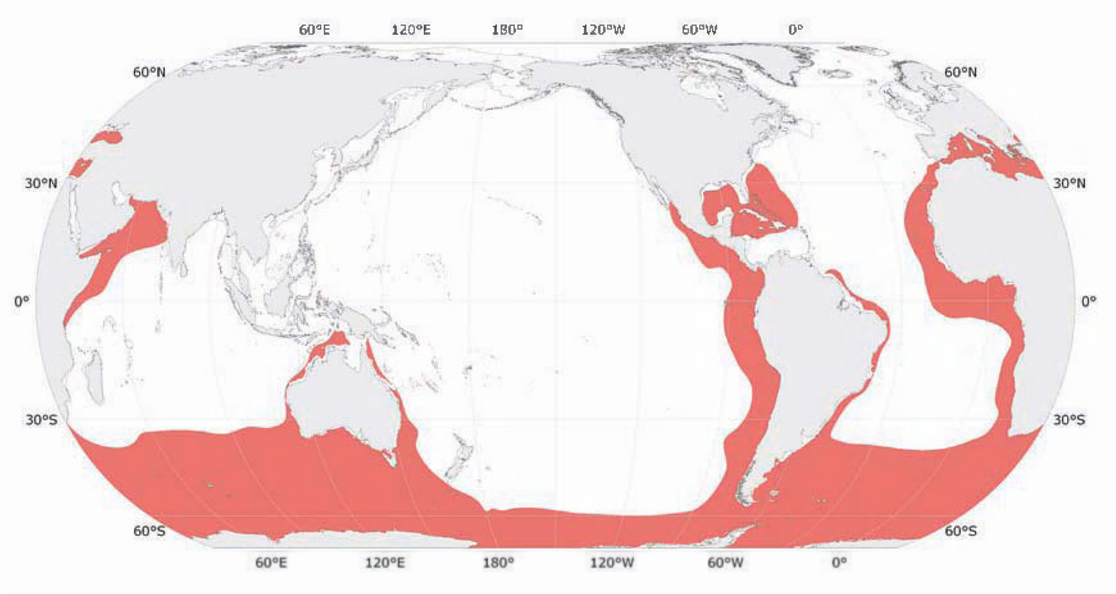


Fig. 168 *Bathyteuthis abyssicola*

🟥 Known distribution

Bathyteuthis bacidifera Roper, 1968

Bathyteuthis bacidifera Roper, 1968, *Proceedings of the Biological Society of Washington*, 81: 161–172 [163]. [Type locality: 07°47'S, 81°23'W, eastern South Pacific Ocean].

Size: The mantle length extends to 40 mm.

Geographical Distribution: A mesopelagic to bathypelagic species in the tropical Indo-Pacific region, principally in the productive waters of the eastern Pacific Equatorial Water Mass. Occurs from 600 to 1 550 m in tropical eastern Pacific (open net captures).

Literature: Roper (1968, 1969), Nesis (1982, 1987).

Bathyteuthis berryi Roper, 1968

Bathyteuthis berryi Roper, 1968, *Proceedings of the Biological Society of Washington*, 81: 161–172 [169]. [Type locality: 33°14'45"N, 118°37'20"W, eastern North Pacific Ocean].

Size: The mantle length attains 50 mm.

Geographical Distribution: A bathypelagic species from the eastern North Pacific Ocean, off southern California. Captured in open nets between 800 and 1 200 m, but probably occurs deeper, as well.

Literature: Roper (1968, 1969), Nesis (1982, 1987).

2.6 Family BATOTEUTHIDAE Young and Roper, 1968

by Clyde F.E. Roper and Patrizia Jereb

Batoteuthidae Young and Roper, 1968, *Antarctic Research Series*, 2: 185–202 [185].

Type Genus: *Batoteuthis* Young and Roper, 1968.

FAO names: En – Bush-club squids; **Fr** – Encornets piquets; **Sp** – Calamars pestillos.

Diagnostic Features: Funnel-mantle locking apparatus distinctly curved. **Buccal connectives attach dorsally to arm pairs I and II, ventrally to arm pairs III and IV**. Large elongate photophores on aboral tips of arms IV in large subadult males; small aboral photophores on tips of arms IV of large subadult females. Gladius with long slender rachis; true vane lacking. **Conus extremely elongate**; **midventral fusion apparent**. **Club 80% or more of tentacle length**; **6 distinct transverse series of very small, very numerous suckers**; **no separate, distinct dactylus and carpus**. **Head disproportionately small and narrow**. Fins short, about 20% of mantle length. Mantle long, slender, produced into long, pointed tail posteriorly. Viscera compact, located near anterior end of mantle cavity (except gonads).

Size: Mantle length up to 300 to 350 mm, exclusive of the elongate, spindle-like tail (supported by secondary conus of gladius) posterior to the fins.

Geographical Distribution: It occurs in the Antarctic and sub-Antarctic waters of the South Atlantic, South Pacific and southern Indian oceans between approximately 45°S to 60°S.

Habitat and Biology: It is a bathypelagic to abyssopelagic circumglobal form.

Interest to Fisheries: Because of its apparent rarity in deep-sea trawls, this species is of no current interest to fisheries, other than its availability as prey to deep-living fishes of commercial interest.

Local Names: USA: Spike-tail squid.

Remarks: This remarkable monotypic squid has been reported infrequently since its original description.

Literature: Young and Roper (1968), Nesis (1982, 1987), Sweeney and Young (2003d), Young and Roper (2008d).

Batoteuthis Young and Roper, 1968

Batoteuthis Young and Roper, 1968, *Antarctic Research Series*, 2: 185–202 [185].

Diagnostic Features: The diagnostic characters for the sole known genus are the same as those given for the family.

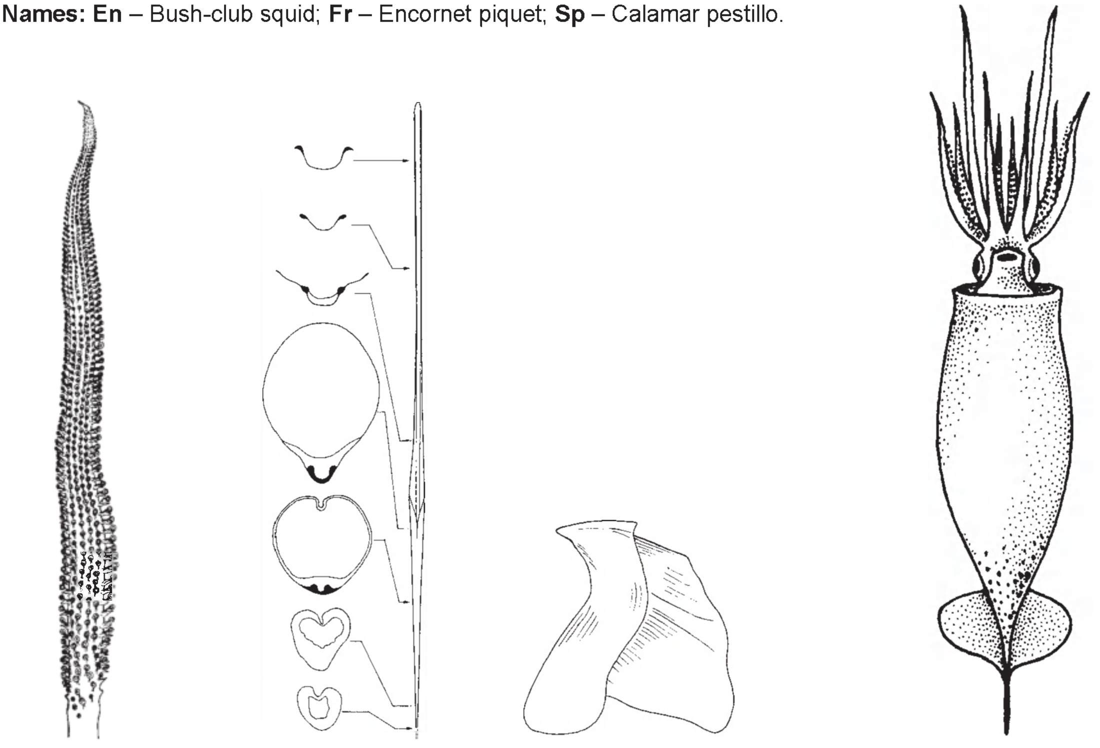
Batoteuthis skolops Young and Roper, 1968

Fig. 169

Batoteuthis skolops Young and Roper, 1968, *Antarctic Research Series*, 2: 185–202 [185]. [Type locality: 49°57’S; 169°01’W, South Pacific Ocean, about 1 000 km southeast of Wellington, New Zealand, in the region of the Antarctic Convergence].

Frequent Synonyms: None.

FAO Names: En – Bush-club squid; **Fr** – Encornet piquet; **Sp** – Calamar pestillo.



tentacular club gladius mouth ventral view

Fig. 169 ***Batoteuthis skolops***

Diagnostic Features: The specific characters are those given for the monotypic family, as well as the following additional characters. The mantle wall is thin but muscular, similar to most cranchiids. **The gladius is visible along the dorsal midline and extends far posteriorly as a supporting element of the long, thin, spindle-like tail**. The tail is about 50% of the mantle length, at least in young specimens. The fins are very short, only 20% of the mantle length. **The head is remarkably small and narrow** in comparison with the mantle size. **The eyes are proportionally very large**. The funnel component of the locking apparatus is deeply grooved, slightly broader and deeper posteriorly. Arms are long, slender, very attenuate at tips. The tentacles are relatively short, only 1.5 times longer than the arms, but quite robust. **The clubs are extremely long, 80% of tentacle length**, not appreciably expanded. Numerous pointed trabeculae are present, but only a trace of a protective membrane exists. **Suckers in 6 transverse series are small and very numerous, with small, conical widely-spaced teeth**. The inner horny rings of the arm suckers have broadly spaced, sharp, pointed teeth on the distal half. **No dactylus or carpus exist**.

Size: The total mantle and tail length extends to 350 mm.

Geographical Distribution: Circumpolar in Antarctic to sub-Antarctic waters, from about 45°S to 60°S (Fig. 170).

Habitat and Biology: The species is a bathypelagic to abyssopelagic form. Recorded depth range from 366 m for a 30 mm mantle length juvenile during the day to 1 200 to 2 500 m for larger juveniles and subadults at night (open net captures only). The largest specimen described with intact tentacles is the holotype. A few growth stages have been described. Paralarvae and mature adults are unknown. The southern elephant seal is one known predator.

Local Names: USA: Antarctic spike-tail squid.

Literature: Young and Roper (1968), Nesis (1999b), Golub (2001), Anderson and Rodhouse (2002), Jackson *et al*. (2002), Young and Roper (2008d).

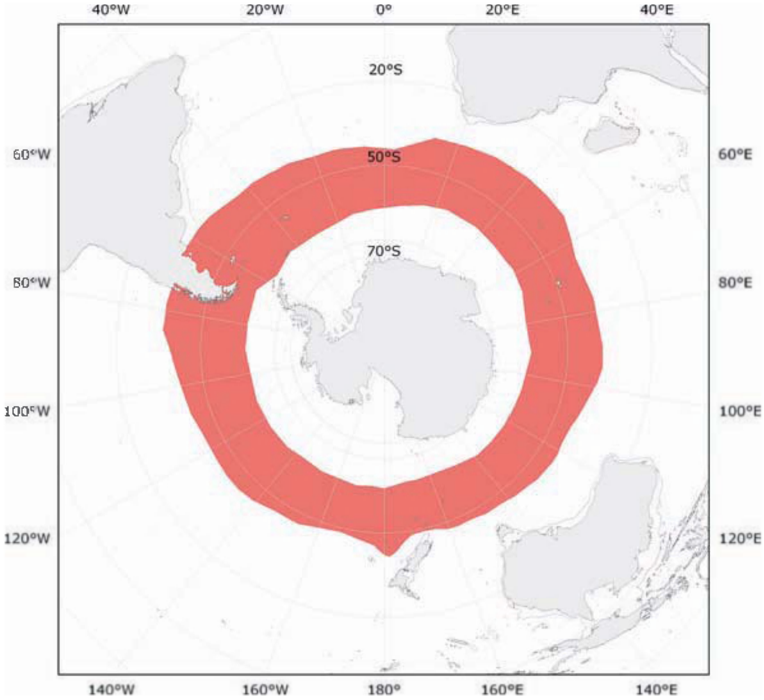


Fig. 170 ***Batoteuthis skolops***

🟥 Known distribution

2.7 Family BRACHIOTEUTHIDAE Pfeffer, 1908

by Clyde F.E. Roper and Patrizia Jereb

Brachioteuthidae Pfeffer, 1908b, *Nordisches Plankton*, 2(9)(4): 9–116 [78].

Type Genus: *Brachioteuthis* Verrill, 1881: [405].

FAO Names: En – Arm squids; **Fr** – Encornets bras courts; **Sp** – Braquilurias.

Diagnostic Features: The adults are characterized primarily by the presence of numerous transverse series (rows) of very small, long-stalked suckers on the greatly expanded proximal portion (manus) of the tentacular clubs; dactylus section with 3 or 4 series of suckers; **carpal-locking apparatus extends along tentacular stalk**; straight, simple groove in funnel-locking cartilage; **ventral attachment of the buccal connectives to ventral margins of arms IV**; 2 series of suckers on the arms; mantle long, slender, muscular, but thin-walled; fins relatively short, terminal, heart-shaped or rhomboidal with free anterior lobes. Gladius with a very thin, narrow rachis, a short vane in the posterior third and a well-developed narrow cone; **photophores present in some species as a single photophore on the ventral surface of each eyeball**; digestive gland compact, displaced well posterior to the cephalic cartilage in the mantle cavity. The diagnostic characters of the paralarvae and juveniles are quite distinct from the adults: mantle elongate to elongate/bulbous; fins separate, terminal, paddle-shaped, transversely oval; distinctive, long, slender neck (no arm-crown stalk); eyes lateral but frequently situated toward ventral part of head; distinctive bump-like swelling on dorsal surface of head; mantle opening wide relative to neck; club suckers develop at hatching and adult-like pattern of numerous suckers on proximal manus well established by about 10 mm mantle length; tentacles large, present at hatching, robust relative to arms.

Size: Small to medium-sized squids up to 200 mm mantle length.

Habitat and Biology: A species of ***Brachioteuthis*** from Hawaiian waters spawns individual eggs into the plankton, a unique phenomenon outside the enoploteuthid squids. Paralarval ***Brachioteuthis*** species apparently orient in the water in a head-down posture to resemble a drifting medusoid bell with dangling tentacles to capture prey. Ontogenetic “breakpoints” of morphological characters during growth of paralarval squids were described; these rapid changes in certain characters seem correlated with rapid ecological changes. While few precise data are available on vertical distribution, closing net data for brachioteuthids off Hawaii showed depths of 830 to 975 m during the day and 100 to 150 m at night and open net captures were made at 975 to 1 000 m during daytime and at 50 to 225 m at night. Also, opening/closing net captures in daylight and darkness were made down to 1 000 m in the Scotia Sea. Closing net captures in the Mediterranean of ***Brachioteuthis riisei*** at night were at a150 m. In the Aegean Sea, open net plankton sampling captured juvenile ***B. riisei*** most frequently at 350 m, while other specimens were caught by trawl during the daylight at depths between 540 and 615 m. These data collectively suggest an extensive diel vertical migration for ***Brachioteuthis*** species. ***Brachioteuthis*** species are prey of numerous epipelagic and mesopelagic fishes, for example, yellowfin tuna and swordfish off eastern Australia.

Interest to Fisheries: The relatively small size, thin-walled mantle and apparent “rarity” of ***Brachioteuthis*** species make them unsuitable for commercial harvesting. However, research has shown the high value of these species as prey for fishes, marine mammals and other components of the marine fauna; consequently, they are not “rare” species in their deep-sea ecosystem.

Remarks: Until 2001 the family had been considered to be monogeneric for many decades, the 5 other nominal genera having been synonymized with ***Brachioteuthis*** Verrill (Sweeney and Young, 2003e). Lipinski (2001), described a new genus, ***Slosarczykovia***, with 1 species, and a new species of ***Brachioteuthis***. Six species currently are recognized as valid in the genus ***Brachioteuthis***: ***B. beanii*** Verrill 1881, (in 1880–1881), ***B. behnii*** Steenstrup, 1882, ***B. bowmani*** Russell, 1909 (with some question), ***B. picta*** Chun, 1910a, ***B. linkovskyi*** Lipinski, 2001 and ***B. riisei*** Steenstrup, 1882. However, the taxonomic status of the new genus has yet to be reviewed and thorough revision of all taxa in the family is required. The unusually long neck in paralarval brachioteuthids distinguishes them from all other families of squids except for the paralarvae of Chiroteuthidae. However, most chiroteuthids have an additional elongation of the arm crown stalk (variable among species). Also, the structure of the elongated neck differs between the 2 families. Brachioteuthids have a neck that appears to be a single, muscular, fluid-filled tube continuous with a large, fluid-filled chamber in the mantle cavity. In contrast, the elongate neck of young chiroteuthids is supported by numerous separate chambers, so the paralarvae and juveniles of the 2 families are easily distinguished (Dunning and Lu, 1998). Even though the systematics of the family are very unsettled, an increasing body of biological information on the species has developed since the early 1990s with regard to geographical distribution, ecology, predation and prey (see Appendix). By far the greatest research information has been attributed to ***B. riisei***, an apparently extremely wide-ranging species. However, because the identification of ***Brachioteuthis*** species is so challenging, it is difficult to know which species and growth stages actually are represented in published reports, both for distribution and biology. Some identifications might need to be adjusted once the systematics are stabilized.

Literature: Roper and Young (1975), Nesis (1982, 1987), Young *et al*. (1985), Dunning and Lu (1998), Roper and Sweeney (1992c), Rodhouse and Piatkowski (1995), Roper and Vecchione (1996), Vecchione *et al*. (2001), Shea and Vecchione (2002), Salman *et al*. (2003), Sweeney and Young (2003e), Lipinski and Young (2008).

Brachioteuthis Verrill, 1881

Brachioteuthis Verrill, 1881 *in* 1880–1881, *Transactions of the Connecticut Academy of Sciences*, 5(6): 259–446 [405].

Type Species: *Brachioteuthis riisei* (Steenstrup, 1882).

Frequent Synonyms: *Tracheloteuthis* Steenstrup, 1882; *Entomopsis* Rochebrune, 1884; *Verrilliola* Pfeffer, 1884.

Diagnostic Features: The skin is smooth; a reticulate structure and/or warts may occur in mature males, especially in late subadult and adult stages. The tentacular club has distinctly differentiated suckers; the largest suckers on the proximal manus are at least 50% smaller than those on the proximal dactylus. A carpal (tentacular) fixing apparatus normally present.

Size: The maximum mantle length is 170 to 200 mm.

Remarks: See family discussion.

Interest to Fisheries: See family discussion.

Literature: See family list.

Brachioteuthis riisei (Steenstrup, 1882)

Fig. 171

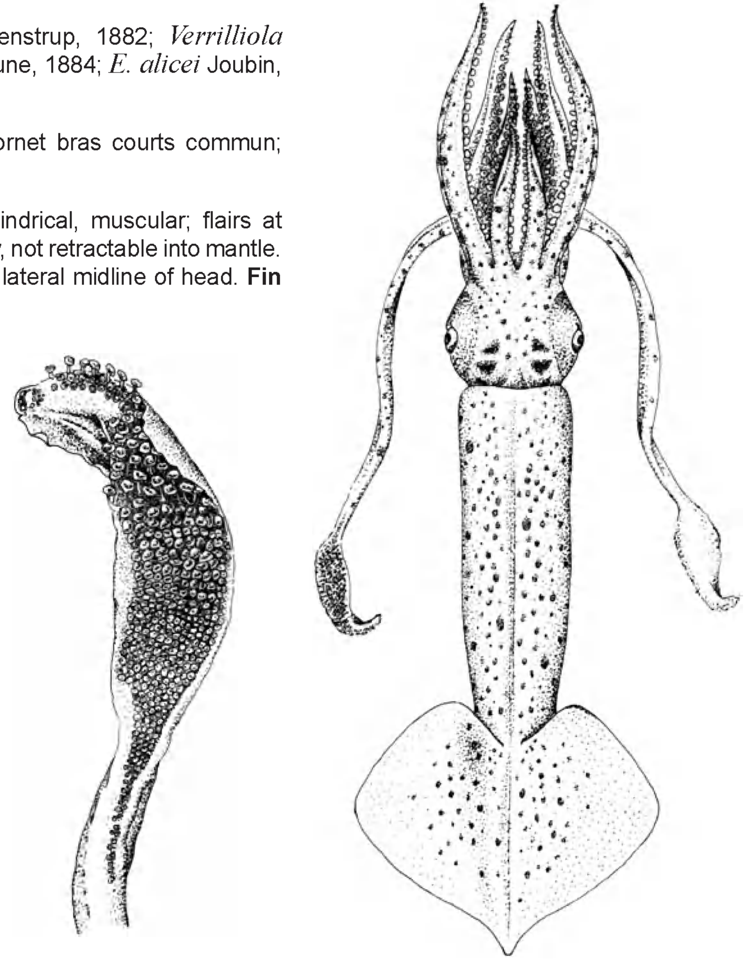
Tracheloteuthis riisei Steenstrup, 1882b, *Videnskabelige Meddelelser fra den Naturhistoriske Forening I Kjrbenhaven*, series 4(3): 293-294 [294]. [Type locality: 34°40'S, 7°W, southeastern Atlantic Ocean].

Frequent Synonyms: *Tracheloteuthis riisei* Steenstrup, 1882; *Verrilliola nympha* Pfeffer, 1884; *Entomopsis velaini* Rochebrune, 1884; *E. alicei* Joubin, 1900.

FAO Names: En – Common arm squid; **Fr** – Encornet bras courts commun; **Sp** – Braquiluria común.

Diagnostic Features: Mantle narrow, elongate, cylindrical, muscular; flairs at mantle opening; conical posteriorly to tip. Head narrow, not retractable into mantle. Neck long to very long in paralarvae; eyes ventral to lateral midline of head. **Fin length from anterior border of fins less than 50% of mantle length and shorter than width**, saggitate to slightly rounded posteriorly, angles rounded, lobes prominent. Tentacles long. **Tentacular clubs wide, with very numerous, minute suckers in the carpal portion**; **4 to 6 transverse series of larger suckers in distal portion**; **4 series at dactylus**. Tentacles in paralarvae and juveniles proportionally much longer than in adults; tentacular clubs broad with 2 to 4 series of "larger" suckers in carpal area, becoming minute in midportion, then 6 to 8 series of knobs in dactyl region. **Carpal-locking apparatus with 2 irregular series of small suckers** along the oral surface of tentacular stalk. Buccal connectives attach to ventral edge of arms IV. Gladius with very long, thin rachis and narrow vane. **A single photophore on ventral surface of each eye** developed in adults. Paralarvae of ***B. riisei*** are characterized by a moderately long neck and eyes that are directed anteriorly at acute angles to the longitudinal axis of the head.

Size: Maximum mantle length to 170 mm in Antarctic populations, to 80 mm in other areas.



tentacular club dorsal view

Fig. 171 ***Brachioteuthis riisei***

Geographical Distribution: A cosmopolitan species. Present in the Atlantic Ocean, from the Norwegian Sea and Iceland (63°N), throughout the Mediterranean Sea (including the Aegean Sea), to the extreme South Atlantic Ocean. (Probably absent in tropical western Atlantic, Gulf of Mexico and Caribbean Sea). In the Indian Ocean, except Arabian Sea and Bay of Bengal; in the South Pacific Ocean, south of central waters; circumglobal in Southern Ocean, but rare in tropics. Zonal designations: boreal, notalian (subantarctic), subtropical, tropical (rare) (Fig. 172).

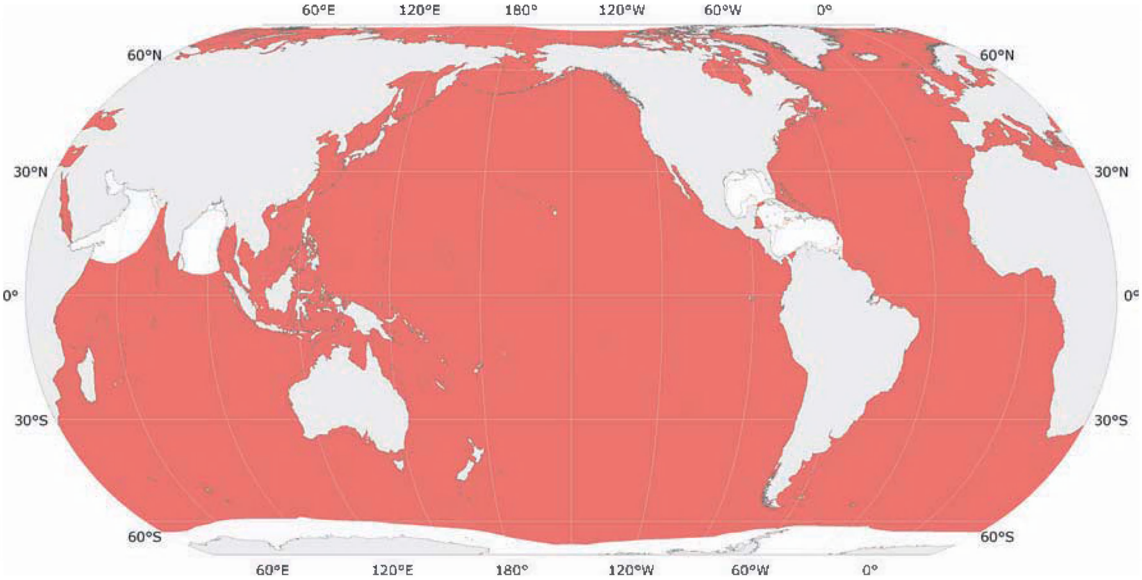


Fig. 172 ***Brachioteuthis riisei***

🟥 Known distribution

Habitat and Biology: An oceanic species that occurs from near the surface through midwaters, the continental slope, to 3 000 m depth. The spawning season appears to be considerably extended with regard to the cosmopolitan distribution of the species complex. Consequently, recently hatched paralarvae and juveniles are found in epipelagic waters throughout the year. In the North Atlantic, paralarvae are particularly abundant from May to August and in February; in the Mediterranean and in upwelling areas off northwestern Africa between 10°N and 30°N, from April to July, September, and from December to February. Paralarvae and juveniles are epipelagic to mesopelagic, then undergo ontogenetic descent to mesopelagic and bathypelagic zones as adults. In the western Atlantic (approximately 39°N 72°W) paralarvae, juveniles and subadults were captured in slope and eddy water masses at 43 to 750 m, with paralarvae and juveniles at less than 300 m and adults greater than 300 m; diurnal vertical migration was indicated. Off Hawaii specimens were caught in closing nets at 830 to 975 m during day and 100 to 150 m at night; open net captures were made at 975 to 1 000 m in daytime and at 50 and 250 m at night. Likewise, in the Mediterranean Sea specimens were caught in closing nets at 150 m during night time, and at 540 to 615 m by trawl nets during the day. Horizontal plankton net sampling at 100 m, 350 m and 650 m during sunrise, noon, sunset and midnight yielded a preponderance of juvenile ***B. riisei*** at 350 m. Paralarval morphology, taxonomy and distribution of ***Brachioteuthis*** sp. (? ***riisei***) were determined in the eastern and western North Atlantic Ocean. ***Brachioteuthis*** (?) ***riisei*** is a frequent prey of sperm whales, striped dolphins, swordfish (*Xiphias gladius*) in Azorean waters, and giant red shrimp (*Aristaeomorpha foliacea*) in the Strait of Sicily, Mediterranean Sea. It is known to prey on krill in Antarctic seas.

Interest to Fisheries: Although this very abundant species/species complex has a nearly cosmopolitan distribution and is a very important food source for higher level predators, it does not appear to have much fishery potential currently.

Local Names: ITALY: Totanello braccio corto.

Remarks: Full extent of distribution undetermined due to uncertain identifications in the literature and probable existence of a currently undifferentiated species complex

Literature: Clarke (1966), Filippova (1972), Roper and Young (1975), Yamamoto and Okutani (1975), Guerra (1992), Nesis (1999b), Lefkaditou *et al*. (2003), Okutani (2005).

Brachioteuthis picta Chun, 1910

Fig. 173

Brachioteuthis picta Chun, 1910a, *Scientific Results of the Expedition Valdivia*, 18(1): 1–401 [207]. [Type locality: 5°6'N, 9°58'E, Benguela Current, South Atlantic Ocean].

Frequent Synonyms: Misidentification as *Brachioteuthis riisei*.

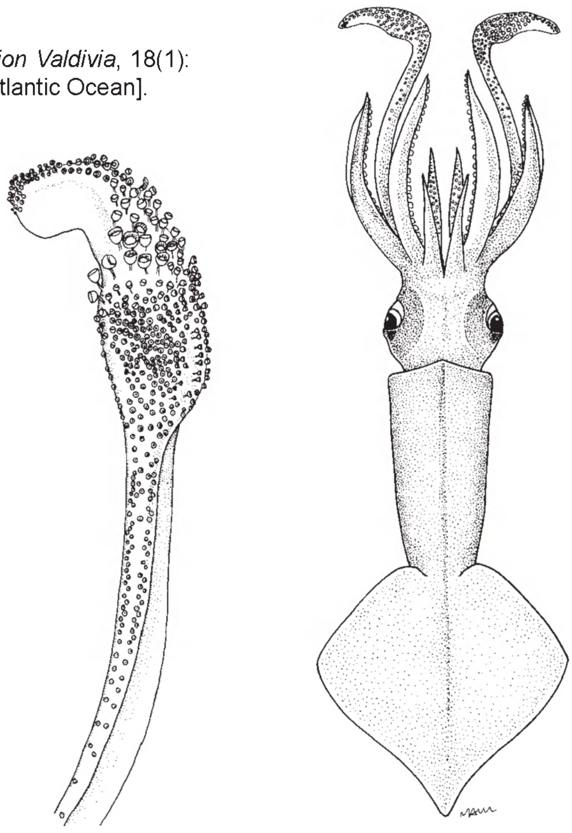
FAO Names: En – Ornate arm squid; **Fr** – Encornet bras courts orné; **Sp** – Braquiluria moteada.

Diagnostic Features: Mantle long, very slender, slightly flared at mantle opening, **abruptly narrows anterior to fins**, extends posteriorly into a pointed tail. Fins saggitate, longitudinally rhomboidal; **fin length and width about 50% of mantle length**; **width: length ratio approximately 0.9:1.1**. Tentacular clubs expanded, covered with numerous minute suckers in the carpal region that extend proximally along the club. **A single sausage-shaped photophore on ventral surface of each eyeball**. Integument consists of reticular, fibrous texture. Colour a light purple-brown or chocolate hue.

Size: Maximum mantle length to 90 mm.

Geographical Distribution: Circumglobal, oceanic from about 30°N to at least 40°S to 45°S (Fig. 174).

Habitat and Biology: An oceanic species occurring in equatorial, southern subtropical, southern peripheral water masses. Paralarvae are epipelagic and mesopelagic; adults are lower epipelagic, mesopelagic and bathypelagic. Predators include the dwarf sperm whale, *Kogia sima*, off Brazil, pygmy sperm whale, *K. breviceps*, off New Zealand, the southern elephant seal, *Miroungia leonina*, and fishes, such as hakes and macrurids. A principal prey item seems to be krill.



tentacular club **dorsal view**

Fig. 173 *Brachioteuthis picta*

Interest to Fisheries: Undetermined.

Remarks: Records of confidence for accurate identification include those from South African waters (e.g. Chun, 1910; Pfeffer, 1912; Nesis, 1982, 1987, 1999b) and from the Antarctic (e.g. Rodhouse, 1989; Piatkowski *et al*. 1994; Rodhouse and Piatkowski, 1995; Roeleveld, 1998).

Literature: Roper (1969), Roper *et al*. (1985), Nesis (1982, 1987), Piatkowski *et al.* (1994), Rodhouse and Piatkowski (1995), Okutani (2005).

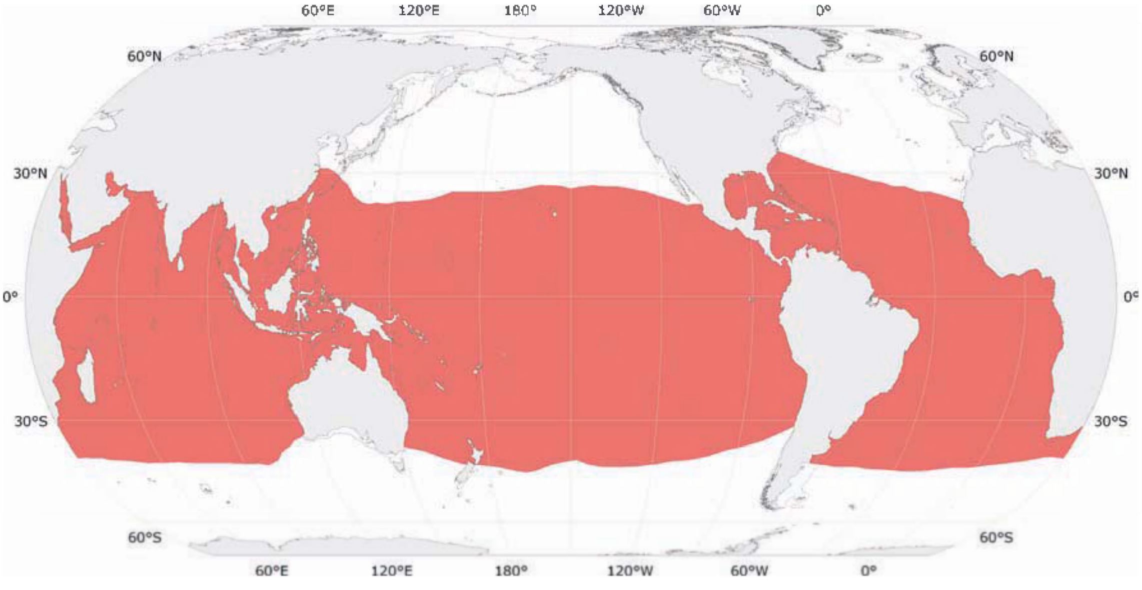


Fig. 174 *Brachioteuthis picta*

🟥 Known distribution

Brachioteuthis beanii Verrill, 1881

Brachioteuthis beanii Verrill, 1881 *in* 1880–1881, *Transactions Connecticut Academy of Science*, 5(6): 259–446 [406]. [Type locality: 39°57'N, 69°19'W and 39°56'N, 69°24'W, western North Atlantic Ocean].

Frequent Synonyms: None.

Size: Maximum mantle length to 100 to 130 mm.

Geographical Distribution: Northwestern Atlantic Ocean off North American east coast, encompassing approximately the region west of 60°W and north of 26°N.

Habitat and Biology: Depths for adults to at least 1 000 m. Although little information exists on this species, its probable mating behaviour was observed and video-taped during 5 submersible dives off Cape Hatteras, North Carolina. The observations were made at 5 to 60 m above the bottom at depths of 500 to 860 m. The squid occurred in schools, and aggregations of 40 to 60 individuals were visible from the submersible at any given time. Three pairs of squid were observed in a tandem position, where the posterior individual grasped the posterior mantle of the anterior squid in its arm crown. The grasped squid bent its head and body posteriorly and vigorously moved its arms around the head and mantle opening of the grasping squid. The coupling had begun prior to the videotaping and continued after the 10-minute sequence was shot, so coupling must continue for an extended period of time.

Literature: Roper and Sweeney (1992c), Roper and Vecchione (1996), Vecchione *et al*. (2001), Okutani (2005).

Brachioteuthis behnii (Steenstrup, 1882)

Tracheloteuthis behni Steenstrup, 1882b, *Videnskabelige Meddelelser fra den Naturhistoriske Forening I Kjrbenhaven*, series (4)3: 293–294 [294]. [Type locality: Indian Ocean (purchased); west coast of New Guinea, western Pacific Ocean; no locality].

Frequent Synonyms: *Tracheloteuthis behnii* Steenstrup, 1882; *Entomposis clouei* Rochebrune, 1884; *Verrilliola gracillis* Pfeffer, 1884.

Size: Mantle length to 60 mm.

Geographical Distribution: Currently considered present in the equatorial and central waters of the Indo-Pacific Ocean, as well as in the equatorial Atlantic.

Habitat and Biology: ***Brachioteuthis behnii*** is considered a tropical-subtropical circumglobal species. Paralarvae are characterized by a very long neck and laterally directed eyes.

Remarks: The species, while currently considered valid, requires further study to confirm its validity or its status as a synonym (Nesis, 1982, 1987).

Literature: Nesis (1982, 1987, 1999b).

Brachioteuthis bowmani Russell, 1909

Brachioteuthis bowmani Russell, 1909, *Annals and Magazine of Natural History*, series 8, 3: 446–455 [449]. [Type locality: northeastern Atlantic Ocean, off Scotland, near the Faeroe-Iceland Ridge; the holotype is not extant (Toll, 1985)].

Frequent Synonyms: None.

Size: Mantle length 61 mm on holotype.

Geographical Distribution: Northeastern Atlantic Ocean, off Scotland near the Faeroe-Iceland Ridge.

Remarks: The systematic status of this species is not resolved, but it is considered to be very closely similar to or synonymous with ***B. beanii*** of the western North Atlantic Ocean (Nesis, 1982, 1987).

Literature: Pfeffer (1912), Nesis (1982, 1987), Sweeney and Young (2003e).

Brachioteuthis linkovskyi (Lipinski, 2001)

Slosarczykovia linkovskyi Lipinski, 2001, *Bulletin of the Sea Fisheries Institute, Gdynia*, 152: 3–14 [5]. [Type locality: 600 miles southeast of Montevideo, Uruguay, South Atlantic Ocean].

Size: The only specimen, a mature male, was 120 mm mantle length.

Geographical Distribution: South Atlantic Ocean.

Remarks: This brachioteuthid (a mature male), known only from the holotype, was collected at night in 720 m water depth in a krill trawl. Characters that differentiate it from other brachioteuthids include: a fibrous integumentary nework with warts covers the mantle (at least in mature males), reticulate but without warts on the head, arms and fins. Sucker dentition on arms with 9 to 12 teeth; tentacular clubs and tentacle very long.

Literature: Lipinski (2001).

Slosarczykovia Lipinski, 2001

Slosarczykovia Lipinski, 2001, *Bulletin of the Sea Fisheries Institute, Gdynia*, 152: 3–14 [5].

Type Species: *Slosarczykovia circumantarctica*, Lipinski 2001.

Diagnostic Features: Surface integument of **mantle, head, arms and fins of both sexes are covered with reticulate fibrous, delicate tissue**. The **tentacular club has only weakly differentiated suckers**; the largest suckers on the proximal manus are about 33% (or slightly larger) of those on the proximal dactylus. **No carpal (tentacular) fixing apparatus exists**.

Remarks: ***Slosarczykovia*** is a monotypic genus, with ***Slosarczykovia circumantarctica*** Lipinski, 2001 the sole recognized species at present. The systematic status of the genus has not yet been reviewed.

Literature: Lipinski (2001).

Slosarczykovia circumantarctica Lipinski, 2001

Slosarczykovia circumantarctica, Lipinski, 2001, *Bulletin of the Sea Fisheries Institute, Gdynia*, 152: 3–14 [6]. [Type locality: the waters adjacent to Wilkes Land, Antarctica].

Frequent Synonyms: *Brachioteuthis picta*, Roper, 1969; *Brachioteuthis* species, Filippova, 1972; *Brachioteuthis* species, Nesis, 1982/1987; *Brachioteuthis picta*, Rodhouse, 1989.

Diagnostic Features: Since the genus is monotypic, the characters of the species are the same as the characters of the genus.

Size: Mantle length 159 mm.

Geographical Distribution: The waters around the Antarctic continent.

Remarks: This brachioteuthid, which often has puzzled teuthologists and has been reported previously from the Antarctic waters, is one of the most common squids in this vast region.

Literature: Lipinski (2001).

2.8 Family CHIROTEUTHIDAE Gray, 1849

by Clyde F.E. Roper and Patrizia Jereb

Chiroteuthidae Gray, 1849, *Catalogue of the Mollusca of the British Museum*, I: 1–164 [42].

Type Genus: *Chiroteuthis* d'Orbigny, 1841.

FAO Names: En – Chiroteuthid squids; **Fr** – Chirocalmars; **Sp** – Quirolurias.

Diagnostic Features: Funnel-locking apparatus oval, generally with 1 or 2 knobs (tragus, anti-tragus) directed toward the centre of the concavity; variable among genera, fused in ***Grimalditeuthis***. Neck elongate. **Mantle narrow, elongate** (usually), up to 800 mm mantle length. **Tentacles generally extremely long, vermiform** (absent in ***Grimalditeuthis***). **Club suckers usually in 4 transverse series** (suckers/tentacles absent in ***Grimalditeuthis***); (suckers in 6 series in an undescribed genus). Arm suckers in 2 series. **Paralarva very distinctive, called *doratopsis* stage**. **Arms, head and mantle with numerous chambers filled with ammonium chloride**, a light-weight fluid that provides near-neutral buoyancy; tissues semi-gelatinous. Eyelid sinus indistinct; **nuchal folds absent**; olfactory organs are long, slender papillae.

All ***doratopsis*** paralarvae possess all of these characters during some phase of their development (Young and Roper, 1999a):

1. Elongate, chambered neck.
2. Chambered brachial pillar.
3. Gladius that extends posteriorly beyond fins and supports floatation structures or "ornamentation".
4. Vesicular tissue in posterior region of mantle, just anterior to tip.
5. Vesiculate arms in advanced stages.
6. Ventral arms greatly elongate in advanced stages.
7. Tentacular clubs of advanced stages with keels parallel to dorsal protective membrane along most of club length.

Size: Small- to large-sized squids; maximum mantle length to about 800 mm.

Geographical Distribution: Members of the family are represented in all geographic zones of all oceans of the world, from sub-Arctic to sub-Antarctic, circumglobally.

Habitat and Biology: Chiroteuthids are bathypelagic or meso-bathypelagic squids and occasionally occur on or in association with the bottom at bathyal depths. Many species have photophores in various configurations on the eyes, ink sac (viscera), ventral arms, tentacular stalks and tips of clubs. No hectocotylus is present, and the penis is developed into an elongate, spearheaded structure. The duration of the *doratopsis* stage is unknown. *Doratopsis* paralarvae occur in oceanic waters in the upper 200 to 300 m; most attain a relatively huge size for a larval form (up to 90 mm mantle length), then gradually transform into the very different-looking subadult stage. Some changes involve the loss of the larval clubs and formation of new clubs, extensive elongation of the tentacular stalks, development of photophores in some species, loss of the remarkable tail in most species, and generally a marked change in proportions of body components. A loosely defined ontogenetic descent occurs following the *doratopsis* stage until adults of various species may occur as deep as 2 000 to 3 000 m. Chiroteuthid species are very important as prey of odontocete cetaceans, e.g. sperm whales, Frasier's dolphin, pygmy and dwarf sperm whales, pilot whales, as well as blue sharks, tunas, toothfish and seabirds.

Interest to Fisheries: The relatively gelatinous consistency and ammoniacal tissue, the dispersed, deep-sea distribution and the generally small size preclude any significant fishery potential.

Remarks: Considerable morphological differences exist among the 4 chiroteuthid genera, ***Chiroteuthis***, ***Asperoteuthis***, ***Planctoteuthis*** and ***Grimalditeuthis***, all of which in the past were placed in separate families. The Chiroteuthidae at present consists of about 20 species, 2 or 3 as yet undescribed. In addition, 2 undescribed new genera exist. The species level taxonomy is poorly understood and the group is very much in need of a comprehensive monograph. The presence of a *doratopsis* paralarva is the only character that is unique to the family. The gladius of the *doratopsis* paralarvae and of the adults of some species extends well posterior to the fins and supports an unusual elongate "tail" that may have oval, fin-like flaps or a series of small flaps and/or oval bulbs, all of unknown function. The bulbs contain canals that are filled with lightweight fluid that probably function as a buoyancy mechanism (Hunt, 1996). The remarkable similarity of some of these ornately-tailed *doratopsis* paralarvae with some siphonophores has been described (Vecchione, *et al*., 1992).

Key to the genera of Chiroteuthidae

1a. Funnel-mantle locking cartilages (apparatus) fused; nuchal-mantle connective not fused; tentacular clubs without suckers . . . . ***Grimalditeuthis***

1b. Funnel-mantle locking cartilages free, not fused; tentacular clubs with suckers . . . . → ***2***

2a. Mantle covered with numerous, minute "cartilaginous" tubercles; fins together oval to elongate/oval with long axis parallel to mantle; arms IV no longer nor thicker than arms II and III . . . . ***Asperoteuthis***

2b. Mantle without tubercles; fins together circular or oval with long axis transverse to mantle; arms IV longer than arms II and III . . . . → ***3***

3a. Fins together roughly oval with long axis transverse to mantle and lobed both posteriorly and anteriorly; arms IV not appreciably thicker than arms II and III; funnel valve absent; funnel-locking apparatus without tragus . . . . ***Planctoteuthis***

3b. Fins together approximately circular, not lobed posteriorly; arms IV usually much thicker than arms II and III; funnel valve present; funnel-locking apparatus with distinct tragus present . . . . ***Chiroteuthis***

Table 2

Key Characters for Genera of Chiroteuthidae[1/]

Character	*Chiroteuthis*	*Asperoteuthis*	*Grimalditeuthis*	*Planctoteuthis*
Funnel valve	Present	Present	Present	Absent
Tentacle pads	Present	Present	Absent	Absent
Arm IV photophores	Present	Absent	Absent	Absent
Arms IV	Enlarged	Not enlarged	Not enlarged	Variable
Visceral photophores	Variable	Absent	Absent	Absent
Funnel-locking apparatus	Tragus & Antitragus	Variable	Fused	Antitragus
Arm IV suckers	Present	Present	Present	Absent distally
Club suckers	Present	Absent proximally	Absent	Present
Club sucker series	4	4	0	4

[1/] from Young and Roper (1998).

Remarks: Two additional genera, yet to be described, have been recognized, but the details of all of their distinguishing characteristics have not been elucidated because so few specimens are available for analysis.

Literature: Nesis (1982, 1987), Young (1992 [1991]), Young and Roper (1998, 1999a), Young *et al.* (1999b), Sweeney and Young (2003f).

Chiroteuthis d'Orbigny, 1841

Plate VI, 34

Chiroteuthis d'Orbigny, 1841 *in* Férussac and d'Orbigny, 1834–1848, *Voyage dans l'Amérique Méridiaonale*: 96 pp. + 1 vi pp. 361 pp. [xxxii].

Type Species: *Chiroteuthis veranyi* (Ferussac, 1834).

Frequent Synonyms: *Doratopsis* Rochebrune, 1884; *Leptoteuthis* Verrill, 1884; (*Chiridioteuthis*) Pfeffer, 1912; (*Tankaia*) Sasaki, 1929; *Diaphanoteuthis* Tomlin, 1931; *Chiropsis* Joubin, 1932; *Bigelowia* MacDonald and Clench, 1934.

Diagnostic Features: Funnel-mantle locking cartilage present, with tragus and antitragus; **tentacular club oral surface with suckers in 4 series** throughout length; **fins together circular**, not lobed posteriorly; **arms IV much longer, thicker than arms I to III**; funnel valve present; **photophores** present on arms IV, often present on viscera.

Literature: Verrill (1884), Nesis (1982, 1987), Roper and Young (1998).

Chiroteuthis veranyi (Ferussac, 1834)

Fig. 175

Loligopsis veranii Ferussac, 1834, *L'Institut, Journal General des Societes et Travaux Scientifiques de la France et de l'Etranger*, 2(77): 355. [Type locality: from dolphin stomach, Mediterranean Sea].

Frequent Synonyms: *Loligopsis vermicolaris* Rüppel, 1844; *L. perlatus* Risso, 1854; *Onychoteuthis perlopsis* Risso, 1854; *Chiroteuthis lacertosa* Verrill, 1881a; *Leptoteuthis diaphana* Verrill, 1884.

FAO Names: En – Verany's long-armed squid; **Fr** – Chirocalmar de Verany; **Sp** – Calamarín volador de Verany.

Size: Mantle length from 100 to 200 mm.

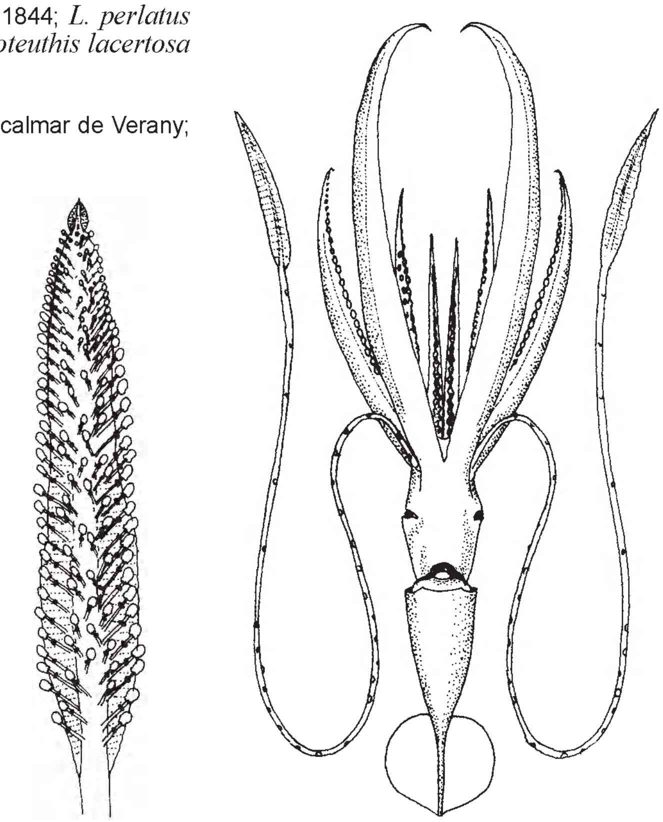
Geographical Distribution: Tropical, subtropical to sub-Antarctic; circumglobal; 55°N to 23°S in Atlantic (Fig. 176).

Habitat and Biology: A mesopelagic to bathypelagic species as adults, ***Chiroteuthis veranyi*** frequently is found in stomach contents of several species of bony fishes, sharks, mammals and seabirds; this confirms that the species is common in its distributional areas, even though seldom captured by commercial fishing gear (e.g. trawls). Its biology is poorly known; paralarvae and juveniles are epipelagic to mesopelagic and widespread in the water column. It has been hypothesized that the species is gregarious, because frequently in deep net tows numerous specimens are captured together, generally an uncommon characteristic with deep sea squids.

Interest to Fisheries: No direct interest for human consumption, but exceedingly important as prey to marine mammals, fishes, other squids and sea birds.

Local Names: ITALY: Totanello volante.

Literature: Verrill (1884), Young (1972a), Nesis (1982, 1987), Vecchione and Roper (1992 [1991]), Roper and Young (1999a).



tentacular club ventral view

Fig. 175 ***Chiroteuthis veranyi***

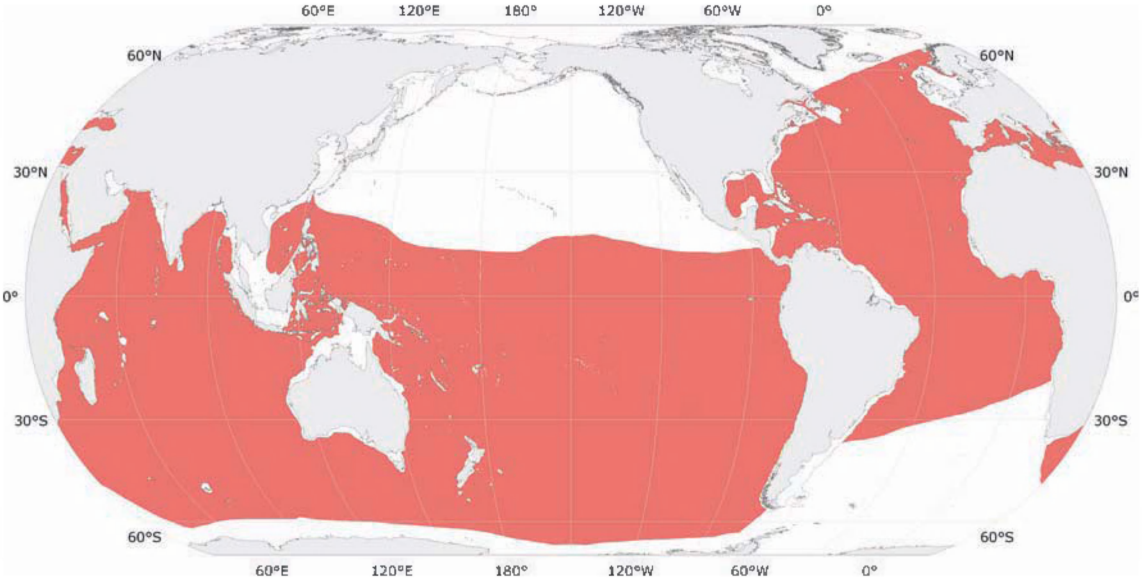


Fig. 176 ***Chiroteuthis veranyi***

🟥 Known distribution

Chiroteuthis calyx Young, 1972

Chiroteuthis calyx Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [69]. [Type locality: "Santa Catalina Basin?", eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 100 mm.

Geographical Distribution: North Pacific Ocean boreal; southern Bering Sea, Gulf of Alaska, Sea of Okhotsk, northeastern Honshu, eastern North Pacific Ocean to southern California (to about 30°N).

Habitat and Biology: A mesopelagic to bathypelagic species. Vertical distribution for smallest stages, 20 to 30 mm mantle length, is in the upper 100 m or so in the eastern Pacific off California. The 30 to 50 mm size group predominates at 300 to 400 m, while the 40 to 60 mm mantle length group is concentrated at 500 to 700 m. Metamorphosis from paralarval to subadult stage occurs at 50 to 60 mm mantle length. Subadults occur at 500 to 800 m during the day, migrate shallower to 100 to 500 m at night.

Interest to Fisheries: No direct interest for human consumption.

Literature: Young (1972a), Nesis (1982, 1987), Roper and Young (1999b).

Chiroteuthis imperator Chun, 1908

Chiroteuthis imperator Chun, 1908, *Zoologischer Anzeiger*, 33(2): 86–89 [88]. [Type locality: 0°15'N, 98°08'E, Sumatra, Indonesia, eastern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 250 mm, possibly to 400 mm.

Geographical Distribution: Indo-Pacific Ocean from Hawaii, Japan, Philippines, Indonesia to 60°E in the Indian Ocean; Australia, Tasman Sea, New Zealand.

Habitat and Biology: Mesopelagic and bathypelagic to bathybenthic. Ontogenetic descent from upper few hundred metres as paralarvae and juveniles to 2 000 m or more as adults. Some adults are captured on the bottom in deep slopewaters.

Remarks: Chun (1908) described ***C. imperator*** from off Sumatra, Indonesia, close to the type locality of ***C. picteti*** Joubin, 1894. Recent examination of the type specimens of ***C. imperator*** by Roper and Young (1999e), however, showed non distinguishing features between the two species. Therefore, ***C. imperator*** is consider a synomym of ***C. picteti*** by these authors.

Literature: Yamamoto and Okutani (1975), Young (1995).

Chiroteuthis joubini Voss, 1967

Chiroteuthis joubini, Voss 1967a, *Annals of the South African Museum*, 50(5): 61–68 [79]. [Type locality: 8°19'N, 44°35'W, western North Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to approximately 100 mm.

Geographical Distribution: Northern subtropical and tropical Atlantic Ocean, Sargasso Sea; western and southern Indian Ocean, 0°S to 45°S, southeastern Africa, southwestern Australia; Banda Sea.

Habitat and Biology: Mesopelagic to bathypelagic.

Literature: Voss (1967a), Clarke (1980), Nesis (1982, 1987), Roper and Young (1999c), Vecchione and Pohle (2002).

Chiroteuthis mega (Joubin, 1932)

Chiropsis mega Joubin, 1932, *Bulletín Societé Zoologie France*, 57: 288–291 [289]. [Type locality: 25°50'N, 76°55'W, western North Atlantic Ocean].

Frequent Synonyms: *Bigelowenia atlanticus* MacDonald and Clench, 1934; *Chiroteuthis capensis* Voss, 1967a.

Size: Mantle length to approximately 100 mm.

Geographical Distribution: Western North Atlantic and eastern South Atlantic in tropical to subtropical waters.

Habitat and Biology: Mesopelagic to bathypelagic.

Literature: Voss (1967a), Roper and Young (1999d), Vecchione *et al.* (2001).

Chiroteuthis picteti Joubin, 1894

Chiroteuthis picteti Joubin, 1894, *Revue Suisse de Zoologie, Genève*, 2: 23–64 [40]. [Type locality: Amboina, Indonesia, eastern Indian Ocean].

Frequent Synonyms: *Chiroteuthis macrosoma* Goodrich, 1896; *C. pellucida* Goodrich, 1896; *C. imperator* Chun, 1908.

Size: Mantle length to approximately 100 mm.

Geographical Distribution: Tropical Indo-West Pacific from Gulf of Aden to southern Honshu, Indonesia and Hawaii; eastern Atlantic (?); southern African waters (?).

Habitat and Biology: Mesopelagic to bathypelagic.

Remarks: Considerable geographical variability has been observed in this species. More detailed studies could indicate that this is a species complex. Salcedo-Vargas (1996) described a subspecies, ***Chiroteuthis picteti somaliensis***, from the western Indian Ocean. (*) ***Chiroteuthis imperator*** Chun, 1908 is considered a synonym of ***C. picteti*** by an authoritative fraction of the scientific community (Roper and Young, 1999e).

Literature: Nesis (1979b), Roeleveld (1998), Bower *et al.* (1999c), Roper and Young (1999e).

Chiroteuthis spoeli Salcedo-Vargas, 1996

Plate VI, 35

Chiroteuthis spoeli, Salcedo-Vargas, 1996, *Beaufortia*, 46(2): 91–108 [17]. [Type locality: Coast of Somalia, western Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length unknown; only small *doratopsis*/juvenile stages known.

Geographical Distribution: Off Somalia, Indian Ocean.

Habitat and Biology: Mesopelagic to bathypelagic.

Literature: Roeleveld (1998), Roper and Young (1999f).

Asperoteuthis Nesis, 1980

Asperoteuthis Nesis, 1980, *Biuletyn Moskovskoe Obshchestvo Ispytatelei Prirody, Otdel Biologicheskii,* 85(4): 59–66 [59].

Type Species: *Asperoteuthis acanthoderma* (Lu, 1977).

Frequent Synonyms: *Chiroteuthis*, Lu, 1977.

Diagnostic Features: Mantle elongate, slender; integument of **mantle, head, arms covered with minute, conical, "cartilaginous" tubercles;** coloration deep violet; **funnel valve present**; funnel-locking apparatus with deep, narrow, curved groove that bifurcates at posterior end; photophores present on extremely long tentacular stalk, absent on arms IV and ink sac; **fins elongate, longitudinally oval, without lobes; lanceolate secondary fins present; arms extremely long, thin**; arms IV not enlarged, are subequal to arms II and III; tentacular stalks with numerous knobs/pads along aboral surface; tentacular clubs short, suckers in 4 transverse series, occupy only distal half of club.

Literature: Nesis (1980).

Asperoteuthis acanthoderma (Lu, 1977)

Fig. 177

Chiroteuthis acanthoderma Lu, 1977, *Steenstrupia*, 4: 179–188 [179]. [Type locality: 6°37'N, 122°02'E, Celebes Sea, western Pacific Ocean].

Frequent Synonyms: None.

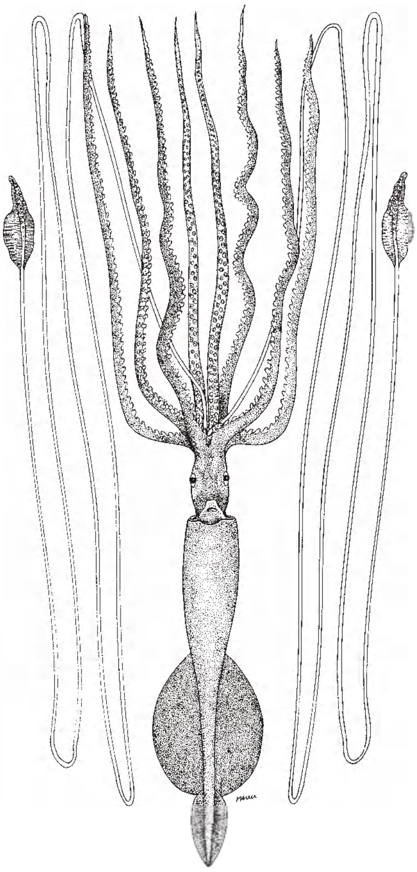
FAO Names: En – Thorny chiroteuthid squid; **Fr** – Chirocalmar épineux; **Sp** – Quiroluria espinosa.

Size: Mantle length to 800 mm.

Geographical Distribution: Indo-West Pacific; Celebes Sea, Ryuku Islands, Molucca Sea, New Guinea, southern Africa; eastern Gulf of Mexico, Gulf Stream Florida, South Atlantic Ocean (Fig. 178).

Habitat and Biology: Mesopelagic to bathypelagic.

Literature: Roper and Lu (1990), Young and Roper (2007), Judkins *et al.* (2009).



ventral view

Fig. 177 ***Asperoteuthis acanthoderma***

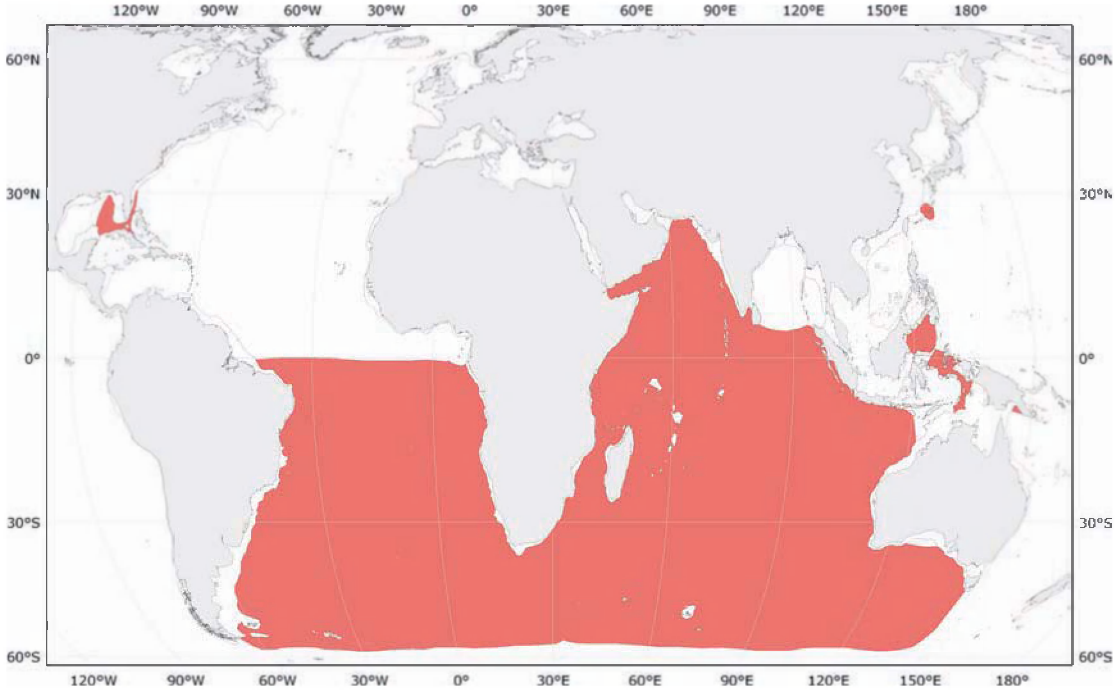


Fig. 178 ***Asperoteuthis acanthoderma***

🟥 Known distribution

Asperoteuthis lui Salcedo-Vargas, 1999

Asperoteuthis lui Salcedo-Vargas 1999, *Mitteilungen aus dem Museum fur Naturkunde in Berlin, Zoologische Reihe*, 75:47-49. [Type locality: Cook Straight, New Zealand. Taken from the stomach of a ling (*Molva molva*)].

Frequent Synonym: None.

Geographical Distribution: Cook Straight, New Zealand.

Remarks: This species is known from a single damaged specimen that was taken from the stomach of a fish (a ling). The specimen was without a funnel or mantle, but had arms, one tentacle and eyes.

Literature: Salcedo-Vargas (1999).

Asperoteuthis mangoldae Young, Vecchione and Roper 2007

Asperoteuthis mangoldae Young, Vecchione and Roper, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 353–365 [354, figs 1–14]. [Type locality: 21°25'N, 158°20.5'W, Hawaiian waters, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length 80 to 128 mm (a mature male at 100 mm mantle length).

Geographical Distribution: Central tropical Pacific Ocean around the Hawaiian Islands at depths of 820 to 900 m.

Literature: Young *et al.* (2007), Young *et al.* (2008c).

Grimalditeuthis Joubin, 1898

Grimalditeuthis Joubin, 1898c, *Bulletín Societé Zoologie France*, 23: 101–113. [111].

Type Species: *Grimalditeuthis bonplandi* (Verany, 1839).

Frequent Synonyms: None.

Diagnostic Features: Mantle elongate, gelatinous, conical anteriorly, very narrow, long, attenuate posteriorly from anterior margin of fins; funnel valve present; **funnel-locking apparatus fused with mantle component; dorsal nuchal mantle-apparatus free**; photophores absent from tip and along arms IV and from viscera; a single, **elongate photophore on tips of arms I to III**; **fins large, elliptical, 50% of mantle length**; **secondary fins extend posterior to mantle *per se* on needle-like extension of the gladius**, elongate, heart-shaped (frequently broken off at juncture with primary fins); arms of about equal-length, slender, not extremely long; tentacular stalks do not bear knobs/pads along aboral surface; **tentacular club reduced, entirely devoid of suckers**; (tentacles fragile, frequently lost on adult specimens). Monotypic genus.

Remarks: Monotypic genus.

Grimalditeuthis bonplandi (Verany, 1839)

Loligopsis bonplandi Verany, 1839, *Memorie della Reale Accademia delle Scienze di Torino*, (series 2)1: 99–101 [99]. [Type locality: 29°N, 39°W, eastern Central Atlantic Ocean].

Frequent Synonyms: *Grimalditeuthis richardi* Joubin, 1898; *Doratopsis sagitta* Chun, 1908.

FAO Names: En – Grimaldi's chiroteuthid squid; **Fr** – Chirocalmar de Grimaldi; **Sp** – Quiroluria de Grimaldi.

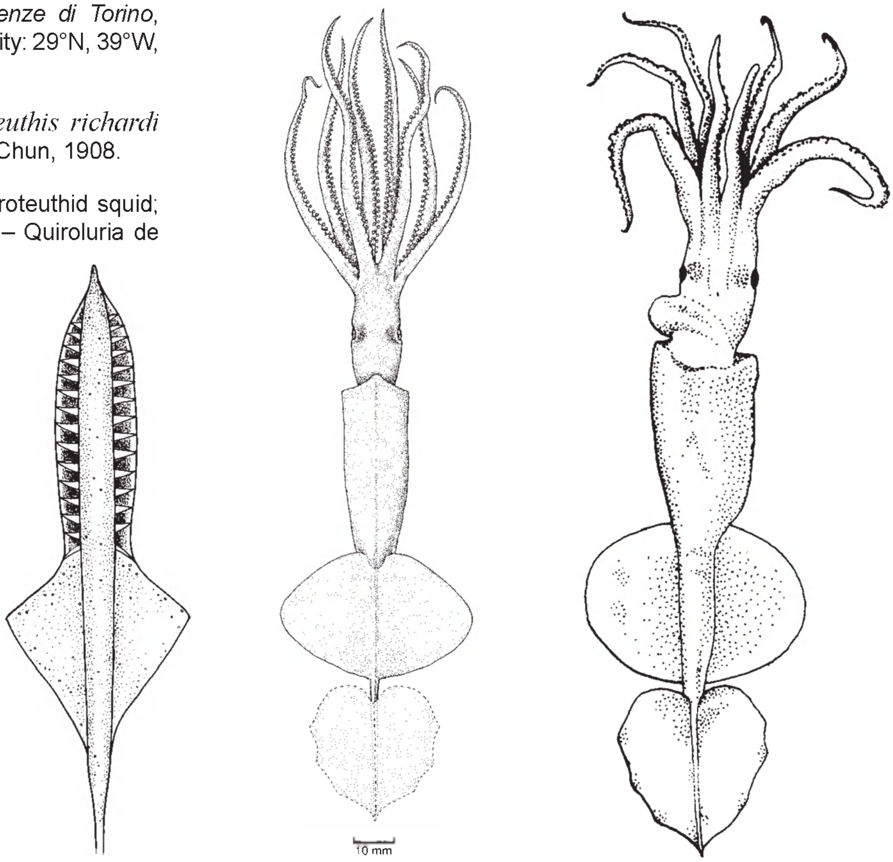
Size: Mantle length to 250 mm.

Geographical Distribution: Circumglobal in tropical, subtropical, temperate waters (Fig. 180).

Habitat and Biology: Mesopelagic to bathypelagic.

Literature: Young (1992 [1991]), Nesis (1982, 1987), Young and Roper (1998, 2008a).

Fig. 179



tentacular club **dorsal view** **ventral view**

Fig. 179 ***Grimalditeuthis bonplandi***

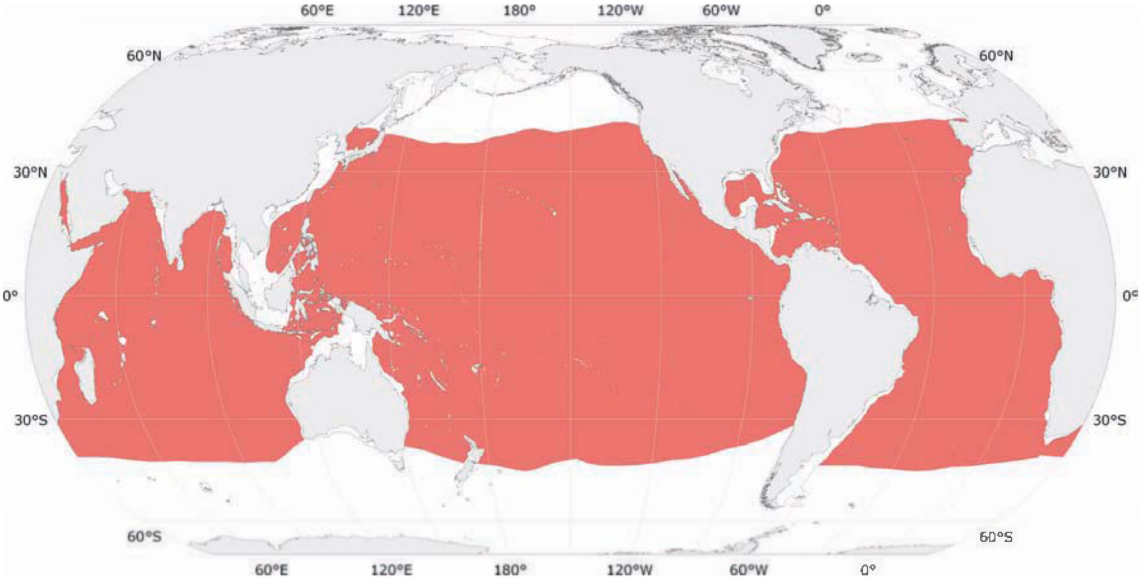


Fig. 180 ***Grimalditeuthis bonplandi***

🟥 Known distribution

Planctoteuthis Pfeffer, 1912

Planctoteuthis Pfeffer, 1912, *Ergebnisse der Plankton Expedition der Humboldt-Stiftung*, 2F(a): 1–815 [571,554].

Type Species: *Planctoteuthis exophthalmica* (Chun, 1908).

Frequent Synonyms: *Valbyteuthis* Joubin, 1931.

Diagnostic Features: Mantle elongate, goblet-shaped, narrows abruptly around anterior third of fin, so the posterior part of mantle is affixed to the narrow conus of the gladius; only integument continues posteriorly over the gladius; eyes project ventrally from the head; **funnel valve absent**; funnel component of locking apparatus with posterior distinct antitragus, oval, deeply concave (tragus absent); mantle component human nose-shaped with tip directed posteriorly and it curves laterally to conform to the deep lateral depression of the funnel component; **photophores entirely absent** on arms IV, viscera, tentacular stalks, club tips; fins subterminal, transversely broad, proportionally large, muscular, width about 85% of mantle length, length about 50% of mantle length; **pronounced anterior and posterior fin margins (lobes)**; arms I to III short, subequal in length, weakly developed; **arms IV extremely long, slender**; **suckers absent distally, a few suckers proximally in uneven single series**; tentacular stalks without knobs/pads or photophores; **tentacular clubs very short, simple, compact, without distinct keels** (except in ***P. lippula***), protective membranes or trabeculae; club suckers present, few in number, in 4 transverse series, on short stalks.

Remarks: Species of ***Planctoteuthis*** usually are rather small and very fragile deepseas squids that often are badly damaged during capture. As a result, few species have been described. Unlike other chiroteuthids, the subadult retains the peculiar doratopsid paralarval tentacular club (Young *et al.*, 2008d).

Literature: See species accounts.

Planctoteuthis exophthalmica (Chun, 1908)

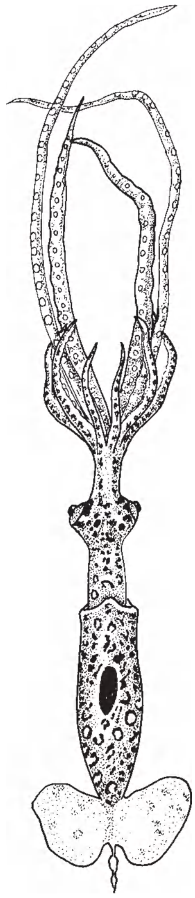
Fig. 181

Doratopsis exophthalmica Chun, 1908, *Zoolisches Anzeiger*, 33: 86–89.
[Type locality: 43°13'S, 80°30'E, South Indian subtropical calm zone].

Frequent Synonyms: *Doratopsis exophthalmica* Chun, 1908.

FAO Names: En – Pop-eye chiroteuthid squid; **Fr** – Chirocalmar exorbité;
Sp – Quiroluria desorbitada.

Size: Mantle length 30 mm, including "spike" tail.



dorsal view

Fig. 181 ***Planctoteuthis exophthalmica***

Geographical Distribution: Eastern Atlantic Ocean, Canaries Current; Indian Ocean (Fig. 182).

Remarks: ***Planctoteuthis exopthalmica*** may eventually prove to be a junior synonym of ***P. levimana***.

Literature: Chun (1910a), Young and Roper (1999b), Young *et al.* (2006b).

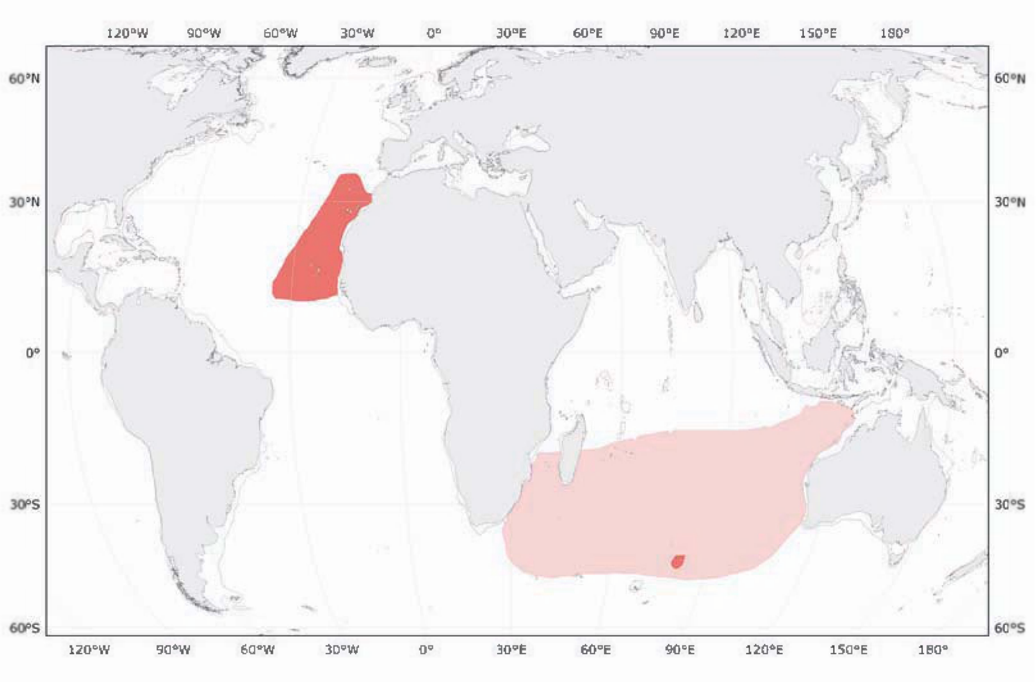


Fig. 182 ***Planctoteuthis exophthalmica***

🟥 Known distribution ▨ Probable presence

Planctoteuthis danae (Joubin, 1931)

Valbyteuthis danae Joubin, 1931, *Annales de l'Institut Océanographique, Monaco*, 10(7): 169–211 [188]. [Type locality: 7°30'N, 79°19'W, eastern Central Pacific Ocean].

Frequent Synonyms: *Valbyteuthis danae* Joubin, 1931.

Size: Mantle length to 55 mm.

Geographical Distribution: Cosmopolitan in tropical and temperate waters; especially in eastern Pacific Ocean to eastern Polynesian Islands.

Habitat and Biology: A bathypelagic species, rarely mesopelagic. Very rarely captured.

Literature: Young (1972a), Roper and Young (1967), Clarke and Lu (1975), Young (1992 [1991]), Young and Roper (1998, 2008b).

Planctoteuthis levimana (Lönnberg, 1896)

Mastigoteuthis levimana Lönnberg, 1896, *Ofversigt af Kongl. Vetenskaps-Akademiens Förhandlingar*, 53(8): 603–612 [605]. [Type locality: 43°30'N, 24°30'W, Central Atlantic Ocean].

Frequent Synonyms: *Valbyteuthis levimana*, Young, 1972a.

Size: Mantle length 70 mm.

Geographical Distribution: North Atlantic Ocean temperate.

Habitat and Biology: Mesopelagic to bathypelagic. Depths of capture for 2 specimens in midwater trawls fished at 800 to 1 800 m and 0 to 2 400 m.

Remarks: Known only from the 4 specimens captured in the North Atlantic, Azores and northward.

Literature: Young *et al.* (1999b), Young *et al.* (2006b).

Planctoteuthis lippula (Chun 1908)

Doratopsis lippula Chun, 1908, *Zoologischer Anzeiger*, 33(2): 86–89 [89]. [Type locality: 11°28'S[sic], 10°24'E, Benguela Current, eastern South Atlantic Ocean].

Frequent Synonyms: *Doratopsis lippula* Chun, 1908.

Size: Known only from *doratopsis*/juvenile; adults unkown.

Geographical Distribution: Eastern South Atlantic Ocean, Benguela Current.

Literature: Pfeffer (1912), Nesis (1982, 1987), Sweeney and Young (2003f), Young *et al.* (2006b), Young and Roper (2008c).

Planctoteuthis oligobessa (Young, 1972)

Valbyteuthis oligobessa Young, 1972, *Smithsonian Contributions to Zoology*, 97: 1–159 [72]. [Type locality: 32°27'N, 120°27'W, eastern North Pacific Ocean].

Frequent Synonyms: *Valbyteuthis oligobessa* Young, 1972.

Size: Mantle length to 76 mm.

Geographical Distribution: Eastern North Pacific Ocean off southern California; equatorial Pacific Ocean to Indonesia.

Habitat and Biology: Bathypelagic. Very rarely captured.

Literature: Young (1972a), Young and Roper (1999c), Young *et al.* (2006b).

2.9 Family CHTENOPTERYGIDAE Grimpe, 1922

by Clyde F.E. Roper and Patrizia Jereb

Chtenopterygidae Grimpe, 1922, *Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig*, 45: 36–52 [36].

Type Genus: *Chtenopteryx* Appellöf, 1890: 1–34[4].

FAO Names: En – Comb-finned squids; **Fr** – Calmars pectiné; **Sp** – Calamars pectinados.

Diagnostic Features: Fins fused posteriorly, extend anteriorly the full length of the mantle in adults; posterior end of mantle broadly rounded; **fins attach to lateral walls of muscular mantle, are comprised of slender muscle bundles (fin ribs) connected by their membranes, to produce a comb-like appearance**. Fins very short in hatchlings, paralarvae; undergo strong ontogenetic growth in length. Arms I to III with suckers in transverse series of 6 to 14 at some point on distal halves of arms. Arms IV with very few small suckers in zig-zag pattern. **Tentacular club suckers small to minute, in 8 to 20 irregular transverse series**. **Tentacles narrow, clubs not expanded, no carpus (fixing apparatus)**. Large oval photophore on viscera (except in ***Chtenopteryx sicula*** and ***C. canariensis***). Large photogenetic patches on ventral surface of eyeballs, (except in ***C. canariensis***). Mature females with an accessory nidamental gland. **Minute suckers on lappets of buccal membrane**. Buccal connectives attach to ventral borders of arm IV. Funnel-locking apparatus straight, simple. **Males without hectocotylus**. Mature males develop a large, dorsally directed photophore in posterior mantle cavity, possibly for mate-attraction.

Size: Small squids to 100 mm mantle length.

Remarks: Members of this monogeneric family are small, muscular, midwater squids that occupy tropical to subtropical waters at depths of 500 to 1 000 m during the day and migrate into near-surface waters at night (upper 200 m). Several undescribed species are present in this genus. Species-level systematic characters in ***Chtenopteryx*** currently seem limited to the following: a) the maximum number of sucker series on the arms and tentacular clubs, b) the presence/absence of visceral and eyeball photophores, c) the relative size of the visceral photophore, d) the mantle width relative to mantle length. Two confirmed species are recognized: ***C. sicula*** (Verany, 1851) and ***C. sepioloides*** Rancurel, 1970. Two other species are currently of undetermined status: ***C. chuni*** Pfeffer, 1912 and ***C. canariensis*** (Salcedo-Vargas and Guerrero-Kommritz, 2000); both species are based on very few, small specimens. Little is known of the biology of any species. Species are preyed upon by lancetfishes (*Alepisauris*), albacore, dolphin fish and mesopelagic viper fishes (Clarke, 1966; Rancurel, 1970; Fujita and Hattori, 1976). The generic name formerly was spelled ***Ctenopteryx***, but that name was preoccupied by a coleopteran. Consequently, Appellöf (1890) spelled the genus ***Chtenopteryx*** and subsequently that spelling has been upheld by the International Code of Zoological Nomenclature (ICZN, 1995) through a petition by Bello and Giannuzzi-Savelli (1993).

Literature: Roper (1969), Nesis (1982, 1987), Roeleveld *et al*. (1992), Bower *et al* (1999c), Shea and Vecchione (2002), Sweeney and Young (2003g), Young and Vecchione (2008a).

Chtenopteryx Appellöf, 1890

Chtenopteryx Appellöf, 1890, *Bergens Museums Aarsberetning*, 1889(3): 1-34 [3].

Type species: *Chtenopteryx sicula* (Verany, 1851).

Chtenopteryx sicula (Verany, 1851)

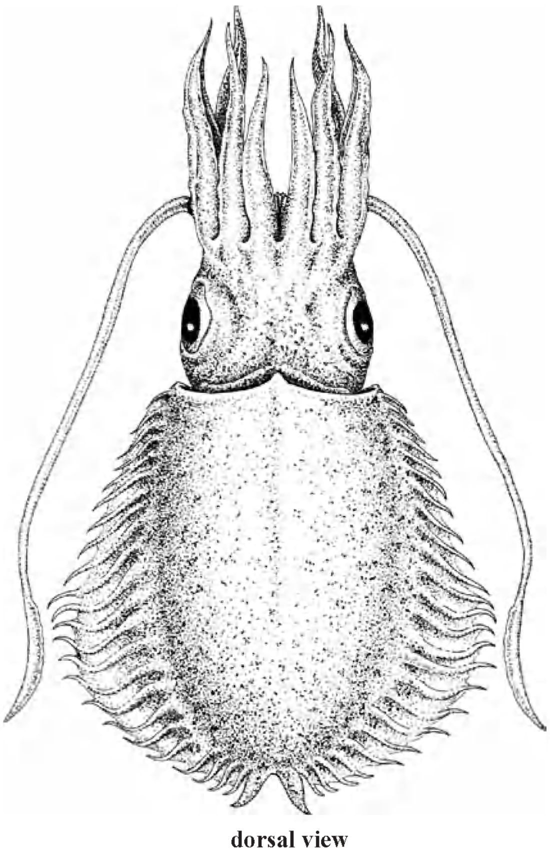
Fig. 183

Type Species: *Chtenopteryx sicula* (Verany, 1851).

Sepioteuthis sicula Verany, 1851, *Mollusques Mèditeranèens observé décrits figurés et chromolithographiés d'après le vivant ouvrage dedie à SM le Roi Charles Albert*, 1: 1–132.

FAO Names: En – Sicilian comb-finned squid; **Fr** – Calmar pectiné sicilienne; **Sp** – Calamarín pectinado siciliano.

Size: Maximum mantle length to 100 mm.



dorsal view

Fig. 183 *Chtenopteryx sicula*

Geographical Distribution: Cosmopolitan (circumglobal) in tropical and subtropical waters. Paralarvae epipelagic; adults descend to mesopelagic and bathypelagic depths, undergo strong diel vertical migrations (Fig. 184).

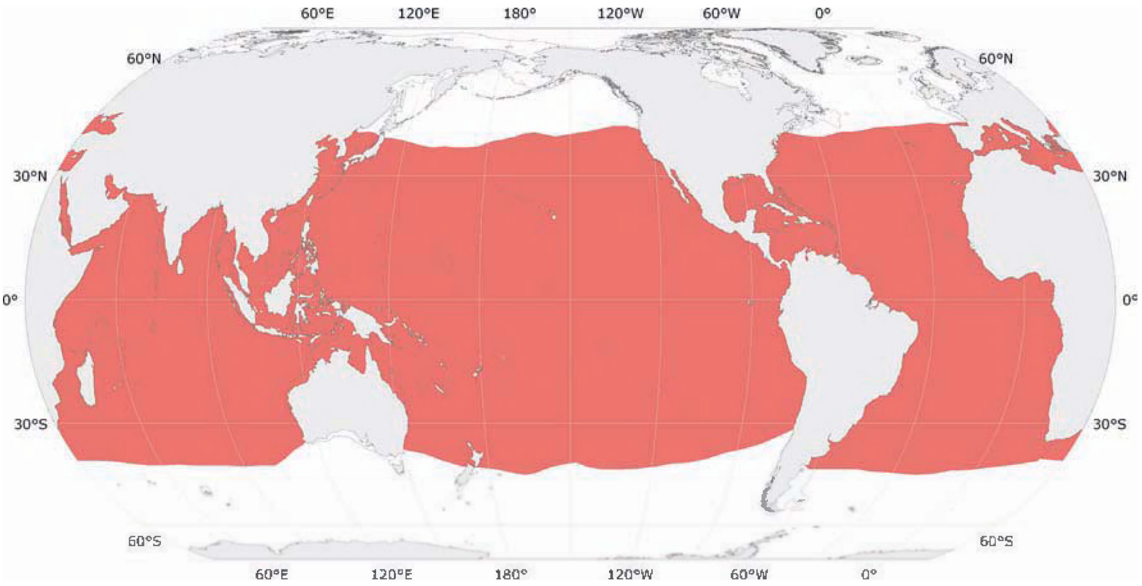


Fig. 184 ***Chtenopteryx sicula***

🟥 Known distribution

Local Names: ITALY: Totanello pinnidentato.

Literature: Roper (1969), Young and Vecchione (2006a), Shea and Vecchione (2002), Diekmann and Piatkowski (2002b). See additional references in the family section.

Chtenopteryx canariensis Salcedo-Vargas and Guerrero-Kommritz, 2000

Chtenopteryx canariensis Salcedo-Vargas, and J. Guerrero-Kommritz, 2000. *Mitteilungen aus dem Hamburgischen zoologische Museum und Institut, Hamburg*, 97: 31–44 [32]. [Type locality: 26° 20'N, 19° 21'W, south of Canary Islands. Other records: 12° 16'N, 23° 05'W; 0° 20'N, 25° 20'W. All known specimens were caught in nets that fished down to 1 000 m depth].

Size: Mantle length to 65 mm, the maximum of only 14 known specimens.

Geographical Distribution: Tropical eastern Atlantic Ocean.

Literature: Salcedo-Vargas and Young (2001a).

Chtenopteryx sepioloides Rancurel, 1970

Chtenopteryx sepioloides Rancurel, 1970, *Cahiers O.R.S.T.O.M., Océanographique*, 8(4): 1–87 [39].

Size: Mantle length less than 100 mm.

Geographical Distribution: Central to western Pacific Ocean, Hawaii to Tuamotu Islands. Paralarvae epipelagic; adults mesopelagic to bathypelagic.

Literature: Rancurel (1970), Young and Vecchione (2001). See additional references in family section.

2.10 Family CRANCHIIDAE Prosch, 1847

by Clyde F.E. Roper and Patrizia Jereb

Cranchiidae Prosch, 1847, *Kongelige Danske Videnskabernes Selskabs Skrifter*, (5)1: 71.

Type Genus: *Cranchia* Leach, 1817: 140.

FAO Names: En – Cranch squids; **Fr** – Encornets-outres; **Sp** – Cranquilurias.

Diagnostic Features:[1/] The family Cranchiidae contains a great diversity of species which exhibit a wide variety of basic characters, as well as significant variation in size, from small (about 100 mm mantle length) to gigantic (over 2 000 mm mantle length). One prominent character, however, easily distinguishes all members of the group from all other species of squids: **the mantle is fused to the head at the nuchal cartilage and to the funnel at its 2 posterolateral corners in the locus of the funnel-mantle locking apparatus**. Mantle cavity is divided into a dorsal and a ventral chamber by a broad horizontal membrane formed by a modification of the funnel retractor muscles. **Buccal membrane** is provided **with 8 connectives (7 lappets) that attach to the ventral borders of arms IV (formula: DDVV)**; the armature of the tentacular clubs generally is in 4 transverse series of suckers (hooded hooks in median series in ***Galiteuthis*** and ***Mesonychoteuthis***); tentacular stalks, variable in length and diameter among species, with 2 to 4 series of alternating carpal suckers and pads for most of tentacle length; the short to medium-length muscular arms have biserial suckers with wide apertures, often without dentition; (hooded hooks occur on midarm in ***Mesonychoteuthis***); well-developed trabeculate protective membranes occur along both margins of all arms; **either right or left ventral arm (IV) hectocotylized (absent in some species)**; photophores are present on the ventral one-half to two-thirds (or more) of the eyes and on the arm tips ("brachial end organs") and ink sac/digestive gland of some species; large buoyancy chamber extends around viscera for entire length of mantle cavity; digestive gland usually spindle-shaped, well posterior to cephalic cartilage. The mantle is stout to elongate, cylindrical, conical or spindle-shaped; the posterior end varies from blunt, rounded (***Bathothauma***) to sharply-pointed, filiform (***Taonius***). **Mantle thin walled, sometimes termed "leathery" but usually muscular; some species develop cartilaginous-like tubercles on external surface of mantle**; midline of rachis and conus of gladius usually visible through skin. Fins normally quite thin (except very thick, muscular in ***Mesonychoteuthis***), insert laterally along lanceola and conus of gladius; shape varies greatly among species: widely separated, small, paddle-shaped, subterminal; medium-sized to large, rounded, terminal; ovate or lanceolate, terminal or terminal-lateral. Gladius with long, narrow rachis, dorsal keel weak or absent anteriorly (except strong in ***Leachia***), bordered posteriorly with short to long vanes that form into a long lanceola (spindle-shaped to broad or diamond-shaped; weakly to strongly keeled) with short, broad to long, filiform, usually hollow, conus (exceptions in ***Helicocranchia*** and ***Bathothauma***). Funnel moderately to very large; funnel valve variably present or absent; dorsal pad of funnel organ an inverted V- or U-shape, normally with 2 or 3 papillae or flaps or both (up to 7 papillae in ***Leachia***); 2 small to very large ventral pads of various shapes: oval, kidney, crescent, L-shaped, etc. **Head short, frequently dominated by large eyes that are sessile, prominent or protruding, usually oriented anteriorly or anterolaterally**; **eyes with photophores**.

Size: Very diverse among species; adults range from 10 to well over 200 cm mantle length.

Geographical Distribution: A family with high species diversity, the Cranchiidae is represented in virtually all of the world's oceans and seas, with the notable exception of the Arctic Ocean. Species diversity predominates in the subtropical and tropical waters. All genera occur circumglobally in tropical and subtropical waters, except ***Egea***, restricted to the tropics, and ***Teuthowenia***, uniquely restricted to the sub-Arctic, north temperate and eastern tropical waters of the Atlantic Ocean and to circumglobal transition waters of the Southern Subtropical Convergence. ***Taonius*** and ***Galiteuthis*** occur in temperate and subpolar waters circumglobally; ***Galiteuthis glacialis*** and ***Mesonychoteuthis hamiltoni*** are circumglobal, but mainly restricted to Antarctic regional waters. Details of geographic and vertical distributions are given in Voss, 1988, Voss, *et al.* 1992b, Nesis, 1999b.

Habitat and Biology: Squids of the Family Cranchiidae are ubiquitous, both in geographical and vertical distribution. The species range in the sub-Arctic, proliferate into the subtropics and tropics and occur even in Antarctic waters. As paralarvae and juveniles they occur in the epipelagic zone, then, with growth, undergo gradual ontogenetic descent into mesopelagic and bathypelagic realms; adults of some species are known to inhabit depths in excess of 2 000 m. Many cranchiid species exhibit varying degrees of diel vertical migration; some seem not to migrate vertically at all. Other species occur in transitional zones and a few even are associated with near-coastal pelagic habitats. The paralarvae and young of cranchiids are characterized by stalked eyes and a stalked arm crown of variable lengths; very short arms and long tentacles; frequently a ventrally-directed rostrum on the eyes; absence of photophores. They do not closely resemble the adults of their species; historically the paralarvae were not connected with their conspecific adults. This has resulted in considerable overnaming, creation of synonyms and taxonomic confusion. The combined characters uniquely possessed by cranchiids have enabled them to develop increased buoyancy and very efficient respiration; these are the fusions of the mantle, head and funnel and the partitioning of the mantle cavity and coelom into 2 chambers in which a weak solution of low density ammonium chloride (NH_4Cl) provides near-neutral buoyancy. Prior to the onset of ontogenetic descent, paralarval/juvenile cranchiids live in near-surface waters where they are readily identified by their long eyestalks. Marked morphological changes occur during ontogenetic descent and maturation, including change of eye shape and position, change of fin shape, increased pigmentation, development of photophores on arm tips, modification of arm structure, and loss of tentacles. A few species of cranchiids have been observed alive in their deep-sea habitats from submersibles. Among other observations, several species have been

---

[1/] Much of the information and data in this chapter has come from the thorough, comprehensive revisionary and monographic works of N.A. Voss (1974, 1980, 1985, 1988), to whom the authors are most grateful.

observed in a stereotypic resting position, with their arms and tentacles held tightly together in a bundle and held dorsally over their heads. This position is known as the “cockatoo” posture because of its general resemblance to the cockatoo bird. Additional observations have been made on behaviour, positions, locomotion, chromatophore patterns, etc. Cranchiids are prey in varying degrees of importance to a number of pelagic predators, e.g. numerous cetacean species including sperm whales, pygmy sperm whales, Orca whales, pot-head whales, dolphins, Dall’s porpoise; also swordfish, tunas, lancetfish, smooth and scalloped hammerhead sharks, blue sharks, tiger sharks and albatrosses.

Interest to Fisheries: Currently no directed fishery of any sort is conducted on any species of Cranchiidae. Indeed, it seems doubtful that a fishery would ever develop, because all species possess a large buoyancy chamber in the mantle cavity filled with low density ammoniacal fluid. Furthermore, the mantle tissue on most species, while “muscular”, is very thin and leathery. The musculature of the mantle in ***Mesonychoteuthis hamiltoni***, which grows in excess of 2 m mantle length, is significantly thicker than on other cranchiids, but its rather soft, gelatinous consistency makes it unsuitable for human consumption. However, future research might reveal other uses, e.g. pharmaceutical, biochemical.

Local Names: USA: Bathyscaphoid squids, Glass squids (Plate VII, 37).

Remarks: The systematics of the group remained in a very confused, unsettled state for most of its history, beginning in the early to mid-nineteenth century. Only since the monumental, critical, monographic works of N.A. Voss in the late twentieth century have the systematics, relationships, distributions been thoroughly enough determined to allow a high degree of understanding and stability to occur (Voss, 1974, 1980, 1985, 1988; Voss and Voss 1983; Voss, *et al.* 1992b).

The Cranchiidae as currently understood consists of 13 genera and in excess of 60 species, a number of which are very poorly known or undescribed. The genera are grouped under 2 subfamilies, the Cranchiinae and the Taoniinae.

Because none of the species of the Cranchiidae appears to have any potential for fishery development at this point, all species in principle are Level 3 Species. However, greater detail than normally provided for in Level 3 taxa is included here when literature is available, because of the ubiquitous occurrence of the family throughout all the world’s oceans and seas, to all bathymetric zones, and to its massive nutritive contribution to the thousands of species of marine mammals, fishes, invertebrates, cephalopods and sea birds that prey on them.

The literature on the Cranchiidae is vast and scattered. Consequently, references cited here for the family level are those with greatest current relevance to systematics and biology and those that are representative of particular aspects of biology, e.g. prey-predator relationships, *in situ* behaviour.

Literature: Voss, N. A. (1974, 1980, 1985, 1988), Voss and Voss (1983), Seapy and Young (1986), Vecchione and Roper (1992 [1991]), Voss *et al.* (1992b), Young and Mangold (2008a), Nesis (1999b), Sweeney and Young (2003h).

Key to the genera of Cranchiidae (adults) (from N. A. Voss, 1980)

1a. Ventral surface of mantle with 1 or 2 cartilaginous strips extending posteriorly from anterior apex of funnel-mantle fusions; funnel fused to head laterally; eyes with 4 or more small, round to oval photophores . . . . **(Subfamily Cranchiinae) → 2**

1b. Ventral surface of mantle without cartilaginous strips extending posteriorly from anterior apex of funnel-mantle fusions; funnel free from head laterally; eyes with 1 usually large photophore, or 2 or 3 markedly dissimilar-sized photophores with the largest usually crescent-shaped . . . . . **(Subfamily Taoniinae) → 4**

2a. Ventral surface of mantle with 2 cartilaginous strips in inverted V-shaped pattern extending posteriorly from anterior apex of funnel-mantle fusions; funnel valve present; dorsal pad of funnel organ with 3 longitudinal, triangular flaps; gladius with short conus . . . . ***→ 3***

2b. Ventral surface of mantle with 1 cartilaginous strip extending posteriorly from anterior apex of funnel-mantle fusions; funnel valve absent; dorsal pad of funnel organ with 3 to 7 narrow papillae; gladius with long slender conus . . . . ***Leachia***

3a. Mantle covered with cartilaginous tubercles; eyes with 14 photophores; brachial photophore present on all arms in near-mature and mature females; suckers in 4 series on midportion of hectocotylized right IV in males . . . . ***Cranchia***

3b. Mantle without cartilaginous tubercles except on ventral cartilaginous strips and sometimes on dorsal median line; eyes with 4 or 14 photophores; brachial photophore present only on arms III in near-mature and mature females; suckers in 2 series on midportion of hectocotylized right or left IV in males . . . . ***Liocranchia***

4a. Fins small, paddle-shaped, subterminal; eyes with 1, usually large, photophore . . . . ***→ 5***

4b. Fins not paddle-shaped, may be short to long, round to lanceola-shaped, terminal or terminal lateral; eyes with 1 large and 1 or 2 small photophores . . . . ***→ 6***

5a. Fins fused distally, inset on short rostrum of gladius which projects dorsally free of end of mantle; eyes small to medium . . . . ***Helicocranchia***
5b. Fins widely separated, insert on lateral expanded ends of transverse extensions of posterior end of gladius; eyes proportionally large to huge . . . . ***Bathothauma***

6a. Gladial conus short, broad to narrow; fins short (<25% mantle length), oval to round; digestive gland long, narrow, spindle-shaped . . . . *→ 7*
6b. Gladial conus medium to long, narrow, or needle-like to filiform; fins medium to long (30 to 60% mantle length), narrow, lanceolate to ovate; digestive gland stout, spindle-shaped or rounded . . . . ***→ 8***

7a. Posterior fin insertions do not extend to tip of gladius; no tubercles present on funnel-mantle fusion cartilages; dorsal pad of funnel organ with large, triangular lobe on each lateral arm; eyes with small, round, anterior photophore indented into median anterior margin of large, round, posterior photophore . . . . ***Sandalops***
7b. Posterior fin insertions extend to tip of gladius; 2 small tubercles present at anterior end of funnel-mantle fusion cartilages; dorsal pad of funnel organ with large, spatulate papilla on each lateral arm; eyes with small, crescent-shaped, anterior photophore lying closely within concavity of large, crescent-shaped, posterior photophore . . . . ***Liguriella***

8a. Anterior fin insertions on lateral margins of lanceola of gladius . . . . *→ 9*
8b. Anterior fin insertions on lateral margins of mantle . . . . ***→ 11***

9a. Tentacular club with hooded hooks, marginal suckers of manus greatly reduced in size or lost; arms IV the longest in juveniles, approximately coequal to III in adults; gladial conus narrow or needle-like . . . . . . ***→ 10***
9b. Tentacular club without hooded hooks (enlarged suckers with 1 or 2 large, central, hook-like teeth on distal margin), marginal suckers of manus not greatly reduced in size or lost; arms III the longest in juveniles, the longest or approximately coequal to II in adults; gladial conus filiform . . . . ***Taonius***

10a. Arms without hooded hooks; fins lanceolate becoming attenuate posteriorly . . . . ***Galiteuthis***
10b. Arms with hooded hooks on midportion; fins stout, ovate (nearly round in combined outline in juvenile), do not become attenuate posteriorly . . . . ***Mesonychoteuthis***

11a. Funnel valve present; dorsal pad of funnel organ with triangular flap on each lateral arm; eyes with 2 photophores (large, roughly crescent-shaped posterior photophore, and within its concavity, smaller, roughly elongate S-shaped anterior photophore); carpal suckers in 2 series on tentacular stalk. . . . . ***→ 12***
11b. Funnel valve absent; dorsal pad of funnel organ with long, spatulate papilla on each lateral arm; eyes with 3 photophores (large, crescent-shaped posterior photophore, and within its concavity, a smaller, crescent-shaped anterior photophore and a third small, oval photophore); carpal suckers in 4 series set in zigzag pattern on tentacular stalk . . . . ***Teuthowenia***

12a. Photophores absent on ventral surface of stout, spindle-shaped, digestive gland; long, single united digestive duct . . . . ***Egea***
12b. Large compound photophore present on ventral surface of rounded digestive gland; 2 short digestive ducts remain separate . . . . ***Megalocranchia***

2.10.1 Subfamily CRANCHIINAE Pfeffer, 1912

Cranchiinae Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2: [644].

Type Genus: *Cranchia* Leach, 1817.

Cranchia Leach, 1817, *Zoological Miscellany*, 3(30): 137–141 [140].

Diagnostic Features: The **Cranchiinae** is characterized by the presence on the ventral surface of the mantle of **1 or 2 cartilaginous strips** (with cartilaginous tubercles) that originate at each funnel-mantle fusion and extend posteriorly along the line(s) of the lateral fusion of the funnel/mantle; funnel fused to head laterally; **1 or more rows of 4 or more small, round to oval photophores** on the eyes; right or left IV hectocotylized in males; secondary sexual modification may be present on tips of arms III (or absent); adult females may have brachial photophore on tip of arm III (or on all 4 pairs); ceacum larger than stomach.

Remarks: This subfamily contains the genera ***Cranchia***, ***Leachia*** and ***Liocranchia***.

Literature: See references listed for the family and for ***Cranchia scabra***.

Cranchia Leach, 1817

Cranchia Leach, 1817, *The Zoological Miscellany; being Descriptions of New or Interesting Animals*, 3(30): 137–141 [140].

Type Species: *Cranchia scabra* Leach, 1817.

Frequent Synonyms: None.

Diagnostic Features: Mantle stout, spindle-shaped, covered with variable-sized, complex, cartilaginous tubercles, with tops bearing spines; tapers to broad posterior point; 2 short cartilaginous strips of co-equal length from each funnel-mantle fusion, V-shaped with complex multipoint tubercle at apex; each fin nearly oval with free posterior lobe; each **eye with 14 photophores**; **brachial end organ (photophore) present on tips of all arms of premature and mature females**; suckers in 4 series on midportion of hectocotylized right arm IV; funnel valve present; gladius with short conus.

Size: Mantle length to 150 mm.

Geographical Distribution: It is distributed circumglobally in subtropical and tropical epipelagic to mesopelagic waters.

Habitat and Biology: Prey to numerous oceanic predators.

Remarks: The genus ***Cranchia*** is monotypic, represented only by ***C. scabra***.

Literature: See references listed for the family and for ***C. scabra***.

Cranchia scabra Leach, 1817

Fig. 185; Plate VII, 36

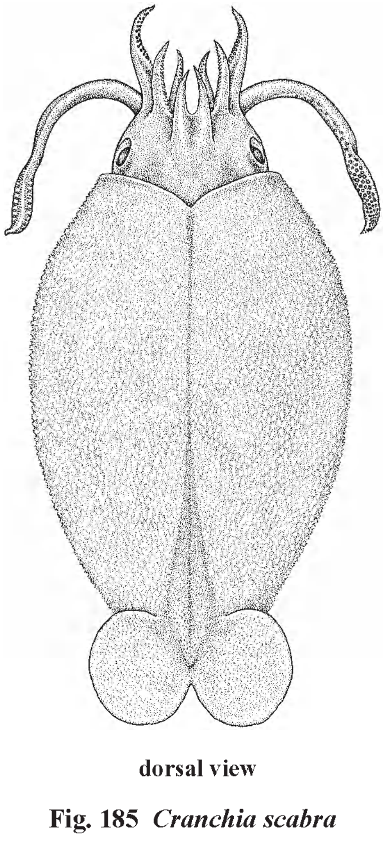
Cranchia scabra Leach, 1817, *Zoological Miscellany*, 3(30): 137–141 [140]. [Type locality: off Congo, West Africa].

Frequent Synonyms: *Loligo cranchia* Blainville, 1823; *Octopus (Philonexis) eylais* d'Orbigny, 1834; *Cranchia hispida* Pfeffer, 1884; *C. tenuitentaculeta* Pfeffer, 1884.

FAO Names: En – Rough cranch squid; **Fr** – Encornet-outre rude; **Sp** – Cranquiluria ruda.

Diagnostic Features: See generic account.

Size: Maximum mantle length to 150 mm.



dorsal view

Fig. 185 ***Cranchia scabra***

Geographical Distribution: This species is circumglobal, oceanic waters in tropical and subtropical open oceanic waters; known from 43°N to 35°S as generally proscribed by the north and south subtropical convergences (Fig. 186).

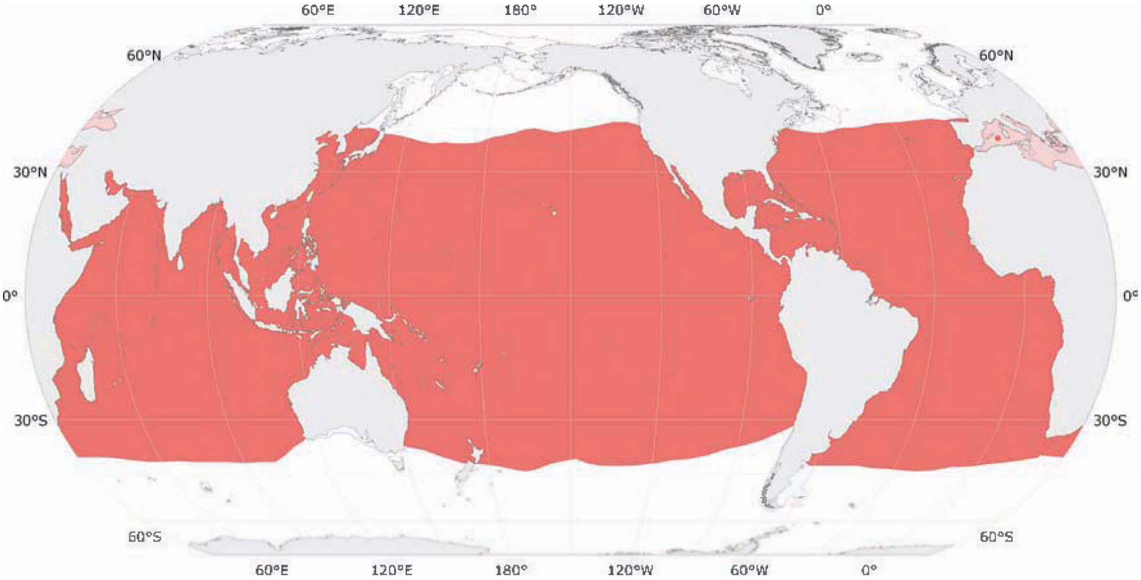


Fig. 186 ***Cranchia scabra***

🟥 Known distribution ▨ Probable presence

Habitat and Biology: Paralarvae and juveniles are epipelagic to upper mesopelagic (upper 400 m), while adults descend to mesopelagic and bathypelagic zones, perhaps to 2 000 m.

Literature: Clarke and Lu (1974, 1975), Lu and Clarke (1975b), Roper and Lu (1990), Roeleveld *et al.* (1992), Arkhipkin (1996c), Quetglas *et al.* (1999a, 2000b).

Leachia Lesueur, 1821

Leachia Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–107 [89].

Type Species: *Leachia cyclura* Lesueur, 1821.

Frequent Synonyms: *Perothis* Rathke, 1833; *Perotis* Gray, 1849 (erroneous spelling of *Perothis* Rathke, 1833); *Dyctydiopsis* Rochebrune, 1884; *Dictydiopsis* Hoyle, 1885a (erroneous spelling of *Dyctydiopsis* Rochebrune, 1884); *Pyrgopsis* Rochebrune, 1884; *Drechselia* Joubin, 1931.

Diagnostic Features: Mantle elongate, slender, spindle-shaped, tapers posteriorly to sharp point; **ventral surface with a single cartilaginous strip that extends posteriorly from the apex of each funnel-mantle fusion**; funnel fused to head laterally; **funnel valve absent**; gladius with long, slender conus; fins barely unite posterior to gladius; fins together transversely elliptical; **eyes with 5 to 21 oval photophores** (species dependent); **brachial photophores present on tips of arms III** in mature or nearly mature females; **median suckers on manus of club greatly enlarged** (unique to the family).

Size: Small to medium-sized squids, mantle length up to 200 mm.

Geographical Distribution: ***Leachia*** is a circumglobal genus in tropical and subtropical waters.

Habitat and Biology: It occurs from the epipelagic (surface) to the bathypelagic zone, to around 2 000 m.

Remarks: Of the 14 nominal species in the genus ***Leachia***, at least 6 species are valid, one yet to be named. The closely related species show contiguous geographical distributions with considerable overlap. While the genus is easily characterized, the species are not easily recognized, because of incomplete descriptions based principally on paralarvae. Currently, geographical location is a most important "character" for identifying species. ***Leachia*** is the only genus in the subfamily Cranchiinae in which the paralarvae have stalked eyes. The cartilaginous tubercles consist of hyaline cartilage and they are covered with epidermis. Some species have been photographed alive, *in situ*.

Literature: Roper and Lu (1990), Voss *et al.* (1992b). See also references listed for the family and for ***Leachia*** species.

Leachia cyclura Lesueur, 1821

Fig. 187

Leachia cyclura Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–107 [90]. [Type locality: southern Indian Ocean at 33°S, 37°E, off South Africa].

Frequent Synonyms: *Loligo leachi* Blainville, 1823; *Perothis eschascholtzi* Rathke, 1833; *Loligopsis guttata* Grant, 1833.

FAO Names: En – Leach's cranch squid; **Fr** – Encornet-outre de Leach; **Sp** – Cranquiluria de Leach.

Diagnostic Features: Length of **cartilaginous tubercle strip about 20 to 30% of mantle length**; **8 eye photophores**, 5 in outer row, 3 near pupil (at 60 to 70 mm mantle length).

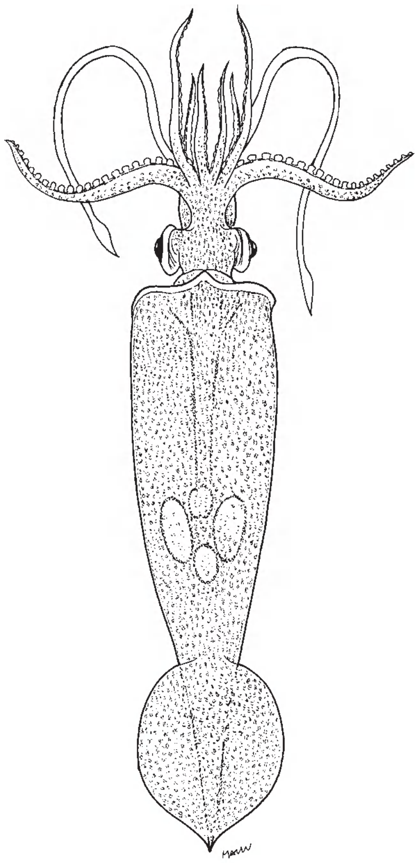
Size: Maximum mantle length 150 to 200 mm.

Geographical Distribution: ***Leachia cyclura*** inhabits tropical and southern subtropical Indo-West Pacific oceanic waters (Fig. 188).

Habitat and Biology: Bathymetric range from surface waters to bathypelagic, around 2 000 m, following a gradual process of ontogenetic descent.

Remarks: The species apparently was originally described from an illustration of the specimen drawn at sea and has not been recorded extensively in the literature.

Literature: Voss (1980), Nesis (1982, 1987).



dorsal view

Fig. 187 ***Leachia cyclura***

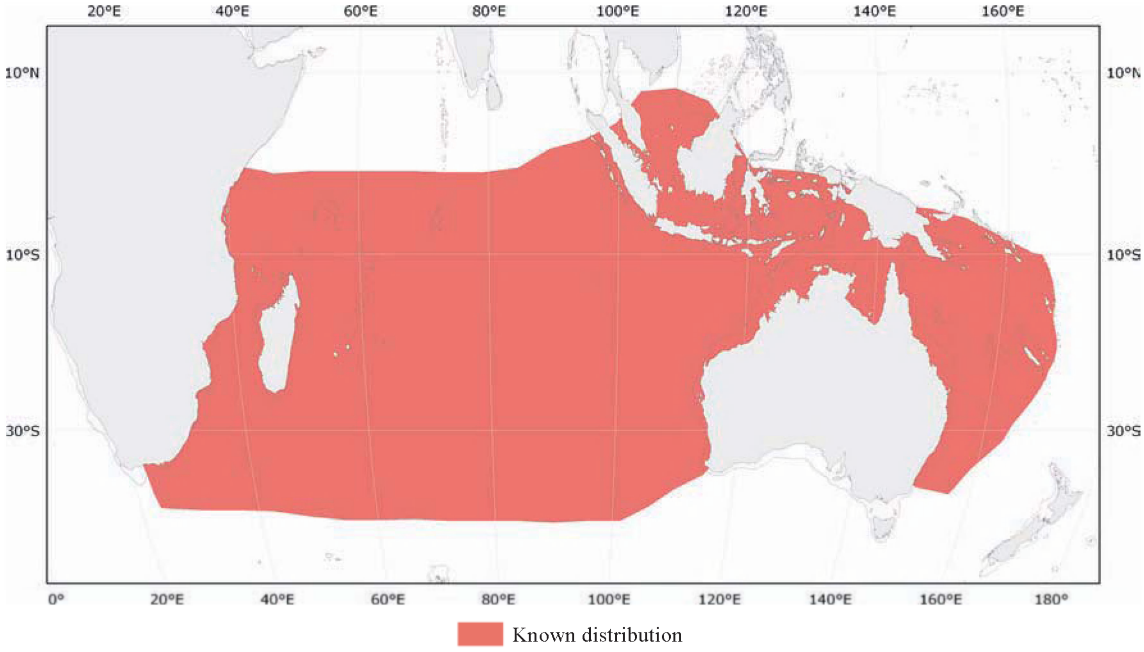


Fig. 188 ***Leachia cyclura***

Leachia atlantica (Degner, 1925)

Pyrgopsis atlantica Degner, 1925, *Report of the Danish Oceanographic Expeditions, 1908 to 1910, Mediterranean and Adjacent Seas*, 2(9): 1–94 [54]. [Type locality: 36°13'N, 09°44'W (Atlantic Ocean)].

Frequent Synonyms: None.

Diagnostic Features: Length of cartilaginous tubercular strip 14 to 15% of mantle length; 6 photophores on eye, 5 in outer row, 1 near pupil; large elongate photophore on tips of arms III in maturing and mature females.

Size: Maximum mantle length to 100 mm.

Geographical Distribution: Broadly distributed in the Atlantic Ocean subtropical and tropical regions; recorded from 50°N to 21°S (carried by the Gulf Stream, meanders as far as the Grand Banks off Newfoundland); Bay of Biscay, Gulf of Mexico, northern Caribbean Sea, Straits of Florida).

Habitat and Biology: An open ocean species, paralarvae and juveniles inhabit epipelagic to mesopelagic zones, while adults occupy mesopelagic to bathypelagic depths to greater than 1 000 m. Some diel vertical dispersal may occur; numerous night and early morning captures of mature and spent females at or near the surface indicate that spawning occurs in near-surface waters. Closing net captures off Bermuda of ***Leachia*** cf. ***atlantica*** juveniles and subadults were recorded at 50 to 60 m during the day; at night most specimens occurred at 50 to 100 m, but largest specimens (26 to 48 mm mantle length) were taken at 135 to 230 m; most large specimens taken during daytime were the deepest captures.

Remarks: This species is sympatric with ***Leachia lemur*** in Atlantic subtropical waters.

Literature: Guerra (1992), Herring *et al.* (2002), Vecchione (2002).

Leachia danae (Joubin, 1931)

Drechselia danae Joubin, 1931, *Annales de l'Institut Océanographique*, (N.S.), 10(7): 169–211 [197]. [Type locality: 06°40'N, 80°47'W, Gulf of Panama, eastern Pacific Ocean].

Frequent Synonyms: None.

Diagnostic Features: Eyes with 21 photophores, 8 in outer row, 5 in middle row, 8 in inner row near the pupil.

Size: Maximum mantle length from 180 to 190 mm.

Geographical Distribution: This species has been recorded in equatorial waters of the eastern tropical Pacific Ocean, between 23°N to about 14°S and west to about 145°W.

Habitat and Biology: Paralarvae and small juveniles occur in the upper few hundred metres of the epipelagic zone, while larger animals descend ontogenetically to depths greater than 1 000 m in the bathypelagic zone. Some diel movement occurs.

Literature: Voss *et al.* (1992b), Young and Mangold (2007a).

Leachia dislocata Young, 1972

Leachia dislocata Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [80]. [Type locality: 32°35'N 118°06'W, off southern California, eastern North Pacific Ocean].

Frequent Synonyms: None.

Diagnostic Features: Cartilaginous tubercerular strip length occupies 12 to 17% of mantle length; second complex tubercle at anterior end of strip noticeably displaced medially; eyes with 15 photophores, 8 in outer row, 7 in inner row (3 large, 4 small).

Size: Maximum mantle length to 150 mm.

Geographical Distribution: This species occurs in oceanic waters of the eastern North Pacific Ocean in the California Current between approximately 25°N and 45°N and westward in North Pacific central waters to 160°W, including the Hawaiian Islands; in the Peru-Chile Current between about 15°S and 25°S.

Habitat and Biology: Juveniles occur in the upper few hundred metres of the epipelagic zone; then with ontogenetic growth they descend into the bathypelagic depths of 1 000 m or more. Mating and spawning appear to occur in the upper 200 m, based on captures of mature males and a spent female in those upper epipelagic waters.

Literature: Young (1972a), Roper and Young (1975).

Leachia lemur (Berry, 1920)

Pyrgopsis lemur Berry, 1920a, *Proceedings of the United States National Museum*, 58(2335): 293–300 [298]. [Type locality: 35°27'N 73°14'W, east of Cape Hatteras, western North Atlantic Ocean].

Frequent Synonyms: None.

Diagnostic Features: Cartilaginous tubercular strip occupies about 35% of mantle length; eyes with 5 photophores, 4 outer, 1 inner.

Size: Maximum mantle length to 70 mm.

Geographical Distribution: ***Leachia lemur*** seems restricted to the North Atlantic subtropical region west of about 50°W in the northern and southern Sargasso Sea.

Habitat and Biology: Paralarvae and juveniles occur in the upper few hundred metres of the epipelagic zone, while larger animals descend progressively with growth (ontogenetic growth) to bathypelagic depths in excess of 1 000 m. Matures at 60 to 70 mm mantle length; apparently mates and spawns in deep water. Very extensive sampling in the western North Atlantic yielded ***L. lemur*** only in the winter months; the species frequently is captured along the offshore edge of the Gulf Stream in its more poorly defined interface with Sargasso Sea water.

Literature: Lea (1985), Vecchione and Roper (1986), Diekmann and Piatkowski (2002a).

Leachia pacifica (Issel, 1908)

Zygaenopsis pacifica Issel, 1908, *Monitore Zoologico Italiano*, 19(4): 102–104 [103]. [Type locality: 14°32'S, 167°43'W, between Tahiti and Pago Pago Islands, central western Pacific Ocean].

Frequent Synonyms: *Liocranchia brocki* Pfeffer, 1884; *L. elongata*, Issel, 1908; *Fusocranchia alpha* Joubin, 1920; *Liocranchia intermedia* Robson, 1924.

Diagnostic Features: Large brachial photophores develop on arms III of mature females. Eyes with 6 photophores, 5 outer, 1 inner; tubercular strips with a second, large anterior tubercle noticeably offset medially from the linear pattern.

Size: Maximum mantle length to 60 mm.

Geographical Distribution: This small oceanic species is geographically broadly distributed in the tropical waters of the North Pacific and Indo-Pacific oceans, and westward into equatorial waters of the Indian Ocean.

Habitat and Biology: The vertical distribution for juveniles is very shallow in the epipelagic zone, from near surface to about 150 m. As sexual maturity occurs, the subadult squid undergo a sudden ontogenetic descent; animals of about 45 to 55 mm mantle length may be found throughout the water column between about 200 to 1 300 m; mature animals occur at depths from about 1 200 to 1 800 m (possibly to 2 300 m) where they become fully mature, mate and spawn.

Remarks: The species co-occurs with ***Leachia dislocata*** in the Indian Ocean.

Literature: Young (1975b, 1978), Young and Mangold (2007a).

Liocranchia Pfeffer, 1884

Liocranchia Pfeffer, 1884, *Abhandlung aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 1–30 [25].

Type Species: *Liocranchia reinhardti* (Steenstrup, 1856).

Frequent Synonyms: *Fusocranchia* Joubin, 1920.

Diagnostic Features: Mantle elongate, spindle-shaped, tapers posteriorly to narrow point, **not covered with cartilaginous tubercles**; **2** moderately long **cartilaginous strips studded with cartilaginous tubercles** extend from each funnel-mantle fusion **in inverted-V pattern, co-equal in length or ventral component the longest**; fins unite posterior to gladius, ovoid to nearly circular; funnel valve present; gladius with short conus; **eyes with 4 or 14 oval photophores**; brachial photophores present only on tip of arms III in premature and mature females; suckers in 2 series on midportion of hectocotylized right or left arm IV in males.

Size: Medium-sized squids up to 250 mm mantle length.

Geographical Distribution: The species are circumglobal in tropical to subtropical oceanic waters.

Habitat and Biology: ***Liocranchia*** squids occupy epipelagic to bathypelagic depth zones. They are prey to numerous oceanic predators.

Remarks: ***Liocranchia*** is comprised of 2 species, ***L. reinhardti*** and ***L. valdiviae***, medium-sized squids up to 250 mm mantle length. The species are circumglobal in tropical to subtropical oceanic waters; they occupy epipelagic to bathypelagic depth zones. Prey to numerous oceanic predators.

Literature: See references listed for family and ***Liocranchia*** species.

Liocranchia reinhardti (Steenstrup, 1856)

Fig. 189

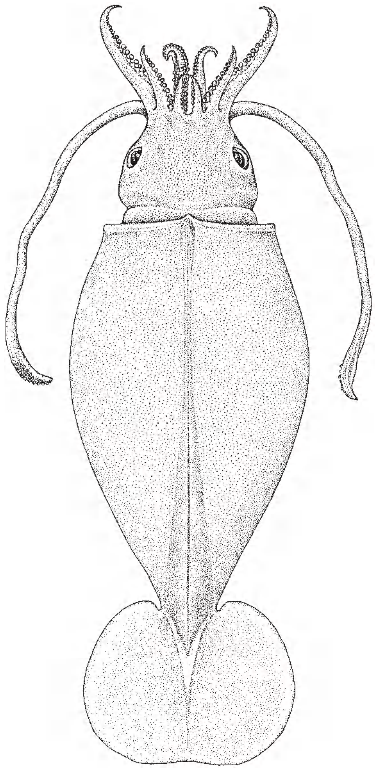
Leachia reinhardti Steenstrup, 1856, *Kongelige Danske Videnskabernes Selskabs Skrifter, series 5*, 4:185–216 [200]. [Type locality: North Atlantic Ocean, 15° 19'N, 24°54'W and 23°N, 32°W].

Frequent Synonyms: *Liocranchia brocki* Pfeffer, 1884; *L. elongata*, Issel, 1908; *Fusocranchia alpha* Joubin, 1920; *Liocranchia intermedia* Robson, 1924.

FAO Names: En – Reinhardt's cranch squid; **Fr** – Encornet-outre de Reinhardt; **Sp** – Cranquiluria de Reinhardt.

Diagnostic Features: Possesses **cartilaginous tubercles along dorsal midline**, overlaying gladius; **14 oval photophores on eye**.

Size: Maximum mantle length to 250 mm.



dorsal view

Fig. 189 ***Liocranchia reinhardti***

Geographical Distribution: ***Liocranchia reinhardti*** is distributed circumglobally in tropical and subtropical waters, recorded from 50°N to about 35°S, generally bounded by the north and south subtropical convergences (Fig. 190).

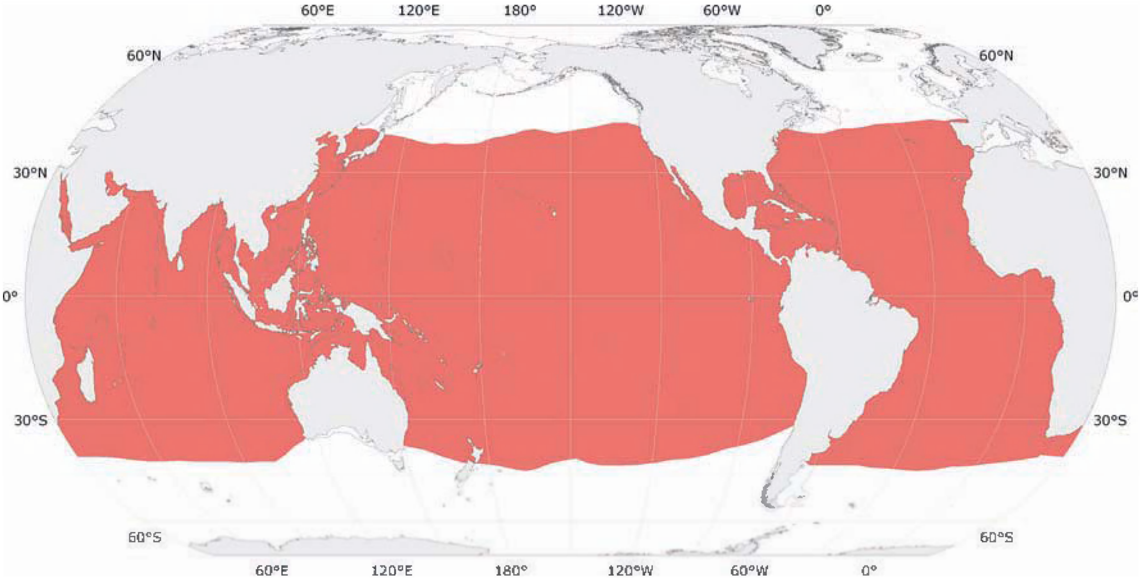


Fig. 190 ***Liocranchia reinhardti***

🟥 Known distribution

Habitat and Biology: Its vertical distribution as paralarvae and juveniles is epipelagic to upper mesopelagic, while the adults occur at lower epipelagic, mesopelagic and bathypelagic depths; surface to 1 200 m. In Hawaiian waters, at least. ***L. reinhardti*** appears to be a strong vertical migrator, probably a component of the mesopelagic boundary fauna where it is most common over bottom depths of 700 m or less, rather than in deeper offshore waters.

Literature: Young (1972a, 1995), Lu and Roper (1979), Piatkowski and Welch (1992 [1991]), Roper and Lu (1990), Voss *et al.* (1992b), Guerra (1992), Arkhipkin (1996c), Chesalin and Zuev (2002b).

Liocranchia valdiviae Chun 1910

Liocranchia valdiviae Chun, 1910, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition dem Dampfer Valdivia, 1898-1899*, 18(1): 1–401 [337]. [Type locality: 04°45'S, 48°58'E, Indian Ocean].

Diagnostic Features: The species is distinguished from ***Liocranchia reinhardti*** by the absence of cartilaginous tubercles along dorsal midline and the presence of only 4 oval photophores on eyeball.

Size: Maximum mantle length unknown, perhaps from 200 to 250 mm.

Geographical Distribution: ***Liocranchia valdiviae*** occurs principally in the Indian and Pacific oceans; it also is present in the southeastern South Atlantic in the Benguela Current off South Africa; it is confined primarily to tropical and equatorial oceanic waters.

Habitat and Biology: The young (of 5 to 15 mm mantle length) are epipelagic, concentrated in the upper few hundred metres; juveniles of approximately 15 to 25 mm mantle length descend to mesopelagic depths of 500 to 700 m and animals greater than 25 mm mantle length are bathypelagic, progressively deeper to in excess of 1 200 m. The species does not undergo a diel vertical migration, but occasional wanderers occur in shallower depths at night off Hawaii.

Literature: Roper and Young (1975), Voss *et al.* (1992b).

2.10.2 Subfamily TAONIINAE Pfeffer, 1912

Taoniinae Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2: [644].

Type genus: *Taonius* Steenstrup, 1861.

Diagnostic Features: The Taoniinae is characterized by the **absence of cartilaginous strips** that extend posteriorly along the lines of the funnel-mantle fusions; the presence of a funnel that is free laterally (not fused to the head); and the presence on the eyes of **1 to 3 markedly dissimilar-sized and -shaped photophores**, **the largest** one usually **crescent-shaped**. Hectocotylus absent in males; secondary sexual modifications may occur on arms I, II, III or all 4 pairs of arms or absent entirely; adult females may have brachial photophore on tips of arms I, II, III (or on all 4 pairs), or absent altogether; ceacum smaller than stomach.

Remarks: This subfamily contains numerous and diverse species that are arranged in several genera, many of which were based on paralarval or juvenile forms (e.g. ***Fusocranchia***, ***Teuthowenia***, ***Taonidium***). The currently recognized genera are: ***Taonius***, ***Bathothauma***, ***Belonella***, ***Egea***, ***Galiteuthis***, ***Helicocranchia***, ***Liguriella***, ***Megalocranchia***, ***Mesonychoteuthis***, ***Sandalops*** and ***Teuthowenia***.

Literature: See references listed in the family section and ***Helicocranchia***.

Taonius Steenstrup, 1861

Taonius Steenstrup, 1861, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1861: 69–86 [83].

Type Species: *Taonius pavo* (Lesueur, 1821).

Frequent Synonyms: *Desmoteuthis* Verrill, 1880–1881; *Toxeuma* Chun, 1906; *Belonella* Lane, 1957.

Diagnostic Features: Mantle very long, slender, widest anteriorly, tapers to sharply filiform posteriorly, **not covered with cartilaginous tubercles**, somewhat gelatinous in adults; funnel-mantle fusion cartilages small, narrow (to stout), oval, without tubercles (a single tubercle may be present in juveniles); mantle-nuchal fusion cartilage oval, extends onto head, tubercles absent; fins long, terminal, narrow, lanceolate, anterior lobes small, very attenuate posteriorly, extend to tip of gladius; funnel large, dorsal pad of funnel organ small, stout, inverted U-shape with 3 short, fat, round papillae, the central one with a thin terminal flap; **funnel valve absent**; eyes very long and stalked in paralarvae, become tubular in juveniles and then huge, nearly spherical in adults, where they dominate head, protruding, anteriorly directed; **2 photophores on ventral surface of eyes: a large posterior crescent-shaped organ that engulfs the small anterior crescent-shaped photophore**; arm-tip photophores absent; **tentacular club without hooded hooks, with enlarged suckers with 1 or 2 large, hook-like central teeth distally**; marginal suckers not reduced in size or lost; tentacular stalk with 2 series of alternating suckers and knobs on distal two-thirds; **conus of gladius very filiform**.

Size: Medium- to large-sized squids, up to 660 mm mantle length.

Geographical Distribution: The genus is oceanic cosmopolitan in tropical, subtropical, temperate and subpolar regions.

Habitat and Biology: Vertical distribution extends from the upper 200 m for paralarvae to the mid-depths of 600 m for juveniles; ontogenetic descent continues until the mature adults occur at 2 000 m and deeper. A diel vertical migration does not seem to occur. Spawning appears to occur suddenly, very near the surface at night.

Remarks: ***Taonius*** currently consists of 3 species, although at least 2 other species are thought to exist in the contiguous geographical distributions that seem to occur among congeners of the genus (Voss *et al*., 1992a; Voss pers.com).

Literature: Voss (1980, 1992); Young and Mangold (2008e). See additional references listed in the species accounts.

Taonius pavo (Lesueur, 1821)

Fig. 191

Loligo pavo Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101 [96]. [Type locality: Sandy Bay, off Massachusetts, western North Atlantic Ocean].

Frequent Synonyms: None.

FAO Names: En – Peacock cranch squid; **Fr** – Encornet-outre paon; **Sp** – Cranquiluria pavo.

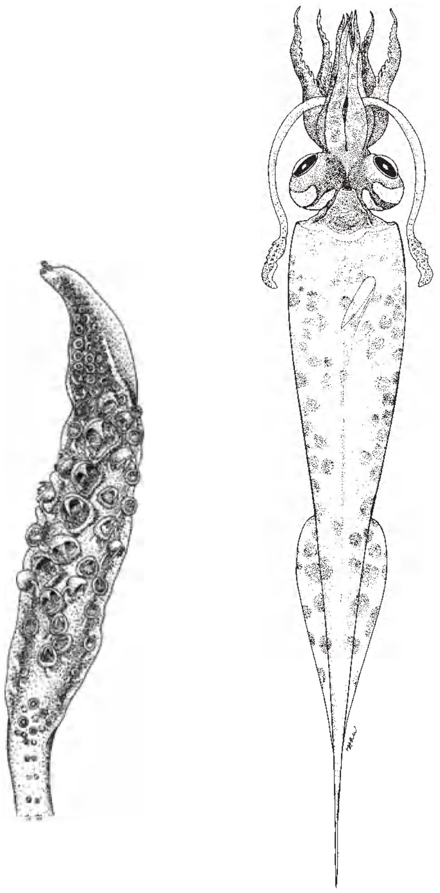
Diagnostic Features: Mantle elongate, thin, tapers posteriorly. **Fins lanceolate, extend half the mantle length**. **Head small, eyes bulbous**. Arms with biserial, spherical suckers. Tentacles a little longer than arms. **Club with 4 series of suckers**; **mesial sucker rings with 2 hook-like curved teeth**. Marginal sucker rings with several sharp teeth.

Size: Maximum mantle length to 660 mm.

Geographical Distribution: *Taonius pavo* is known to be widely distributed in the open Atlantic Ocean midwaters from about 45°N to the Southern Subtropical Convergence; it may extend into the Indian Ocean in association with the Agulhas Current (Fig. 192).

Habitat and Biology: Vertical distribution as noted for the genus. See Literature.

Literature: Clarke and Lu (1974, 1975); Roper and Young (1975), Vecchione and Roper (1992 [1991]), Roeleveld *et al.* (1992), Moreno and Pereira (1998), Vecchione (2002).



tentacular club ventral view

Fig. 191 *Taonius pavo*

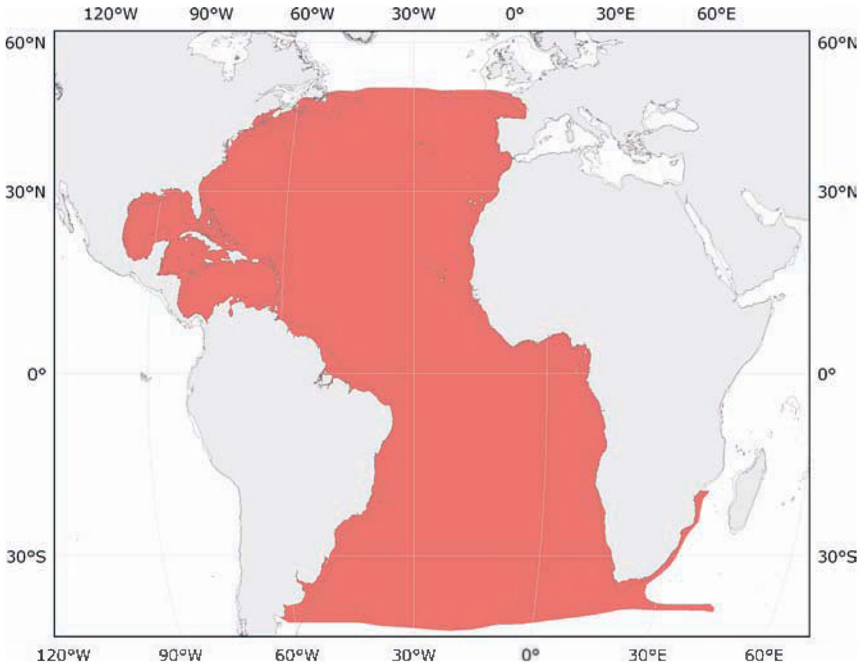


Fig. 192 *Taonius pavo*

🟥 Known distribution

Taonius belone (Chun 1906)

Toxeuma belone (Chun, 1906), *Zoologischer Anzeiger*, 31(2): 92–86 [86]. [Type locality: 10°08'S, 97°14'E, central Indian Ocean].

Frequent Synonyms: *Belonella pacifica pacifica* Nesis, 1972a, *Belonella belone* Nesis (1982, 1987).

Diagnostic Features: Mantle very slender, thin, leathery; fins long, width about 15% of mantle length. Eyeball large, with lunate and bilobal crescent photophore. Arms short; sucker rings with broad, low teeth. Mesial 6 pairs of manal suckers transformed into 2 hooks; lateral accessory denticles vestigial.

Size: Maximum mantle length to about 530 mm.

Geographical Distribution: North subtropical and tropical/equatorial waters of the Pacific and Indian Oceans.

Remarks: Chun (1906) named ***Toxeuma belone*** from the Indian Ocean at 10°08'S, 97°14'E on the basis of a single specimen of 51 mm mantle length. Lane (1957) pointed out that the generic name ***Toxeuma*** was preoccupied and proposed the name ***Belonella belone***. Nesis (1972a) maintained a generic separation between ***Belonella*** and ***Taonius*** based in part on his observation of the different consistency of the tissues (gelatinous in ***Taonius*** and leathery in ***Belonella***). ***Belonella*** and ***Taonius*** were synonymised by Voss (1980), even though some authors did not accept this action (e.g. Nesis, 1982, 1987; Okutani, 2005). The identity/validity of Chun's species, however, was long considered uncertain; ongoing research (Voss, pers. comm.), supporting previously published data (Nesis, 1982, 1987; Voss, 1988; Voss *et al.*, 1992b) and working hypotheses (Young and Mangold, 2008e), strongly indicate that ***Taonius belone*** be synonymised with ***T. pacificus***, the latter species name obtained by synonymising ***Belonella pacifica pacifica***, Nesis, 1972a with ***Taonius***. Thus, the new combination is derived, ***Taonius belone*** (Chun, 1906), the specific name ***belone*** having priority (Jereb and Roper *in* Young and Mangold, 2008e).

Literature: Chun (1906), Lane (1957), Voss (1980), Nesis (1982, 1987), Voss (1988), Voss *et al*. (1992b), Young and Mangold (2008e).

Taonius borealis (Nesis, 1972)

Belonella borealis Nesis, 1972a, *Zoologicheskij Zhurnal*, 51(3): 341–350 [343]. [Type locality: 44°07.8'N, 150°26.7'E, North Pacific Ocean].

Frequent Synonyms: None.

Diagnostic Features: Mantle leathery; photophores on eyeball crescent-shaped. Sucker rings dentate. Tentacular suckers with 1 or 2 major hooks and 1 to 3 accessory small lateral hooks.

Size: Maximum mantle length to about 500 mm.

Geographical Distribution: ***Taonius borealis*** is an oceanic species that occurs in the boreal, sub-Arctic region of the North Pacific Ocean, from the Bering Sea to eastern Honshu, Japan, Sea of Okhotsk to southern California.

Habitat and Biology: Paralarvae occur in the upper 200 m, undergo ontogenetic descent as juveniles to 400 to 600 m, then with continued growth descend to in excess of 2 000 m where sexual maturity occurs. Some diel vertical movement might occur.

Literature: Nesis (1982, 1987), Arkhipkin (1996b), Katugin *et al.* (2006b).

Bathothauma Chun, 1906

Bathothauma Chun, 1906, *Zoologischer Anzeiger*, 31(2): 82–86. [86].

Frequent Synonyms: *Leucocranchia* Joubin, 1912.

Diagnostic Features: Medium-sized taoniids. Mantle elongate cylindrical, sac-shaped, rounded posteriorly. Cartilaginous tubercles absent (or nearly so) on funnel/mantle fusion. Fins small, widely separated, rounded, paddle-shaped, subterminal, inserted on lateral expanded ends of transverse extensions of posterior end of gladius (unique to this genus). Funnel valve absent, funnel organ with inverted V-shaped dorsal pad. Eyes large to huge, protruding, anteriorly oriented, nearly spherical; most of posteroventral surface covered with a single, very large, half-round photophore (unusual in family, shared only with ***Helicocranchia***), indented in midanterior margin. Brachial photophores on arm tips of adult females unknown. Paralarva and juvenile exceptionally distinct with very long eye stalks, distinct rostrum on each eye, a long brachial pillar, widely separated fins.

Size: Medium-sized species: maximum mantle length to 200 mm.

Geographical Distribution: The genus is circumglobal in tropical and subtropical zones.

Habitat and Biology: ***Bathothauma*** occupy the open oceans and occur from the near-surface epipelagic waters, as young, to the bathypelagic realm in excess of 2 000 m, as adults. The paralarval stage is extended to a very large size, about 100 mm mantle length, while adults attain 200 mm mantle length.

Remarks: ***Bathothauma*** currently is monotypic; the only species is ***B. lyromma***. However, ongoing research indicates that at least 4 very closely related species exist throughout their contiguous distributions.

Literature: Voss (1980), Voss *et al.* (1992b).

Bathothauma lyromma Chun, 1906

Fig. 193

Bathothauma lyromma Chun, 1906, *Zoologischer Anzeiger*, 31(2): 82–86. [86]. [Type locality: 17°28'N, 29°42'W, West of Cape Verde Islands, southeastern Atlantic Ocean.

Frequent Synonyms: *Leucocranchia pfefferi* Joubin, 1912.

FAO Names: En – Lyre cranch squid; **Fr** – Encornet-outre lyre; **Sp** – Cranquiluria cítara.

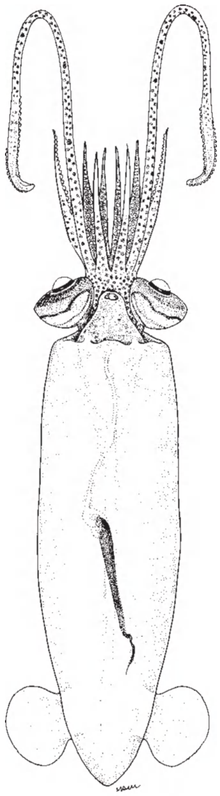
Diagnostic Features: As given for the genus.

Size: Maximum mantle length to 200 mm.

Geographical Distribution: ***Bathothauma lyromma*** is an extremely broadly distributed oceanic species throughout the world oceans in tropical and subtropical zones; in the Atlantic known from 35° to 45°N to 35° to 40°S (Fig. 194).

Habitat and Biology: Its vertical range extends from subsurface epipelagic depths as paralarvae and undergoes very clear ontogenetic descent through the mesopelagic zone and into the bathypelagic waters to in excess of 2 000 m.

Literature: See references listed for the genus. Young (1970), Aldred (1974), Roper and Young (1975), Vecchione *et al.* (1989), Kubodera (1994).



ventral view

Fig. 193 ***Bathothauma lyromma***

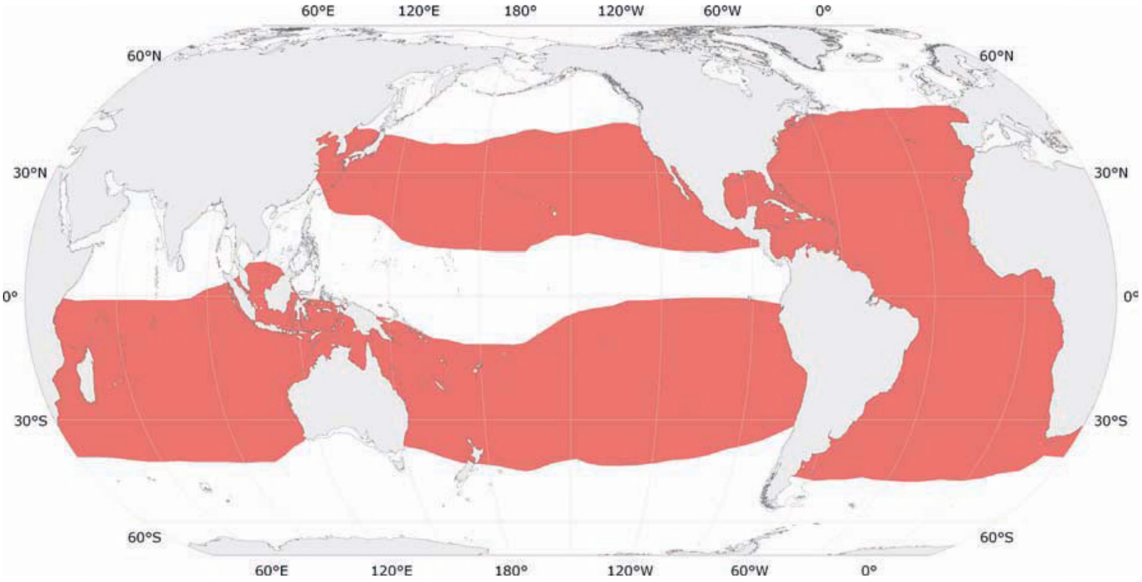


Fig. 194 ***Bathothauma lyromma***

🟥 Known distribution

Egea Joubin, 1933

Egea Joubin, 1933, *Annales de l'Institut Océanographique*, 13(1): 1–49 [43].

Frequent Synonyms: None.

Diagnostic Features: Mantle long, narrow, spindle-shaped, thin-walled, leathery, tapers posteriorly to attenuated tip; funnel-mantle fusion cartilage elongate, triangular, without tubercles; nuchal fusion cartilage conspicuous, spindle-shaped without tubercles; internal funnel-mantle fusion lines appear externally as non-cartilaginous, non-tubercular, inverted-V marks that originate on the mantle-funnel cartilages; fins lanceolate, terminal lateral, taper posteriorly to tip of gladius, no anterior lobes; fins attach laterally on mantle for one-third or more of mantle length (unusual in subfamily, shared only with ***Teuthowenia***); funnel moderately large; **dorsal pad of funnel organ large**, inverted V-shaped, broad anterior margin, **triangular flap on each lateral limb**, no midanterior papilla, ventral pads with anterior V-shaped notch; funnel valve present, well developed (unusual in subfamily, shared only with ***Megalocranchia***); **eyes spherical, protruding**, anterolaterally oriented, ventral surface **with 2 long, narrow photophores: 1 long, crescent-shaped, posterior (medial)**; **1 anterior (lateral) encircles two-thirds of lens, crescent-shaped with out-curved terminal curve at posterior end**; brachial end organs (photophores) present on arms III in subadult females (adult females unknown); hectocotylus absent in mature males, all arm tips secondarily modified with 4 transverse series of minute suckers; tentacles medium length, muscular, stalk with 2 series of suckers and pads on distal three-fourths; clubs slightly expanded, without carpal cluster, suckers on manus medium-sized, set on long stalks; gladius with very long, delicate, narrow rachis without anterior expansion; delicate vanes on posterior third of rachis form narrow, elongate lanceola; distal posterolateral margins of vanes in-roll ventrally without fusing to form hollow needle-like conus.

Size: Moderately large cranchiids; maximum reported mantle length 420 mm.

Geographical Distribution: Circumglobal in equatorial, tropical to subtropical waters (35°N to 42°N, to 25°S), in the Atlantic, Indian and western Pacific oceans. It occurs in the Gulf of Mexico, the western North Atlantic Gulf Stream system and the western North Pacific Kuroshiro Current system.

Habitat and Biology: The vertical distribution of paralarvae to approximately 35 mm mantle length is epipelagic, concentrated in subsurface water to 200 m both day and night. With growth and metamorphosis (around 35 to 40 mm mantle length) juveniles broaden their range in the mesopelagic zone to 800 m or more. One subadult female was captured in a closing net at night at 800 to 600 m in the western North Atlantic. Subadults and adults descend into the bathypelagic zone where maturation occurs in the 2 000 m zone. Captures of juveniles and large subadults at night in subsurface waters to about 300 m suggests that a portion of the population undergoes a diel vertical migration.

Remarks: The genus ***Egea*** currently is monotypic, represented by ***Egea inermis***, but Voss *et al*. (1992b) indicate that a second species may exist.

Literature: Voss *et al*. (1992b), Young and Mangold (1999a).

Egea inermis Joubin, 1933

Fig. 195

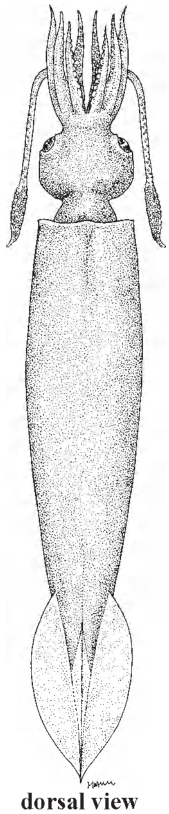
Egea inermis Joubin, 1933, *Annales de l'Institut Océanographique*, 13(1): 1–49 [48]. [Type locality: 33°51'N, 66°43'W, North Atlantic Ocean].

Frequent Synonyms: *Phasmatopsis lucifer* Voss, 1963b.

FAO Names: En – Unarmed cranch squid; **Fr** – Encornet-outre désarmé; **Sp** – Cranquiluria desarmada.

Diagnostic Features: See under ***Egea***.

Size: Maximum mantle length to 420 mm.



dorsal view

Fig. 195 ***Egea inermis***

Geographic Distribution: See under ***Egea*** (Fig. 196).

Habitat and Biology: See under ***Egea*** generic account.

Literature: Zuev and Nesis (1971), Voss (1974), Lu and Roper (1979), Vecchione *et al*. (1989). Additional references are listed under ***Egea***.

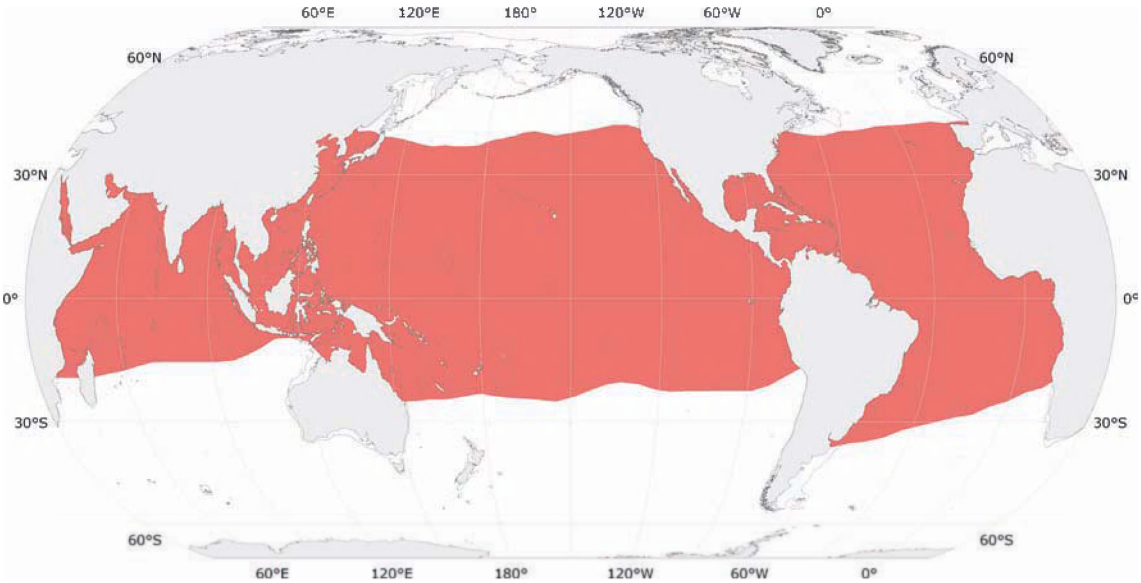


Fig. 196 ***Egea inermis***

🟥 Known distribution

Galiteuthis Joubin, 1898

Galiteuthis Joubin, 1898a, *Annals of Scientific Naturalist, Zoology, series 8*, 6: 279-292 [292].

Type Species: *Galiteuthis armata* Joubin, 1898a.

Frequent Synonyms: *Taonidium* Pfeffer, 1900; *Crystalloteuthis* Chun, 1906; *Phasmatoteuthion* Pfeffer, 1912; *Cristalloteuthis* Naef, 1921a (erroneus spelling of *Crystalloteuthis* Chun, 1906).

Diagnostic Features: Mantle long, slender, broadest in anterior half, tapers posteriorly to long, slender, pointed tip; mantle spindle shape, fins small in juvenile; numerous rounded cartilaginous tubercles present on mantle from about 10 mm mantle length, occasionally very numerous with growth (species-dependent); comma-shaped mantle-funnel fusion cartilages may have 2 elongate tubercles each with 2 or 3 cusps present on anterior portions; broad, triangular mantle-nuchal fusion cartilage, with 2 small turbercles on each side with 2 or 3 cusps; **fins terminal**, medium to long, **lanceolate, variously attenuate posteriorly, with stout gladial spine** and low delicate fringe to tip of gladius; anterior margin of fins insert on posterolateral margins of lanceola; funnel medium-sized, extends to mideye level; dorsal pad of funnel organ approximately inverted U-shape with 3 large, slightly flattened papillae; **funnel valve absent**; **large, protruding, anterior laterally-directed eyes** dominate head, their ventral (medial) surface **with 1 large, very elongate, crescent-shaped posterior photophore that envelopes 1 small, slightly crescent-shaped to round anterior (lateral) photophore**; **arms short; arms without hooded hooks**; arm tips without brachial end-organ photophores; tentacles short to medium, muscular, 2 series of carpal suckers in pairs along distal two-thirds to three-fourths of stalk, carpal cluster present; club short, slightly expanded, **4 to 8 pairs median suckers on manus** that with growth (from about 35 to 60 mm mantle length) **become conspicuous, large, hooded hooks**; suckers on lateral rows greatly reduced or lost; medium-width protective membrane with weak trabeculae; gladius with long, slender rachis, long narrow vanes that in-roll posteriorly, overlap, and form long, hollow, needle-like conus.

Size: Moderately large-sized squids. Some species may attain a large size to nearly 2 m total length (unconfirmed).

Geographical Distribution: Species within the genus are oceanic, pelagic, found variously circumglobally in all oceans in tropical, subtropical, temperate, subpolar and Antarctic waters; absent in Arctic Ocean.

Habitat and Biology: Squids vertical range extends from immediate subsurface depths as paralarvae into depths in excess of 1 500 m as adults.

Remarks: ***Galiteuthis*** is comprised of 5 nominal species and at least 1 or 2 additional species are yet to be validated.

Literature: Voss (1980), Rodhouse *et al*. (1992a). Additional references listed in individual species sections.

Galiteuthis armata Joubin, 1898

Fig. 197

Galiteuthis armata Joubin, 1898a, *Annals of Scientific Naturalist, Zoology, series 8*, 6: 279–292 [292]. [Type locality: ?Nice, Mediterranean Sea].

Frequent Synonyms: *Taonidium pfefferi* Russell, 1909.

FAO Names: En – Armed helmet squid; **Fr** – Encornet-outre armé; **Sp** – Cranquiluria armada.

Diagnostic Features: Mantle long, lanceolated, fused with funnel and head in the occipital area. **Mantel surface smooth**. Fins lanceolated, reach the pinted tail of the mantle. **Two to 4 small conical tubercles** on the mantle-funnel fusion sites.

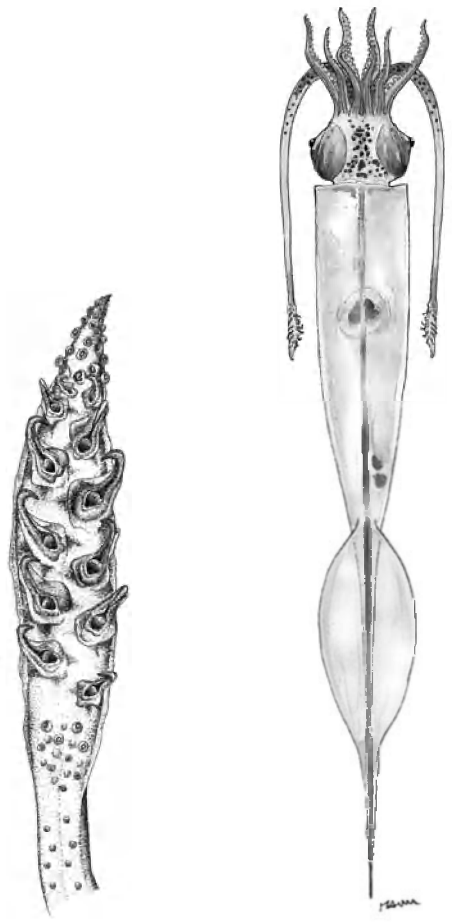
Size: Maximum mantle length to 610 mm.

Geographical Distribution: ***Galiteuthis armata*** occurs in the North Atlantic Ocean to 62°N southward to about 25°S, in tropical, northern subtropical, northern temperate waters; Straits of Florida, Gulf of Guinea, Bay of Biscay and Mediterranean Sea (Fig. 198).

Habitat and Biology: This species occurs over a very broad vertical range of depths and demonstrates a definite ontogenetic descent. Juveniles and paralarvae less than 30 mm mantle length have been captured in closing nets from subsurface depths to 1 000 m, with greatest concentrations in the upper 200 m. By about 35 mm mantle length, juveniles descend below 600 m, while large subadults have been captured between 500 to greater than 2 500 m, with greatest numbers deeper than 1 300 m.

Local Names: ITALY: Totano armato.

Literature: Berdar and Cavallaro (1975), Lea (1985), Lefkaditou and Maiorano (2001), Vecchione and Pohle (2002), Okutani (2005).



tentacular club dorsal view

Fig. 197 *Galiteuthis armata*

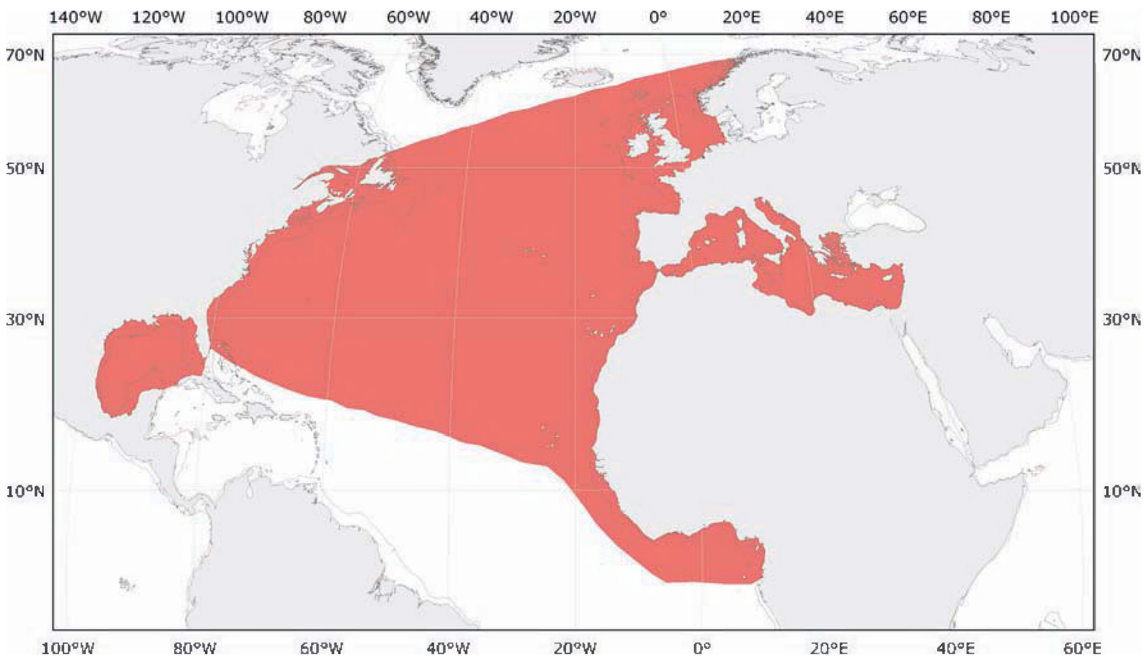


Fig. 198 *Galiteuthis armata*

🟥 Known distribution

Galiteuthis glacialis (Chun, 1906)

Crystalloteuthis glacialis Chun, 1906, *Zoologischer Anzeiger*, 31(2): 82–86 [85]. [Type locality: 59°16'S, 40°13'E, Antarctic Drift Current].

Frequent Synonyms: *Teuthowenia antarctica* Chun, 1910; *Galiteuthis aspera* Filippova, 1972.

Diagnostic Features: Two linear, multicuspid tubercles at each funnel-mantle fusion; 2 or 3 small, conical tubercles/cusps on each side of nuchal head-mantle fusion. Mantle surface rough, with many rounded cartilaginous tubercles in subadults.

Size: Maximum mantle length to 500 mm.

Geographical Distribution: ***Galiteuthis glacialis*** occurs in oceanic Antarctic circumpolar water masses (45°S to 70°S) and northward only where great masses of Antarctic intermediate waters flow out northward of the Antarctic Convergence (Fig. 199).

Habitat and Biology: The vertical distribution of paralarvae and juveniles extends from the lower epipelagic zone, concentrated around 200 m, but as shallow as around 75 m. With continued growth ontogentic descent finds larger juveniles concentrated at 300 to 1 000 m, subadults to 2 000 m; then sexual maturation occurs in very deep water in excess of 2 500 m. Significant diel vertical shifting appears to occur. ***Galiteuthis glacialis*** is one of the most abundant of Antarctic species of squid and is significant prey for albatrosses, Patagonian toothfish, southern elephant seals and cetaceans and it is a predator on *Euphausia superba* krill.

Literature: Roper (1969), Filippova (1992 [1991]), Rodhouse and Piatkowski (1995), Piatkowski *et al.* (2002), Laptikhovsky and Arkhipkin (2003a).

Galiteuthis pacifica (Robson, 1948)

Taonidium pacificum Robson, 1948, *Zoologica, Scientific Contributions of the New York Zoological Society*, 33(3): 115–132 [130]. [Type locality: off Cocos Island, eastern tropical Pacific Ocean].

Frequent Synonyms: None.

Diagnostic Features: Lateral (near lens) ocular photophore, circular. No tubercles at fusion of mantle-locking apparatus.

Size: Maximum mantle length to 200 mm.

Geographical Distribution: ***Galiteuthis pacifica*** is widely distributed throughout the equatorial tropical Indo-Pacific waters, from northern Chile (north of about 30°S) to southern California waters (about 34°N) in the eastern Pacific; Hawaii and the central Pacific Ocean to about 28°N and westward to New Caledonia and through to the eastern Indian Ocean.

Habitat and Biology: The vertical distribution for paralarvae of less than 20 mm mantle length extends from very shallow subsurface depths to about 800 m. The eyes become sessile at around 45 mm mantle length by which time these larger paralarvae concentrate around 600 to 800 m. Ontogenetic descent continues as juveniles and subadults occur increasingly deeper from 700 to 2 000 m. This species appears not to undergo diel vertical migration.

Literature: Young (1972a), Roper and Young (1975), Okutani (1995).

Galiteuthis phyllura Berry, 1911

Galiteuthis phyllura Berry, 1911b, *Proceedings of the United States National Museum*, 40(1838): 589–592 [592]. [Type locality: off Point Piños, Monterey Bay, California].

Frequent Synonyms: *Crystalloteuthis beringiana* Sasaki, 1920.

Diagnostic Features: Lateral (near lens) ocular photophore bar-shaped. Two to 4 small, conical tubercles at mantle-funnel fusion; none at mantle-nuchal fusion.

Size: Maximum mantle length reported to be 2.7 m, but this is considered a doubtful record that might refer to total length; probably the maximum mantle length is less than 400 to 500 mm.

Geographical Distribution: ***Galiteuthis phyllura*** is distributed in the temperate eastern North Pacific Ocean from off Baja California, about 25°N, and boreal, northward to the Bering Sea, westward to northern Japan and the Sea of Okhotsk.

Habitat and Biology: The vertical distribution of the species extends from shallow subsurface depths in the upper 100 m for the paralarvae around 10 mm mantle length, while larger paralarvae descent to 500 to 600 m. Juveniles with sessile eyes developed, generally occur deeper than 800 m. Ontogenetic descent continues as juveniles and subadults extend to over 1 200 m. No clear diel vertical migration has been confirmed, but a vertical wandering of larger individuals occurs into shallower depths at night, to 500 m or so.

Literature: Young (1972a), Nesis (1989b), Arkhipkin (1996b), Katugin *et al.* (2006b).

Galiteuthis suhmi (Hoyle, 1886)

Taonius suhmi Hoyle, 1886, *Report of the Scientific Results of the Voyage of the HMS Challenger, Zoology*, 16(44): 1–245 [192]. [Type locality: 47°25'S, 130°22'E in the southern Ocean from about 20°S to 45°S].

Frequent Synonyms: None.

Diagnostic Features:

Size: Maximum mantle length 300 to 400 mm.

Geographical Distribution: ***Galiteuthis suhmi*** is a very rarely reported species that occurs in the southern subtropical to sub-Antarctic circumglobal waters.

Habitat and Biology: ***Galiteuthis suhmi*** is a mesopelagic to bathypelagic species.

Literature: Nesis (1982, 1987), Lipinski *et al.* (2000).

Helicocranchia Massy, 1907

Helicocranchia Massy, 1907, *Annals and Magazine of Natural History (series 7)*, 20: 377–384 [382].

Type Species: *Helicocranchia pfefferi* Massy, 1907.

Frequent Synonyms: *Ascocranchia* Voss, 1962b.

Diagnostic Features: Mantle long, slender, cylindrical, most stout in midportion; tapers posteriorly to blunt terminal point that is not supported by the gladius. **Fins very small, paddle-shaped, subterminal, fused distally**, insert on short rostrum of gladius that projects dorsally free of end of gladius (free posterior lobes). **Eyes small to medium with 1, usually large, oval to round, protruding, anteriorly-oriented photophore**. **Funnel very large, long, broad**. Funnel-mantle fusion broad, indistinct cartilage, no tubercles. Funnel valve absent. Sexual dimorphism in arms and suckers; males with all arms more robust than on females, all arms with enlarged suckers (especially arms III); ends of male arms I to IV also secondarily modified with multiple series of suckers, variably expanded protective membranes, especially on arms I to II. Females occasionally with a few pairs of enlarged suckers on arms III; brachial photophores absent.

Size: Small-sized cranchiids; maximum mantle length to 100 mm.

Geographical Distribution: ***Helicocranchia*** members are circumglobal squids, widely distributed in tropical, subtropical and temperate (at least in the Atlantic Ocean) waters.

Habitat and Biology: Paralarvae and juveniles typically occur in upper epipelagic waters then with growth gradually undergo ontogenetic descent through the mesopelagic stratum and into the upper bathypelagic zone. Diel vertical migrations, if they occur at all, apparently are weak.

Remarks: ***Helicocranchia*** currently consists of 3 species considered valid; an additional 11 species throughout the world's oceans are recognized as valid, but they all are undescribed. The genus is easy to identify because of the **exceptionally large funnel** that extends anteriorly well anterior to the beaks and the very small, paddle-like fins that attach to the posterior gladius that projects dorsally above the mantle musculature.

Literature: See references listed for the family and for species, as well as the following: Voss, (1980), Young and Mangold (2008b).

Helicocranchia pfefferi Massy, 1907

Fig. 199

Helicocranchia pfefferi Massy, 1907, *Annals and Magazine of Natural History, series 7*, 20: 377–384. [382]. [Type locality: 51°44'N, 11°57'W, off the southwestern Irish coast, temperate western North Atlantic Ocean].

Frequent Synonyms: *Helicocranchia beebei*, Nesis (1982, 1987).

FAO Names: En – Pfeffer's cranch squid; **Fr** – Encornet-outre de Pfeffer; **Sp** – Cranquiluria de Pfeffer.

Diagnostic Features: Absence of cartilaginous papillae on the mantle, no enlarged suckers on the arms III of adult females (or on tentacular clubs), presence of bands of orange/brown chromatophores on sides of mantle; moderately long, robust tentacles, less than 100% of the mantle length; **L-shaped ventral pads on funnel organ**.

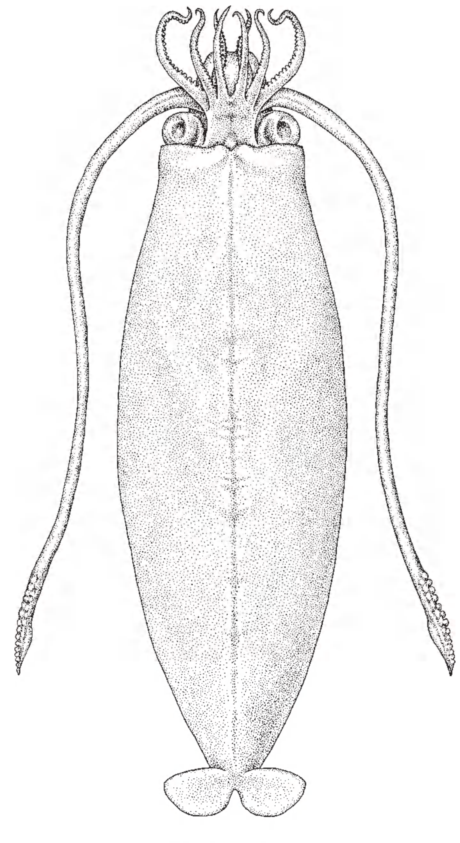
Size: Maximum mantle length to 90 to 100 mm.

Geographical Distribution: ***Helicocranchia pfefferi*** probably is a complex of species that together are circumglobal in open oceanic waters of the tropical, subtropical and North Atlantic temperate zones. In the Atlantic it occurs from 50° to 55°N to 30° to 35°S. Complete distributional pattern as yet undetermined (Fig. 200).

Habitat and Biology: Paralarvae and juveniles occur in the upper few hundred metres of the epipelagic zone, then descend gradually to the upper mesopelagic; finally, adults descend into the lower mesopelagic and the bathypelagic zones to at least 2 000 m. Some diel vertical migration might occur; paralarvae and mated/spent females captured at or near the surface suggest that adults return to the surface to mate and spawn.

Remarks: A considerable body of literature exists for ***H. pfefferi*** that documents details of geographic and vertical distribution, as well as other aspects of development and biology.

Literature: See generic references as well as the following: Lu and Clarke (1975a), Cairns (1976), Okutani and Tsukada (1988), Guerra (1992), Young and Mangold (2008b, c).



dorsal view

Fig. 199 ***Helicocranchia pfefferi***

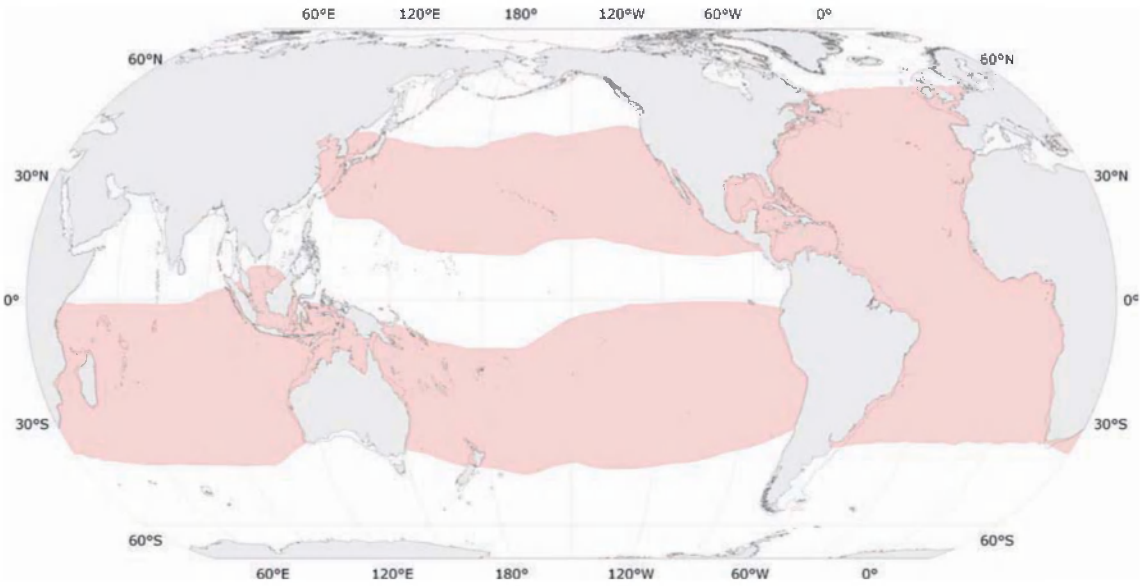


Fig. 200 ***Helicocranchia pfefferi***

🟥 Probable presence

Helicocranchia joubini (Voss, 1962)

Ascocranchia joubini Voss, 1962a, *Bulletin de l'Institut Océanographique, Monaco*, 1242: 1–6. [2]. [Type locality: 45° 02'N, 13° 05'W Sargasso Sea, western North Atlantic].

Frequent Synonyms: None.

Size: Maximum mantle length from 50 to 60 mm.

Geographical Distribution: It occurs in the tropical and subtropical Atlantic and the southwestern Pacific ocean in mesopelagic and bathypelagic realms.

Remarks: This poorly known species, considered by Nesis (1982, 1987) to be valid, but not listed in Voss *et al*. (1992b), possibly it is a synonym of ***Helicocranchia pfefferi***.

Literature: Nesis (1982, 1987), Voss *et al*. (1992b).

Helicocranchia papillata (Voss, 1960)

Megalocranchia papillata Voss, 1960, *Fieldiana, Zoology*, 39(40): 419–446. [430]. [Type locality: 32°05'N, 64°38'W, Sargasso Sea, off Bermuda, subtropical western North Atlantic Ocean].

Frequent Synonyms: None.

Diagnostic Features: Distinguishing characters include enlarged suckers on midportion of arms III and on ventral row of tentacular club; long, narrow tentacles more than 100% of mantle length in paralarvae and juveniles; ventral pads of funnel organ oval, elongate, crescent-shaped.

Size: Maximum mantle length from 50 to 60 mm.

Geographical Distribution: The geographical distribution of ***H. papillata*** occupies a broad portion of the western, central and eastern subtropical North Atlantic Ocean; Caribbean Sea and Gulf of Mexico, northeastern African waters.

Habitat and Biology: Vertical distribution of paralarvae and juveniles occurs in the upper 300 m, followed by ontogenetic descent of individuals into the mesopelagic zone with growth. Adults mature in the bathypelagic waters of 2 000 m or more; shallow depth captures of paralarvae and nearly spent females in the upper 100 m point to an epipelagic spawning habit.

Literature: Voss (1960), Clarke and Lu (1974), Nesis (1982, 1987), Vecchione *et al*. (2001).

Liguriella Issel, 1908

Liguriella Issel, 1908, *Monitore Zoologico Italiano*, 19(4): 102–104 [103].

Type Species: *Liguriella podophthalma* Issel, 1908.

Frequent Synonyms: *Vossoteuthis* Nesis, 1974a.

Diagnostic Features: Mantle elongate, moderately stout, tapers to blunt point posteriorly; anterodorsal mantle margin free, except at midline cartilaginous fusion; **without tubercles**; funnel-mantle fusion small, slightly curved, with 2 small cartilaginous tubercles at anterior end; funnel valve absent; **dorsal pad of funnel organ with 3 spatulate papillae**; **fins terminal, small, posterior fin insertions extend to tip of gladius and fuse along distal end of vane of gladius**; gladius with long, slender, delicate rachis, vanes along distal third expand to form diamond-shaped lanceola; posterolateral margins at very posterior tip infold, fuse to form short, narrow conus; **eyes with 2 contiguous photophores**, the anterior 1 small, crescent-shaped lies closely within the concavity of the large crescent-shaped posterior photophore; **arm tip photophores absent**; tentacular club with suckers, no hooks, no carpal cluster, 2 series of suckers and knobs along tentacular stalk.

Size: Medium-sized squids; maximum mantle length to over 240 mm.

Remarks: *Liguriella* contains 1 recognized species to date, ***L. podophthalma***, but as many as 2 or more additional mesopelagic species may exist (Voss *et al*. 1992b).

Literature: Voss (1980), Voss *et al*. (1992b), Young and Mangold (1999c).

Liguriella podophthalma Issel, 1908

Fig. 201

Liguriella podophthalma Issel, 1908, *Monitore Zoologico Italiano*, 19(4): 102–104[103, by monotypy]. [Type locality: 28°38'S, 47°31'W, South Atlantic Ocean].

Frequent Synonyms: None.

FAO Names: En – Bigeye cranch squid; **Fr** – Encornet-outre grand-oeil; **Sp** – Cranquiluria ojo-grande.

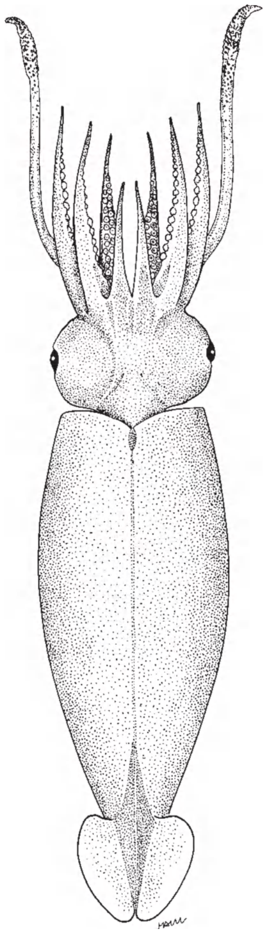
Diagnostic Features: See generic account.

Size: Maximum mantle length known 243 mm.

Geographical Distribution: ***Liguriella podophthalma*** occurs circumglobally in tropical, subtropical and northern sub-Antarctic waters (Southern Subtropical Convergence) of the world's oceans (Fig. 202).

Habitat and Biology: The species overall vertical distribution extends from subsurface waters to depths in excess of 1 000 to 1 500 m. Paralarvae and juveniles up to about 40 mm mantle length occur from subsurface depths to around 400 m, while older animals extend progressively deeper with growth. This ontogenetic descent extends to about 1 500 m where the largest specimen caught to date was a 243 mm mantle length subadult.

Literature: Nesis (1982, 1987), Voss *et al.* (1992b), Moreno and Pereira (1998).



dorsal view

Fig. 201 *Liguriella podophthalma*

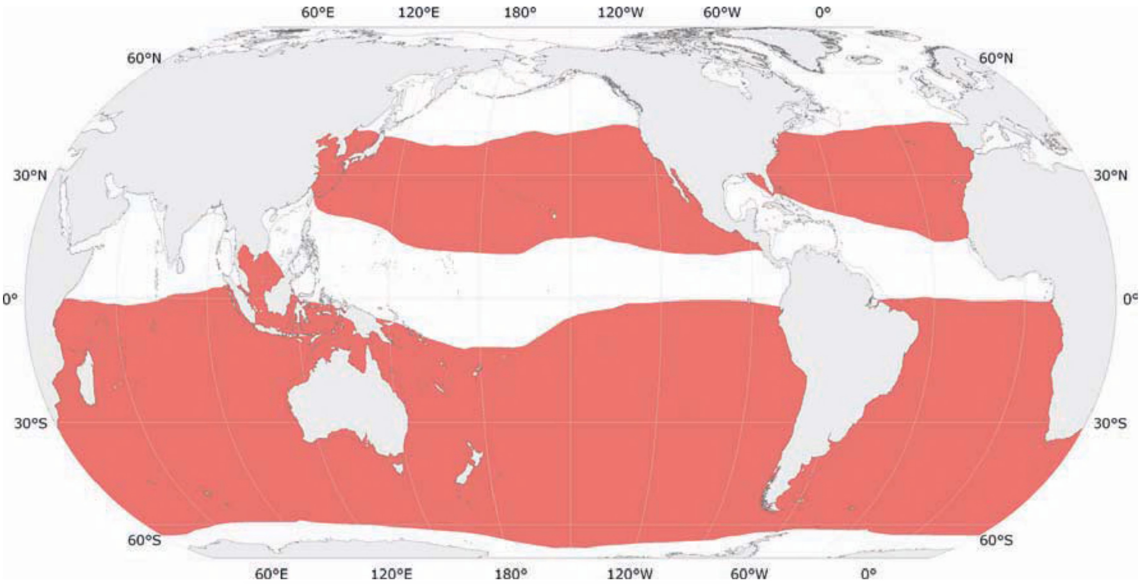


Fig. 202 *Liguriella podophthalma*

🟥 Known distribution

Megalocranchia Pfeffer, 1884

Megalocranchia Pfeffer, 1884, *Abhandlung aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 1–30 [24].

Type Species: *Megalocranchia maxima* Pfeffer, 1884.

Frequent Synonyms: *Corynomma* Chun, 1906; *Xenoteuthis* Berry, 1909; *Ascoteuthis* Berry, 1920a; *Carynoteuthis* Voss, 1960.

Diagnostic Features: Mantle slender, elongate, tapers dramatically posteriorly to thin, sharp tip; mantle wall very thin, leathery, transparent; paralarvae (to about 50 mm mantle length) with thick, gelatinous dermis on mantle (unique within family); tubercles absent on elongate, subtriangular mantle-funnel fusion cartilages and conspicuous spindle-shaped mantle nuchal fusion cartilage; **fins long** (about 50% of mantle length), lanceolate, terminal-lateral, **anterior 10 to 15% insert along lateral margin of mantle for about one-half mantle length**, no anterior lobes (fusion of anterior 10 to 15% of fins to mantle is unique in family; only ***Egea*** and ***Teuthowenia*** fins are fused to mantle but for 30% or more of their length; all other cranchiid fins attach to the gladius); funnel well developed, with well-developed funnel valve, funnel organ dorsal pad large, stout, with triangular flap on each lateral limb, anterior margin broad; head dominated by **very large, spherical, protruding, anterolaterally oriented eyes**; most of **ventral hemisphere of eyes covered with 2 photophores: one large, crescent-shaped posterior (medial) organ with irregularly shaped inner margin and central bulge, and within its concavity one smaller narrow, roughly elongate, irregularly S-shaped, anterior (lateral) organ**; arm tips I to III in large males secondarily modified by abrupt attenuation and reduced-size suckers, minute suckers in 2 series; subadult and adult females with brachial end organ (photophore) on I to III, or only on III, or occasionally only on II; tentacle short, strong, with 2 series of carpal suckers on mid-third of stalk then 4 transverse series distally to merge into a strong carpal group; clubs moderately long, strong, slightly expanded, with suckers in 4 series only moderately enlarged, on short to medium stalks; **a complex, bilobed, large, multilens (4) visceral photophore occurs on the ventral surface of the digestive gland and ink sac** (unique within the family); gladius with very slender, long rachis without anterior expansion; long, moderately expanded vanes border posterior half of rachis, dorsolateral margins roll-inward, fuse and form long, hollow, needle-like conus.

Size: Species of ***Megalocranchia*** are moderately to very large, up to 1.8 m mantle length.

Geographical Distribution: ***Megalocranchia*** species occur circumglobally in equatorial and bicentral tropical and subtropical waters.

Habitat and Biology: Paralarvae are epipelagic from very near-surface waters to about 200 m day and night. Juveniles metamorphose at about 40 to 50 mm mantle length, are concentrated in the upper 200 m at night, then descend to 600 to 800 m during the day. Subadults undergo further ontogenetic vertical descent through the mesopelagic and into the bathypelagic zone to greater than 2 000 m during daytime and some appear to migrate at night back toward lower epipelagic and mesopelagic depths (about 100 to 700 m). While adults probably mature in the bathypelagic water, they apparently reverse migrate back into epipelagic waters to spawn, as indicated by specimens caught at or near the surface at night. The species of ***Megalocranchia*** are neutrally buoyant.

Remarks: The systematics of this complex genus needs cnsiderable additional research and marterial to be clarified. Current thoughts agree in recognizing 2 valid named species, ***Megalocranchia maxima*** Pfeffer, 1884 and ***M. oceanica*** Voss, 1960 (Okutani, 2005, Young and Mangold, 2008d, Voss, pers. comm). At least 4 other entities were recognized and designated by letters but not named by Voss (1988), Voss *et al.* (1992b), Clarke (1986); one of these entities is considered, by part of the scientific community, to be a validly named species: ***M. fisheri*** (Berry, 1909), from the central North Pacific Ocean, particularly Hawaii (Young and Mangold, 2008e).

Literature: Young (1978), Clarke *et al.* (1979), Vecchione and Roper (1992 [1991]), Young and Mangold (1996a), Okutani (1998), Bello and Biagi (1999), Young and Mangold (2008d)

Megalocranchia maxima Pfeffer, 1884

Fig. 203

Megalocranchia maxima Pfeffer, 1884, *Abhandlung aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 1–30 [24]. [Type locality: off Cape of Good Hope, South Africa].

Frequent Synonyms: None.

FAO Names: En – Large cranch squid; **Fr** – Encornet-outre grand; **Sp** – Cranquiluria grande.

Diagnostic Features: See generic account.

Size: Maximum mantle length to 1.8 m.

Geographical Distribution: ***Megalocranchia maxima*** ranges the subtropical waters of the South Atlantic, sub-Antarctic and into the southwestern Indian Ocean. Japanese waters (Fig. 204).

Literature: Kubodera (in Okutani) (2000), Okutani (2005).

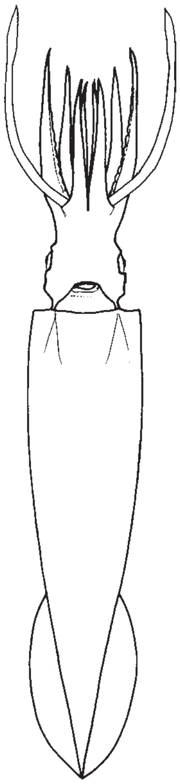


Fig. 203 ***Megalocranchia maxima***

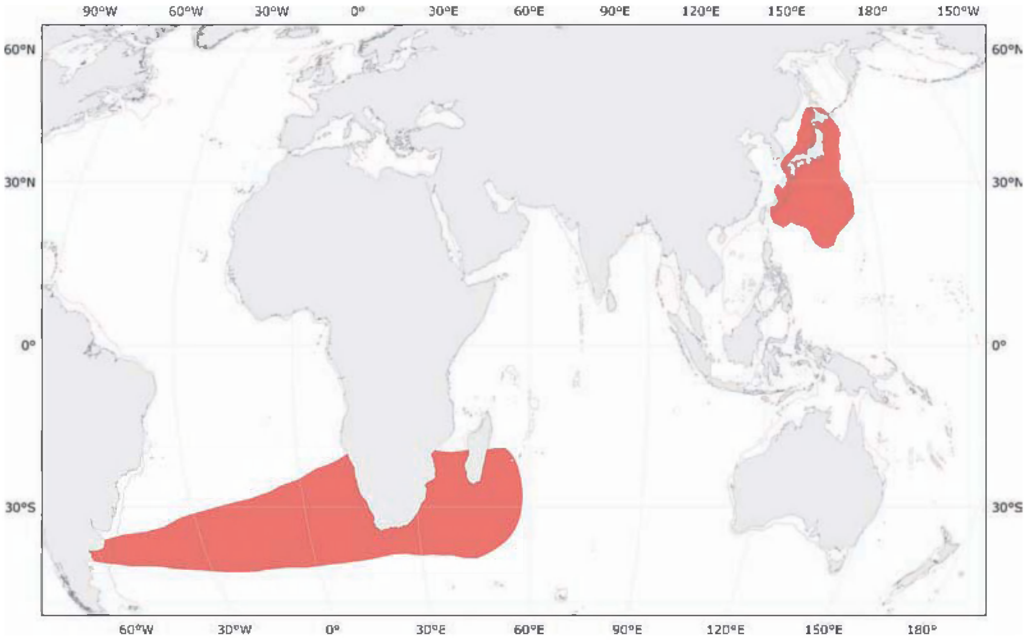


Fig. 204 ***Megalocranchia maxima***

🟥 Known distribution

Megalocranchia oceanica (Voss, 1960)

Carymoteuthis oceanica Voss, 1960, *Fieldiana, Zoology*, 39(40): 419–446 [434]. [Type locality: 32°08'N, 64°33'W, western North Atlantic Ocean].

Frequent Synonyms: None.

Diagnostic Features: See generic account.

Size: Maximum mantle length to 810 mm.

Geographical Distribution: ***Megalocranchia oceanica*** is a tropical to subtropical species in the North and South Atlantic Oceans from about 40°N to 35°S.

Habitat and Biology: Paralarvae were captured with closing nets off Bermuda between 50 and 200 m day and night. Ontogenetic descent occurs when paralarvae in the epipelagic zone gradually descend through the mesopelagic zone as juveniles and subadults; late subadult and adult stages occur in bathypelagic waters to 2 000 m or deeper. Two specimens were observed *in situ* from submersibles at 800 to 900 m in the Bahamas during daytime.

Literature: Vecchione and Roper (1992 [1991]), Nesis (1999b), Okutani (2005).

Mesonychoteuthis Robson, 1925

Mesonychoteuthis Robson, 1925, *Annals and Magazine of Natural History, series 9*, 16: 272–277 [272].

Type Species: *Mesonychoteuthis hamiltoni*, Robson, 1925.

Frequent Synonyms: None.

Diagnostic Features: The mantle is elongate, moderately stout in anterior quarter, tapers sharply anterior to fins then tapers gradually to form long, very narrow posterior half; **mantle wall thin, muscular to leathery and tough in juveniles and adults**, semigelatinous in mature females, up to 50 mm thick in adults, smooth; funnel-mantle fusion cartilages short, stout, curved, a complex of 4 to 6 conical cartilaginous tubercles anteriorly in paralarvae and juveniles; **nuchal fusion cartilage triangular, without tubercles in adults**, a single anterior tubercle in paralarvae and early juveniles; fins terminal, large, stoutly ovate, without anterior lobes, taper posteriorly to broad point at tip of gladius, anterior fin insertions extend along posterolateral margins of lanceola, except at anterior most margin; length up to 60% of mantle length in adults, **fins very muscular medially, taper to thin lateral margins; funnel valve absent**, inverted V-shaped dorsal pad of funnel organ with a short, stout papilla on each lobe and a long, narrow conical papilla on the midanterior section; **head large, dominated by huge, nearly spherical, protruding anterolaterally directed eyes**; **2 photophores on ventral hemisphere of each eye, a small, oblong anterior one encircled by a large, wide, crescent-shaped posterior one**; arms robust, moderately long, about 50% of mantle length, subequal; arm suckers in 2 series with dentate rings, about **3 to 10 pairs in midarm section develop into large, hooded hooks** beginning at about 45 mm mantle length (increasing numbers of hooks in arms I through IV), a unique character within the Cranchiidae; **brachial end organs (photophores) absent**; tentacles moderately long, robust; stalks with diagonally oriented pairs of suckers and pads along distal two-thirds, carpal cluster present, **club short**, strongly built, slightly expanded, with all suckers in medial series of manus developed into about **12 pairs of large, hooded hooks**; suckers of lateral series minute; gladius with long, moderately wide vanes that border posterior three-fourths of narrow rachis, posterolateral margins roll in ventrally, overlap posteriorly and fuse into long, narrow, strong, hollow conus.

Size: This is a gigantic squid with maximum mantle lengths of 2.25 to about 3 m, maximum recorded weight of 495 kg.

Geographical Distribution: It occurs circumglobally in Antarctic waters to 70°S, only rarely crossing the Antarctic Convergence to about 40°S, or very occasionally into southern waters off South Africa.

Habitat and Biology: This is a fully oceanic squid that occurs as shallow as 20 m for paralarvae, down to mesopelagic depths around 500 m. Larger paralarvae, juveniles and subadults range into the bathypelagic realm of around 500 m to in excess of 2 000 m. Nearly mature female ***Mesonychoteuthis hamiltoni*** have been taken in Antarctic waters hooked on long lines set to fish the upper few hundred metres. This suggests that the females at least, like females of other, better known species of cranchiids, may migrate vertically from great depths to near-surface waters to spawn; mating depths are unknown. ***Mesonychoteuthis hamiltoni*** is the major source of prey for sperm whales that migrate into Antarctic waters in summertime to crop the seasonal population explosions of cephalopods and fishes.

Remarks: ***Mesonychoteuthis*** is monotypic, represented only by ***M. hamiltoni***, one of the largest squids known.

Literature: Voss (1980), Roper *et al*. (1984), Rodhouse and Clarke (1985), Young and Mangold (2008a).

Mesonychoteuthis hamiltoni Robson, 1925

Fig. 205

Mesonychoteuthis hamiltoni Robson, 1925, *Annals and Magazine of Natural History, (series 9)*, 16: 272–277 [272]. [Type locality: 50 miles south of Smith Island, South Shetland Islands, from the stomach of a sperm whale].

Frequent Synonyms: None.

FAO Names: En – Colossal squid; **Fr** – Encornet-outre colossal; **Sp** – Cranquiluria colosal.

Diagnostic Features: See generic account.

Size: Maximum mantle length around 3 m; total length approaches 9 to 10 m; maximum weight recorded 495 kg (1 089 pounds).

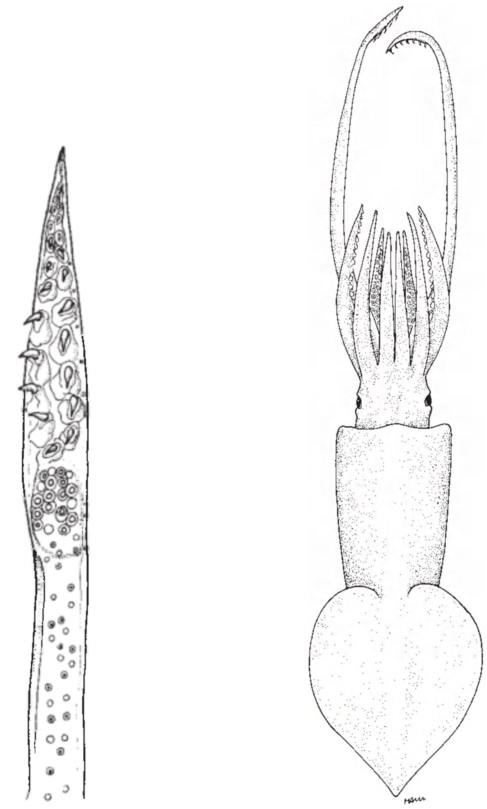
Geographical Distribution: This broadly distributed species occurs in the Southern Ocean, circumpolar region, primarily south of the Antarctic Convergence, occasionally north in cold waters to off South Africa. See generic section for additional details and for vertical distribution (Fig. 206).

Habitat and Biology: A mesopelagic to bathypelagic species in late juvenile, subadult and adult stages that range in depth from 500 m, then through ontogenetic descent to greater than 2 000 m; a relatively passive swimmer. Matures at mantle lengths greater than 1 m and 25 to 30 kg weight; spermatophores are 170 to 270 m long. It has a potential fecundity of 4 to 4.2 million oocytes. Feeds on mesopelagic fishes (Myctophidae, Paralepididae), Patagonian toothfish, sleeper shark and squids, and it is very heavily preyed upon by sperm whales at 400 to 600 m during the sperm whale feeding migration to the Southern Ocean in summertime; other predators include Patagonian toothfish. Juveniles also are preyed upon by albatrosses and Antarctic fulmars.

Interest to Fisheries: This species is believed to have some potential for a fishery. The flesh is rumored to be of "excellent quality and very flavourful", but this needs to be reconfirmed in view of changes in world cephalopod fishery exploitation since the 1970s and 1980s. It has been estimated that 1 or 2 million tonnes could easily be harvested in view of the reduced sperm whale predation at the time, due to that major predator's population decline. However, with the restoration of sperm whale populations to significantly higher levels in the late twentieth and early twenty-first centuries, such estimates might be invalid. Total reserves were estimated at 90 million tonnes (biomass), but no specific fishing methods have been developed yet, nor has any directed fishery been reported.

Local Names: RUSSIA: Antarkticheskyi gigantskyi kalmar.

Literature: Clarke (1980), Roper *et al.* (1984), Rodhouse and Clarke (1985), Filippova (1992 [1991]), Anderson and Rodhouse (2002), Xavier, *et al.* (2002c). Additional references are listed in the generic section.


tentacular club

dorsal view

Fig. 205 *Mesonychoteuthis hamiltoni*

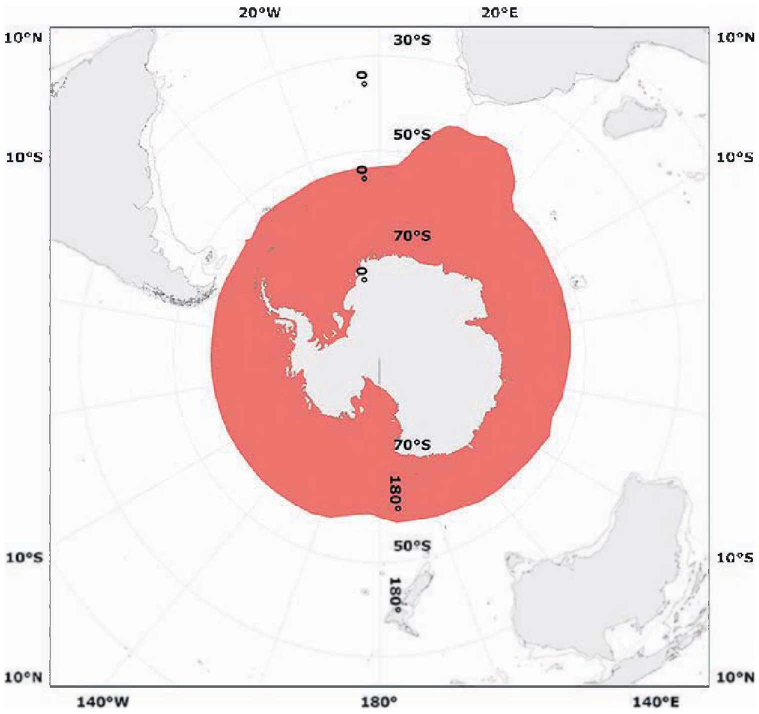


Fig. 206 *Mesonychoteuthis hamiltoni*

🟥 Known distribution

Sandalops Chun, 1906

Sandalops Chun, 1906, *Zoologischer Anzeiger*, 31(2): 82–86. [86].

Type Species: *Sandalops melancholicus* Chun, 1906.

Frequent Synonyms: *Uranoteuthis* Lu and Clarke, 1974.

Diagnostic Features: The mantle is stout, broadest at about one-third from anterior end, cylindrical, tapers gradually to broad posterior point; **no tubercles present on narrow funnel-mantle fusion or on small nuchal cartilage**. Fins small, short, oval to round, subterminal, with anterior and posterior lobes, posterior insertion does not reach terminal end of gladius, anterior insertion at broadest point on vanes of gladius (attach to posterolateral margins of lanceola). Conus short. Funnel valve absent; **dorsal pad of funnel organ with 2 large triangular flaps**. **Eyes large, protruding, nearly spherical, anteriorly oriented, each with 1 very large, round posterior photophore and 1 very small, round to elliptical anterior photophore contiguous with and indented into anterior margin of posterior photophore**. Brachial photophores absent.

Size: A medium-sized taoniid. Maximum mantle length known to 110 mm.

Geographical Distribution: ***Sandalops*** occurs circumglobally in oceanic tropical and subtropical waters at depths from the upper epipelagic into the lower mesopelagic and bathypelagic, following ontogenetic descent. In the Atlantic it occurs roughly between 40°N and 37°S.

Remarks: Currently only 1 species, ***Sandalops melancholicus***, is described, but Voss *et al*. (1992b) indicate that the genus is comprised of 3 or 4 closely related species.

Literature: Voss *et al*. (1992b), Young and Mangold (1996c), Nesis (1999b).

Sandalops melancholicus Chun, 1906

Fig. 207; Plate VII, 38

Sandalops melancholicus Chun, 1906, *Zoologischer Anzeiger*, 31(2): 82–86. [86]. [Type locality: 32°08'S, 08°28'W, off Tristan da Cunha Island, central South Atlantic Ocean].

Frequent Synonyms: *Uranoteuthis bilucifer* Lu and Clarke, 1974.

FAO Names: En – Melancholy cranch squid; **Fr** – Encornet-outre mélancolie; **Sp** – Cranquiluria afligida.

Diagnostic Features: The eyes are long, tubular in paralarvae and particularly in juveniles when they occupy the upper mesopelagic zone; **eyes oriented vertically upward**. **In subadults the eyes become nearly hemispherical**.

Size: Maximum mantle length to 110 mm.

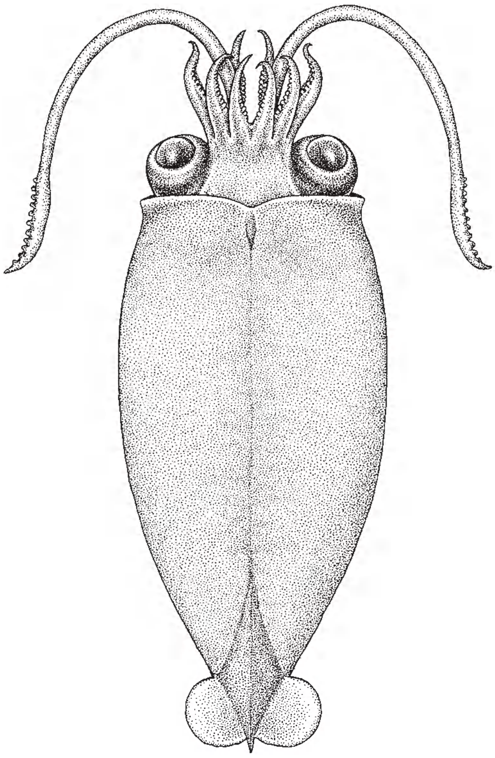


Fig. 207 ***Sandalops melancholicus***

Geographical Distribution: The species is cosmopolitan in tropical and subtropical waters (Fig. 208).

Habitat and Biology: ***Sandalops melancholicus*** lives in epipelagic, mesopelagic and bathypelagic zones, following the general cranchiid pattern of ontogenetic descent. By full growth, animals have descended into the bathypelagic zone beyond 2 000 m depth, where maturation and mating occur. No evidence currently exists for diel vertical migration.

Literature: Okutani (1974a), Kubodera (1996), Vecchione (2002). Additional references are listed in the generic section.

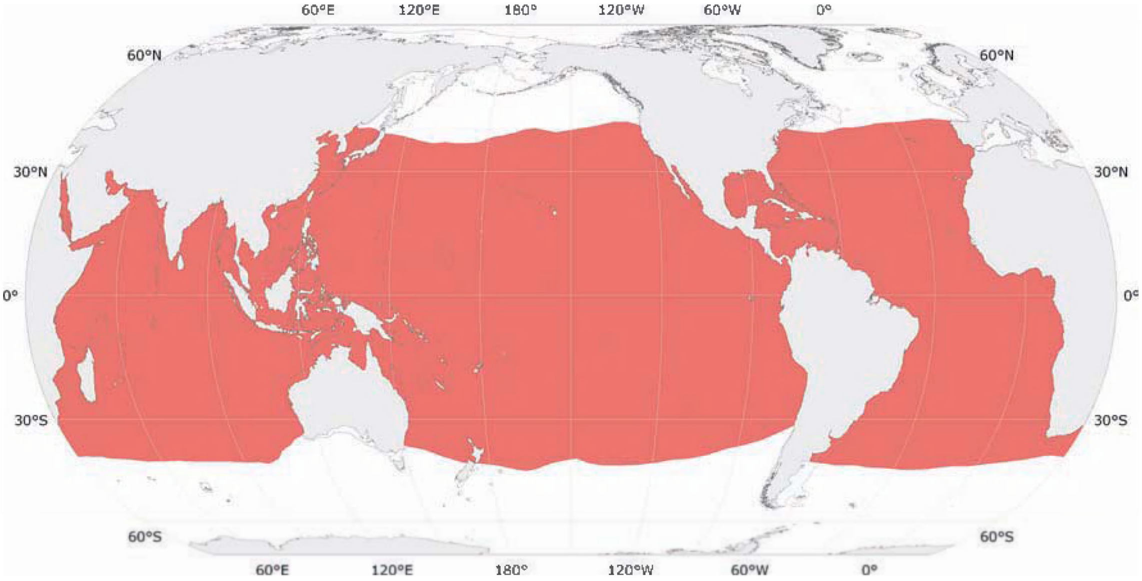


Fig. 208 ***Sandalops melancholicus***

🟥 Known distribution

Teuthowenia Chun, 1910

Teuthowenia Chun, 1910a, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition dem Dampfer Valdivia, 1898–1899*, 18(1): 1–401 [376].

Type Species: *Teuthowenia megalops* (Prosch, 1847).

Frequent Synonyms: *Owenia* Prosch, 1847; *Teuthowenia* Chun, 1910a; *Verrilliteuthis*, Berry, 1916; *Anomalocranchia* Robson, 1924.

Diagnostic Features: Mantle conical, elongate, tapers gradually posteriorly to narrow posterior tip, **mantle wall thin, leathery**; **funnel-mantle fusion cartilages small, oval to spindle-shaped, with 1 to 4 cartilaginous tubercles** at mantle margin; nuchal-mantle fusion cartilage small, elongate, diamond-shaped, without tubercles; fins long, narrow, terminal-lateral, taper gradually posteriorly, terminate in small lobes that extend posterior to tip of gladius and fuse with median cleft, anterior lobes absent, anterior one-third or more of fins insert on lateral margin of mantle for 40 to 60% of mantle length (unusual in family, shared only with ***Egea***) rather than on the shell sac of the gladius; funnel large, long, broad; funnel valve absent; **funnel organ dorsal pad with 3 long papillae, 1 lanceolate in middle section, 2 spatulate on narrow lateral arms**; head dominated by **huge eyes, anteriorly oriented, with 3 photophores each (unique in the family)**: 1 large crescent-shaped posterior (medial) organ with 1 smaller, narrow, crescent-shaped anterior (lateral) organ within concavity of larger, 1 small, oval organ on inner anterodorsal margin near lens; brachial end-organ (photophore) present on arms I to IV of maturing and mature females; tentacles short, muscular, **4 series of carpal suckers and pads in zig-zag pattern on distal one-half to one-third of stalk** (unique in family, but see other digressions in ***Megalocranchia*** and ***Bathothauma***); no carpal cluster; club slightly expanded, with suckers on long pedestals; gladius with long, narrow-rachis, vanes moderately wide along posterior one-third to one-half, in-fold ventrally, edges overlap without fusing, extend posteriorly into narrow, non-needle-like, hollow conus.

Size: Medium-sized to moderately large cranchiids. Maximum reported mantle length about 380 to 400 mm.

Geographical Distribution: ***Teuthowenia*** is comprised of 3 species that in aggregate display allopatric (disjunct) distributions circumglobally in the Southern Subtropical Convergence Zone, and the sub-Arctic, north temperate and eastern tropical waters of the Atlantic Ocean.

Habitat and Biology: The vertical distributions of ***Teuthowenia*** species in general show ontogenetic descent from the near-surface, epipelagic to upper mesopelagic waters, to about 200 to 300 m for paralarvae; mesopelagic for juveniles (300 to 600 m) and increasingly deeper into the upper bathypelagic for early subadults to around 1 000 m; late subadults and adults range to 1 500 m and maturation occurs from there to around 2 700 m. A degree of diel vertical movement also is evident in these near-neutrally buoyant species. ***Teuthowenia*** species are prey for large pelagic fishes (swordfish, tuna, lancetfish, blue shark, goblin shark, scalloped hammerhead shark, sooty albatrosses and cetaceans, e.g. sperm whales, pilot whales, northern bottlenose whales, dolphins).

Remarks: Typical of most genera in the family, ***Teuthowenia*** has undergone numerous nomenclatural changes, with the following genera now considered synonymous: ***Owenia*** Prosch, 1847, ***Verrilliteuthis*** Berry, 1916, ***Desmoteuthis*** Verrill, 1881 (in 1880–1881), ***Anomalocranchia*** Robson, 1924, ***Hensenioteuthis*** Thiele, 1934. The chromatophore pattern and number and configuration of tubercles on the funnel-mantle fusion cartilage are useful characters for distinguishing species.

Literature: Voss (1985), Vecchione and Roper (1992 [1991]), Sweeney and Young (2003h).

Teuthowenia megalops (Prosch, 1847)

Fig. 209; Plate VII, 39

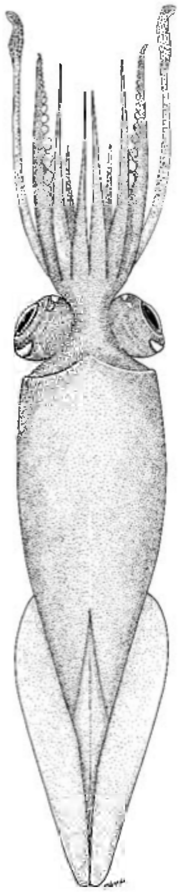
Cranchia (Owenia) megalops Prosch, 1847, *Kongelige Danske Videnskabernes Selskabs Skrifter, series 5*, 1 [1849]: 53–72 [71] (published as separate, 1847). [Type locality: off the Faeroe Islands, eastern North Atlantic Ocean].

Frequent Synonyms: *Leachia hyperborea* Steenstrup, 1856; *Desmoteuthis tenera* Verrill, 1881 (in 1880–1881); *Desmoteuthis thori* Degner, 1925; (See Voss, 1985: 15 for complete synonymy).

FAO Names: En – Atlantic cranch squid; **Fr** – Encornet-outre Atlantique; **Sp** – Cranquiluria Atlantica.

Diagnostic Features: See generic account.

Size: Maximum mantle length to 400 mm.



dorsal view

Fig. 209 ***Teuthowenia megalops***

Geographical Distribution: ***Teuthowenia megalops*** occupies the highly productive waters of the sub-Arctic and northern temperate Atlantic Ocean. In the western North Atlantic it occurs from the northern limit of the subtropical waters off Bermuda (31°N to 33°N) to 55°N, or so, off Labrador in sub-Arctic water. In the eastern Atlantic, ***T. megalops*** occurs from between Greenland and Iceland (65°N to 66°N) to about 44°N to 45°N in the Azores-Britain region of the North Atlantic temperate zone. Possibly down to 32° to 35°N. One record from the Mediterranean Sea (Fig. 210).

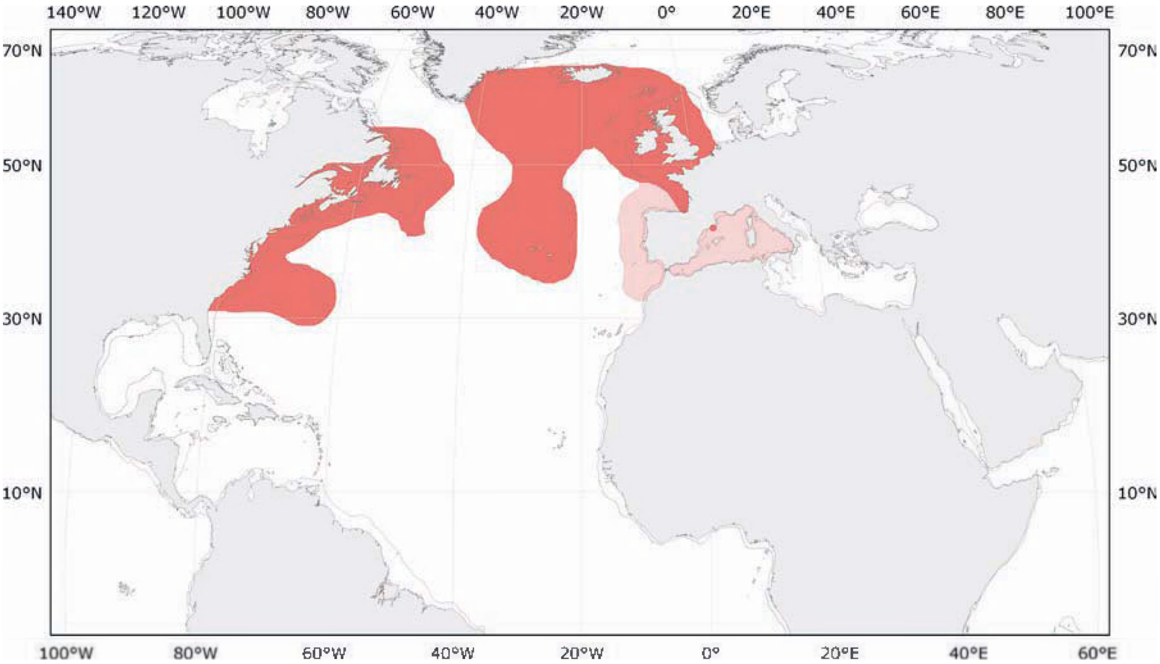


Fig. 210 ***Teuthowenia megalops***

🟥 Known distribution ▨ Probable presence

Habitat and Biology: The vertical distribution ranges from about 40 m to nearly 2 700 m with evidence of both significant ontogenetic descent as well as some diel vertical movement. Juveniles, subadults and adults inhabit waters where bottom depth exceeds 1 000 m. The species is heavily preyed upon by sperm whales, northern bottlenose whales, Cuvier's beaked whales, swordfish, blue shark.

Local Names: ITALY: Totano tutt'occhi.

Literature: Zuev and Nesis (1971), Dilly (1972), Lu and Roper (1979), Nixon (1983), Vecchione and Roper (1992 [1991]), Santos *et al.* (1999), Unger *et al.* (2006), Young and Mangold (2007b).

Teuthowenia maculata (Leach, 1817)

Cranchia maculata Leach, 1817, *Zoological Miscellany*, 3(30): 137–141 [140]. [Type locality: 01°36'S, 08°47'E, eastern equatorial South Atlantic Ocean].

Frequent Synonyms: *Cranchia (Cranchia) maculata* Prosch, 1847; ?*Verrilliteuthis hyperborea* Adam, 1962a; *Taonius megalops* Lu and Clarke, 1975b; *Teuthowenia megalops* Morales and Guerra, 1977.

Diagnostic Features: See generic account.

Size: Maximum mantle length known estimated to 370 mm (calculated from beaks in sperm whale stomachs).

Geographical Distribution: ***Teuthowenia maculata*** has a relatively limited distribution, restricted to the moderately to highly productive waters of the tropical, subtropical eastern North and South Atlantic Ocean. The species is limited to east of 20°W to 23°W and occurs from about 20°N to 22°N southward to around 20°S and eastward to about 11°E.

Habitat and Biology: The vertical distribution of ***T. maculata*** extends from 25 m to about 2 000 m. Truly an oceanic species, as all captures have occurred in waters where bottom depth exceeds 1 000 m. The paralarvae and juveniles undergo ontogenetic descent during growth and some diel vertical movement seems to occur.

Literature: Voss (1985), Young and Mangold (2007b).

Teuthowenia pellucida (Chun, 1910)

Desmoteuthis pellucida Chun, 1910, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition dem Dampfer Valdivia, 1898–1899*, 18(1): 1–401 [357]. [Type locality: 33°20'S, 15°58' W in the Benguela Current, South Atlantic Ocean].

Frequent Synonyms: *Megalocranchia megalops australis* Voss, 1967a; *Anomalocranchia impennis* Robson, 1924; *Megalocranchia richardsoni* Dell, 1959; (see Voss, 1985: 41 for complete synonymy).

Diagnostic Features: See generic account.

Size: Maximum mantle length recorded is 210 mm (unsexed) and 201 mm for mature females and 140 mm for mature males.

Geographical Distribution: ***Teuthowenia pellucida*** occurs in a circumglobal belt centred on a band width of about 6° to 7° associated with the Southern Subtropical Convergence and to a certain extent into the boundary waters that fringe the Convergence zone to the north and south. The total north-south extent of distribution is about 32°S to 48°S in the waters with the hydrologic characteristics of the Convergence.

Habitat and Biology: The vertical distribution extends from the surface to 2 400 m, with ontogenetic descent. Juveniles and subadults appear to undergo diel vertical displacement from 700 to 800 m during the day into the upper 300 m at night. Mature adults seem to occur below about 1 500 m and remain from there down to 2 400 m or more. This species is prey to sperm whales, goblin shark, scalloped hammerhead shark, sooty albatross.

Literature: Voss (1985), Roeleveld (1998), Smale and Cliff (1998), Dunning and Lu (1998), Nesis (1999b).

2.11 Family CYCLOTEUTHIDAE Naef, 1923

by Clyde F.E. Roper and Patrizia Jereb

Cycloteuthidae Naef, 1923, *Fauna e Flora del Golfo di Napoli*, 35, 1(1,2): 149–863 [312].

Type Genus: *Cycloteuthis* Joubin, 1919.

FAO Names: En – Discfin squids; **Fr** – Discoloutènes; **Sp** – Discolurias.

Diagnostic Features: Mantle broadly conical, goblet-shaped. **Fins long, broad, disk-like, greater than 70% of mantle length** in adults (including tail when present). **Funnel component of funnel-mantle locking apparatus subtriangular to irregularly oval, with deep pit to receive prominent, protruding, nose-shaped or tubercular mantle cartilage component**; mantle component does not reach anterior mantle margin. Arm suckers biserial. Tentacular club suckers tetraserial. Club compact, expanded with well-defined manus and dactylus, ill-defined carpus, with about 7 small knobs and suckers. Buccal connectives attach to ventral borders of arms IV. **Photophores present variously on eyes, head, mantle, ink sac**. **Hectocotylus absent**.

Size: Moderate to large-sized squids; maximum mantle length about 600 mm.

Geographical Distribution: Cosmopolitan in tropical and subtropical waters.

Habitat and Biology: Very little is known about the biology of any species in the family. Members of the family occur in lower epipelagic to mesopelagic zones, occasionally to the bottom in bathyal waters. While records are relatively few, species of cycloteuthids appear to undergo diel vertical displacement; specimens have been taken in the upper 200 m at night and at 500 to 1 000 m during daytime. Members of the family provide significant prey to numerous predatory species, e.g. sperm whales, swordfish, blue shark, short-finned pilot whale.

Interest to Fisheries: The small size of most species, the soft consistency of the flesh and the relative rarity of specimens in deep-set trawls preclude an interesting potential for fisheries. Species, however, are heavily preyed upon by cetaceans, fishes, sea birds and other cephalopods.

Local Names: USA: Roundfin squids, Cycloteuthids.

Remarks: The family Cycloteuthidae contains 2 rather dissimilar genera, ***Cycloteuthis*** and ***Discoteuthis***. These 2 genera are united principally by the single character of the subtriangular funnel-locking component. Otherwise there is little morphological evidence for a close relationship. Molecular analysis, however, confirms the close relationship of these genera in the Cycloteuthidae (Carlini, 1998). Although 4 species currently are recognized, recent findings suggest that other species may be included in the 2 genera in the future. Familial treatments of systematics, distribution, paralarvae and juveniles are presented in Nesis (1982, 1987, 1999b) and Jefferts and Roper (1992) and Young (1999a). The genera are distinguished in the key below.

Literature: Young and Roper (1969a), Roper and Young (1975), Jefferts and Roper (1992), Dunning and Lu (1998), Young (1999a), Vecchione (2002), Sweeney and Young (2003i).

Key to the genera of Cycloteuthidae

1a. Mantle in adults drawn out posteriorly into tail; fin length in adults to 75% of mantle length, including tail; suckers in 4 series on manus of club of equal/subequal size; a single photophore present on ink sac; a series of 15 to 30 very small, irregularly-shaped photophores on iris of eye around pupil; no photophores embedded on surface of body; gladius thin, narrow, with long, terminal cone . . . . . . ***Cycloteuthis***

1b. Mantle in adults not drawn out into a tail; fin length equals or slightly exceeds mantle length in adults; suckers in central 2 series on clubs greatly enlarged, suckers in the 2 marginal rows greatly reduced in size; no photophore on ink sac; 1 to several photophores embedded on surface of body; vane of gladius wide, heavily thickened, posteriorly rounded, terminal cone absent or minimal . . . . ***Discoteuthis***

Cycloteuthis Joubin, 1919

Cycloteuthis Joubin, 1919, *Bulletin de l'Institut Océanographique, Monaco*, 351: 7 pp. [1].

Type Species: *Cycloteuthis sirventi* Joubin, 1919.

Frequent Synonyms: None.

Diagnostic Features: See generic key.

Remarks: Two species are recognized in the genus, but they are poorly known because they are relatively rare in collections. They are cosmopolitan in mesopelagic waters in tropical, subtropical (***C. sirventi***) and tropical, subtropical to subantarctic (***C. akimushkini***) waters.

Literature: See family list.

Cycloteuthis sirventi Joubin, 1919

Cycloteuthis sirventi Joubin, 1919, *Bulletin de l'Institut Océanographique, Monaco*, 351: 7 pp. [1]. [Type locality: 30°45'40"N, 25°47'W, off Madeira, eastern North Atlantic Ocean].

Frequent Synonyms: None.

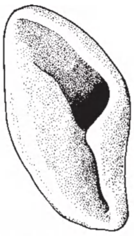
FAO Names: En – Sirvent's disc-fin squid; **Fr** – Discoloutène de Sirvent; **Sp** – Discoluria de Sirvent.

Size: Mantle length to about 500 mm.

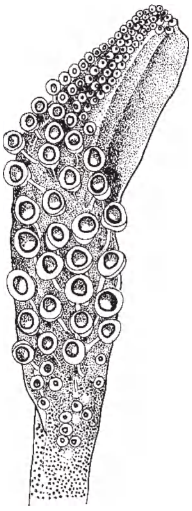
Geographical Distribution: Tropical, subtropical, temperate waters of the Atlantic, Mediterranean, Indo-West Pacific. Lower epipelagic, mesopelagic, rarely bathybenthic (Fig. 212).

Literature: Young and Roper (1969a), Nesis (1982, 1987, 1999b), Guerra (1992). See also family literature list.

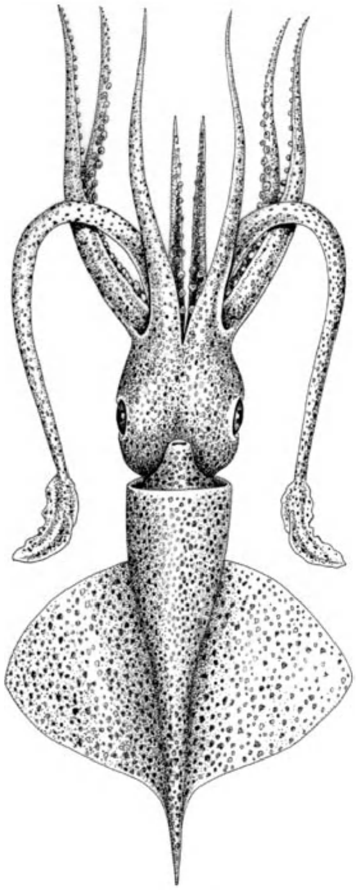
Fig. 211



funnel-locking apparatus



tentacular club



ventral view

Fig. 211 ***Cycloteuthis sirventi***

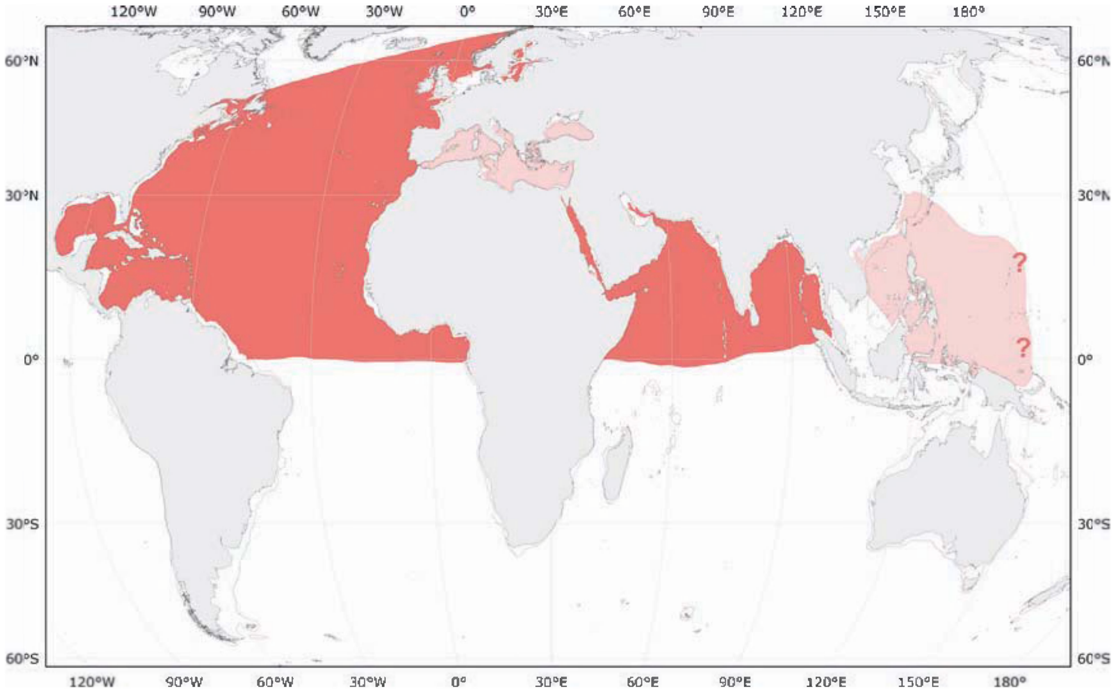


Fig. 212 ***Cycloteuthis sirventi***

🟥 Known distribution ▨ Probable presence

Cycloteuthis akimushkini Filippova, 1968

Cycloteuthis akimushkini Filippova, 1968a, *Malacological Reviews*, 1: 119–124 [119]. [Type locality: 9°57'S, 91°31'E, eastern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 600 mm.

Geographical Distribution: Tropical, subtropical to subantarctic Indian and western Pacific Oceans, southern subtropical Atlantic. Lower epipelagic to mesopelagic.

Literature: Nesis (1982, 1987, 1999b), Jefferts and Roper (1992). See also family literature list.

Discoteuthis Young and Roper, 1969

Discoteuthis Young and Roper, 1969a, *Smithsonian Contributions to Zoology*, 5: 24 pp. [5].

Type Species: *Discoteuthis discus* Young and Roper, 1969.

Frequent Synonyms: None.

Diagnostic Features: See generic key.

Remarks: ***Discoteuthis*** currently is represented by 2 species ***D. discus*** and ***D. laciniosa***, each of which is rare in collections. However, an unusual specimen of ***Discoteuthis*** that has a distinctive array of photophores was recently described (Salcedo-Vargas and Guerrero Kommritz, 2000) that may represent a third species in the genus (Salcedo-Vargas and Young, 2001a). Further, another badly damaged, immature male squid recently was taken in the Atlantic Ocean in which the large suckers of the club remains had an unusual dentition. This, also, may turn out to represent another species in the genus (Young and Vecchione, 2005c).

Literature: Young (1999c), Young and Vecchione (2005c).

Discoteuthis discus Young and Roper, 1969

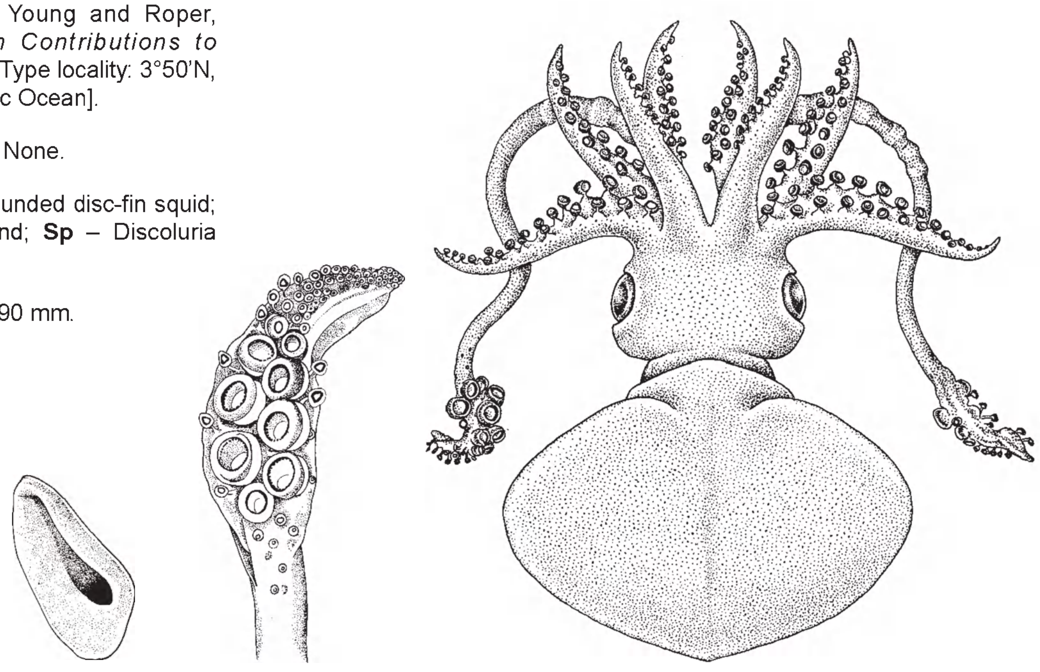
Fig. 213

Discoteuthis discus Young and Roper, 1969a, *Smithsonian Contributions to Zoology*, 5: 24 pp. [5]. [Type locality: 3°50'N, 2°37'W, eastern Atlantic Ocean].

Frequent Synonyms: None.

FAO Names: En – Rounded disc-fin squid; **Fr** – Discoloutène rond; **Sp** – Discoluria rotunda.

Size: Mantle length to 90 mm.



funnel-locking apparatus **tentacular club** **dorsal view**

Fig. 213 ***Discoteuthis discus***

Geographical Distribution: Tropical and subtropical Atlantic, Pacific and Indian Oceans. Lower epipelagic to mesopelagic (Fig. 214).

Literature: Young and Roper (1969a), Roper and Young (1975), Vecchione (2002). See also family literature list.

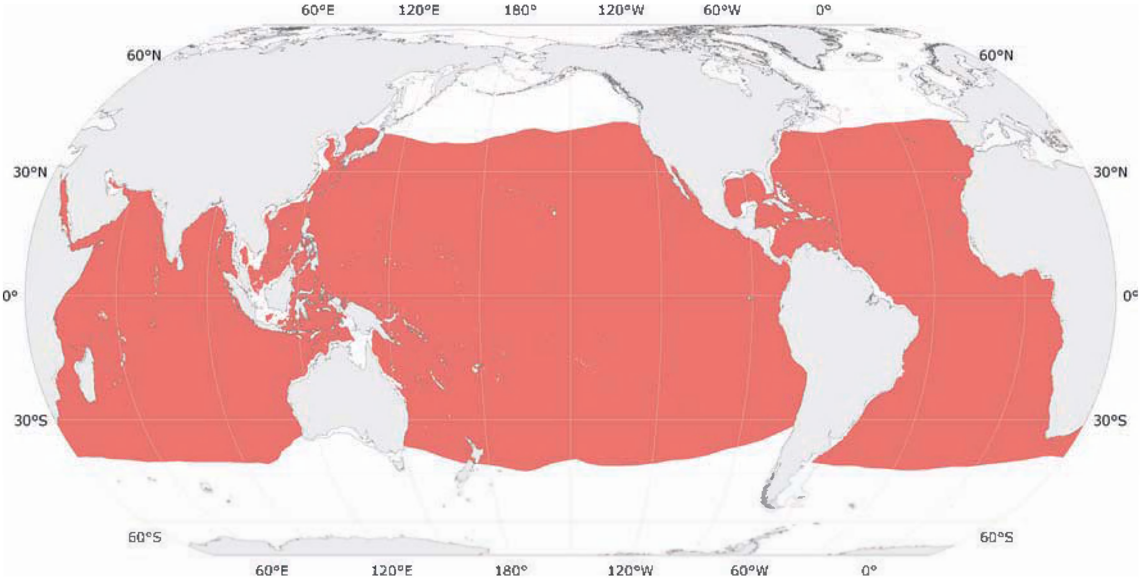


Fig. 214 ***Discoteuthis discus***

🟥 Known distribution

Discoteuthis laciniosa Young and Roper, 1969

Discoteuthis laciniosa Young and Roper, 1969a, *Smithsonian Contributions to Zoology*, 5: 24 pp. [9]. [Type locality: 33°04'N, 64°37'W, western Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 70 mm.

Geographical Distribution: Tropical, subtropical Atlantic, Pacific and Indian Oceans.

Literature: Young and Roper (1969a), Jefferts and Roper (1992), Vecchione, (2002). See also family literature list.

2.12 Family ENOPLOTEUTHIDAE Pfeffer, 1900

by Clyde F.E. Roper and Patrizia Jereb

Enoploteuthidae Pfeffer, 1900, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2): 145–198 [163].

Type Genus: *Enoploteuthis* d'Orbigny *in* Rüppel, 1844: [129].

FAO Names: En – Enope squids; **Fr** – Enoplolоutènes; **Sp** – Enoplolurias.

Diagnostic Features: Funnel-mantle locking apparatus straight; biserial armature (except occasionally at the arm tips) with at least **some hooks on all the arms**. **Buccal crown with 8 supports**; **buccal connectives attached to dorsal margins of arms IV**. No secondary buccal connectives attached to ventral margins of arms I and II. (***Enoploteuthis dubia*** Adam, 1960a, is unique in having connectives that attach dorsally to all arms). **Tentacular clubs with 1 or 2 series of hooks on manus** (arrangement varies with genus); armature on manus in 2 or 3 series. **Photophores present on mantle, funnel, head, eyeballs, and arms**. Photophores absent from tentacles, viscera, and most of fins. **Nidamental glands absent**; oviducal glands enlarged; oviducts unpaired. **Fins usually terminal**; **always lack posterior lobes**. Tail fleshy, extends well beyond conus of gladius. Photosensitive vesicles present. **Nuchal folds present**. Tentacles not modified near base; stalk "ligament" and vein leave tentacle at base in membrane. **Ink sac not embedded in digestive gland**. Gladius with small, blunt conus and elongate cone field; rostrum absent.

Size: Small-sized squid up to 130 mm mantle length.

Geographical Distribution: Inhabitants of the tropical, subtropical and temperate oceans of the world.

Habitat and Biology: Enoploteuthids are mesopelagic squids that undergo extensive diel vertical migrations. Paralarvae and juveniles are epipelagic and inhabit the upper 200 m.

Interest to Fisheries: Generally enoploteuthids are not fished on a commercial basis. There are exceptions, however, most notably the intense, seasonal fishery for ***Watasenia scintillans*** in Japan, especially in Toyama Bay, where annual commercial landings approach 4 000 tonnes. ***Enoploteuthis chunii*** is sympatric with ***W. scintillans*** and also enters the fishery as bycatch with ***Watasenia***. A third species is known to be used in Singapore, but no data currently are available.

Remarks: The Enoploteuthidae formerly was comprised of three long-established subfamilies: Enoploteuthinae (***Enoploteuthis***, ***Abralia***, ***Abraliopsis***, ***Watasenia***); Pyroteuthinae (***Pyroteuthis***, ***Pterygioteuthis***); and Ancistrocheirinae (***Ancistrocheirus***, ***Thelidioteuthis***). Now these are recognized as separate, closely-related families of the Enoploteuthid group (Clarke, 1988b; Young and Harman, 1998; Young *et al*., 1998a). ***Thelidioteuthis*** now is considered as an immature ***Ancistrocheirus***, with which it is synonymized. The young of ***Abralia*** and ***Enoploteuthis*** are not easily distinguished: the presence of 2 photophores on the developing eyes of ***Enoploteuthis*** versus 3 enlarged photophores on ***Abralia*** seems to apply for most species but not necessarily all. ***Abraliopsis*** species generally are distinctive from other related genera from a very small size by the development of the bulbous photophores on the tips of the ventral arms (IV), by relatively longer arms (greater than or equal to the mantle length) and tentacles. Other characters useful for species discrimination include chromatophore patterns, size of largest club suckers versus arm suckers, relative sizes among club suckers, number of club suckers, photophore patterns and photophore sizes.

Key to the families of the Enoploteuthid Group[1/]

1a. Photophores on mantle, surface of head and arms (>4 mm ML); not on viscera . . . . → ***2***
1b. Photophores on viscera, not on mantle or surface of head or arms . . . . **Pyroteuthidae**

2a. Photophores on mantle, head, eyes, and arms, not on tentacles . . . . **Enoploteuthidae**
2b. Photophores on mantle, head, arms, and tentacles, but not on eyes (>5 to 7 mm ML) . . . . . **Ancistrocheiridae**

Key to the Genera of the family Enoploteuthidae

1a. One or more enlarged photophores on distal tip of arms IV (>3 to 5 mm ML). . . . . → ***2***
1b. No enlarged photophores on distal tip of arms IV. . . . . → ***4***

2a. Squid collected from seas around Japan. . . . . → ***3***
2b. Squid collected also from other geographic regions . . . . ***Abraliopsis***

3a. Tentacle hooks in 2 rows (appear at about 5 to 10 mm ML). . . . . ***Abraliopsis***
3b. Tentacle hooks in 1 row (appear at about 5 mm ML). . . . . ***Watasenia***

4a. Two enlarged photophores develop on eye (>2.5 mm ML). . . . . ***Enoploteuthis***
4b. Three enlarged photophores develop on eye (>2.0 to 2.5 mm ML) . . . . ***Abralia***

Literature: Okiyama and Kasahara (1975), Roper and Young (1975), Kluchnik and Starobogatov (1978), Tsuchiya (1993), Young *et al*. (1998b), Bower *et al*. (1999c), Sweeney and Young (2003j), Tsuchiya and Young (2008).

[1/] Young *et al*. (1992). A more detailed key for genera is found in Dunning, 1998e.

Enoploteuthis d'Orbigny *in* Rüppell, 1844

Enoploteuthis d'Orbigny in Rüppell, 1844, *Giornale del Gabinetto Letterario di Messina*, 5(27 –28): 129–135 [129].

Type Species: *Enoploteuthis leptura* (Leach, 1817).

Frequent Synonyms: None.

Diagnostic Features: Manus of club with 2 series of hooks; marginal suckers absent. **No enlarged photophores at tips of arms IV**. Fins subterminal. Buccal crown with typical chromatophores on aboral surface, possibly with light epithelial pigmentation on oral surface. **Nine or 10 photophores on eyeball**. **Right arm IV hectocotylized**. Suckers present distally on arms IV. Spermatophore receptacles at posterior junction of retractor muscles of funnel and head. Complex photophores of integument, in life, without red colour filters. Radula with heterodont rhachidian tooth. **Large arm hooks with open apertures**. **Mantle with tail-like projection beyond posterior end of fin insertion**. Anterior and posterior ocular photophores small, subequal.

Remarks: ***Enoploteuthis*** is a speciose genus with most species having been described in recent decades as a result of exploratory midwater trawling in the mesopelagic realm. While all ***Enoploteuthis*** species are important in the economy of the sea as abundant food sources for fishes and odontocetes, they have little commercial value at the present time, with the exception of ***Enoploteuthis chunii*** which is taken as bycatch in the Japanese fishery for ***Watasenia scintillans***.

Literature: Roper (1964, 1966), Nesis (1982, 1987), Nesis (1993b), Young *et al*. (1998b), Jivaluk (2001), Tsuchiya (2009).

Enoploteuthis leptura leptura (Leach, 1817) **(Type Species) Fig. 215**

Loligo lepturo Leach, 1817, *Zoological Miscellany*, 3(30): 137–141 [141]. [Type locality: Not designated; 01°08'N, 07°26'E, Gulf of Guinea, eastern Atlantic Ocean, fide Lipinski *et al*. (2000: 107)].

Frequent Synonyms: None.

FAO Names: En – Hooked enope squid; **Fr** – Enoploloutène crochu; **Sp** – Enoploluria uncinada.

Diagnostic Features: Seven distinct light organ rows on ventral side of the mantle. Two rows of hooks extend along arm.

Size: Maximum mantle length to 92 mm.

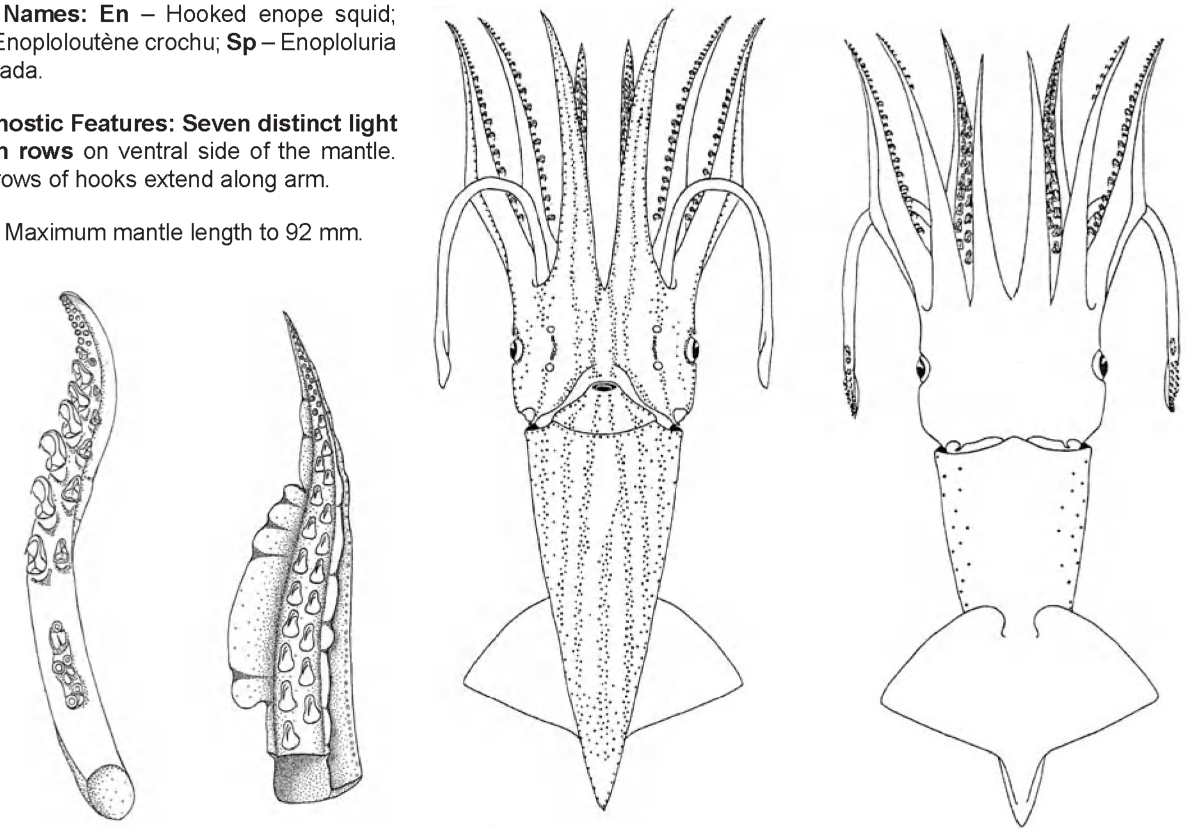


Fig. 215 ***Enoploteuthis leptura leptura***

Geographical Distribution: Gulf of Guinea, eastern and western central Atlantic Ocean, Indo-West Pacific Ocean (Fig. 216).

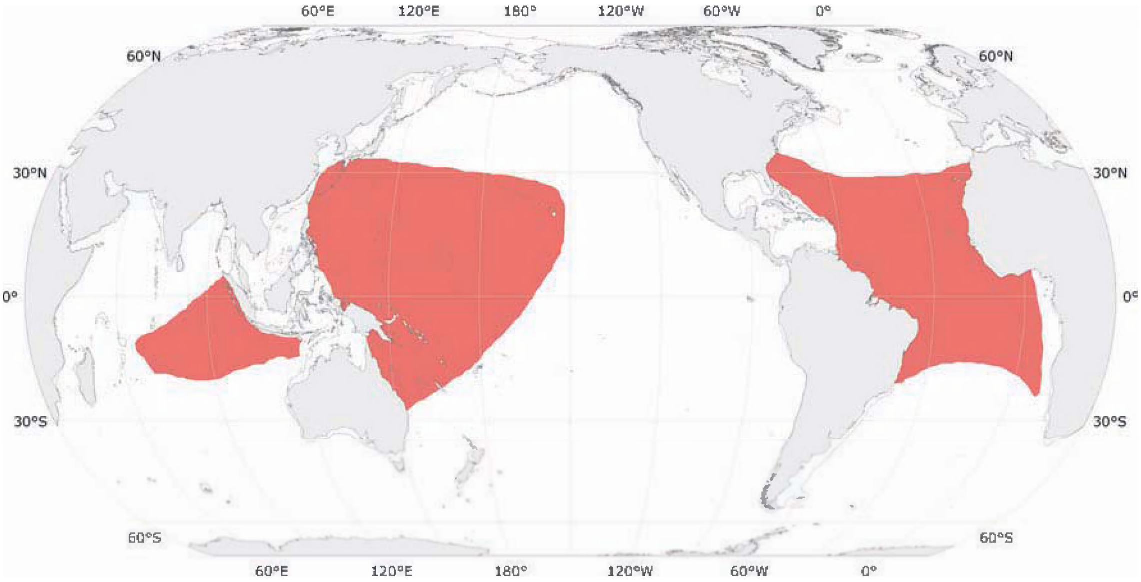


Fig. 216 ***Enoploteuthis leptura leptura***

🟥 Known distribution

Habitat and Biology: Mesopelagic to epipelagic in tropical, subtropical (rarely temperate) waters as diel vertical migrators.

Remarks: Records from Pacific and Indian Oceans probably refer to subspecies ***Enoploteuthis magnoceani*** Nesis (1982, 1987).

Literature: Roper (1966), Arkhipkin (1994).

Enoploteuthis leptura magnoceani Nesis, 1982

Enoploteuthis leptura magnoceani Nesis, 1982, *Light and Food Industry Publishing*, 358 pp. [162]. [Type locality: Pacific Ocean, exact locality unknown].

Frequent Synonyms: None.

Size: Mantle length to 80 mm.

Geographical Distribution: Tropical western and central Pacific Ocean and Indian Ocean; South China Sea; equatorial waters.

Habitat and Biology: Mesopelagic to epipelagic diel vertical migrator.

Literature: Tsuchiya (1993).

Enoploteuthis anapsis Roper, 1964

Enoploteuthis anapsis Roper, 1964, *Bulletin of Marine Science of the Gulf and Caribbean*, 14(1): 140–148 [140]. [Type locality: 16°55’N, 81°10’W, Caribbean Sea, western Atlantic].

Frequent Synonyms: None.

Size: Mantle length to 80 mm.

Geographical Distribution: Tropical and subtropical Atlantic Ocean; Gulf of Mexico and Caribbean Sea.

Habitat and Biology: Mesopelagic to epipelagic as diel vertical migrator.

Literature: Roper (1964, 1966), Laptikhovsky (1999b).

Enoploteuthis chunii Ishikawa, 1914

Enoploteuthis chunii Ishikawa, 1914, *Journal of the College of Agriculture, Imperial University of Tokyo*, 4(7): 401–413 [401]. [Type locality: Toyama Bay, Etchu Province, Japan, western Pacific Ocean].

Frequent Synonyms: *Enoploteuthis theragrae* Taki, 1964.

Size: Mantle length to 100 mm.

Geographical Distribution: Western Pacific Ocean; Sea of Japan, off central and southern Japan, approximately 20°N to 40°N, 120°E to 150°E.

Habitat and Biology: A nerito-oceanic, mesopelagic boundary species that undergoes diel vertical migrations of the migrant pattern: day and night patterns are clearly separated with peak abundance deeper than 300 m during the day and shallower than 300 m at night. This species is restricted to warm Core Ring waters in the northwestern North Pacific Ocean. Captured as bycatch in the ***Watasenia scintillans*** fishery. Prey of odontocete whales and dolphins, walleye pollack.

Interest to fisheries: This species co-occurs with ***Watasenia scintillans*** and it constitutes a bycatch that is not sorted out from the target species.

Literature: Okiyama and Kasahara (1975), Okutani (1987, 1995), Hayashi (1991).

Enoploteuthis galaxias Berry, 1918

Enoploteuthis galaxias Berry, 1918, *Biological Results of the Fishing Experiments Carried on by the F.I.S. Endeavour, 1909–1914*, 4(5): 201–298 [211]. [Type locality: Victoria, Australia, Tasman Sea, western South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 110 mm.

Geographical Distribution: Southwestern South Pacific Ocean: southern, eastern Australia and northern New Zealand.

Habitat and Biology: A southern subtropical, nerito-oceanic mesopelagic and benthic-bathyal species.

Literature: Riddell (1985).

Enoploteuthis higginsi Burgess, 1982

Enoploteuthis higginsi Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [718]. [Type locality: off Waianae, Oahu Island, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 60 mm.

Geographical Distribution: Hawaiian waters, equatorial region of central Pacific Ocean; Indian Ocean.

Habitat and Biology: Mesopelagic to epipelagic as a diel vertical migrator.

Literature: Tsuchiya (1993).

Enoploteuthis jonesi Burgess, 1982

Enoploteuthis jonesi Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [713]. [Type locality: off Milolii, Hawaii Island, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 85 mm.

Geographical Distribution: Hawaiian waters and equatorial region of western central Pacific Ocean.

Habitat and Biology: Mesopelagic to epipelagic as a diel vertical migrator.

Remarks: Nesis (1982, 1987) considers ***Enoploteuthis jonesi*** to be a subspecies of ***E. anapsis*** Roper, 1964.

Literature: Roper (1966), Young *et al*. (1998b).

Enoploteuthis obliqua (Burgess, 1982)

Enoploteuthis migrato Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [704]. [Type locality: 11°47’N, 144°47’W, central Pacific Ocean].

Frequent Synonyms: *Enoploteuthis migrato* Burgess, 1982.

Size: Mantle length to 60 mm.

Geographical Distribution: Eastern equatorial central Pacific Ocean from east of Line Islands eastward to Central American region.

Habitat and Biology: A mesopelagic to epipelagic species as a diel vertical migratory.

Literature: Young *et al*. (1998b).

Enoploteuthis octolineata Burgess, 1982

Enoploteuthis octolineata Burgess, 1982, *Fishery Bulletin, US*, 80(4): 703–734 [708]. [Type locality: 2°56’N, 150°03’W, central Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 80 mm.

Geographical Distribution: Equatorial region of the central Pacific Ocean.

Habitat and Biology: Presumed diel vertical migratory in mesopelagic to epipelagic waters.

Literature: Young *et al.* (1998b).

Enoploteuthis reticulata (Rancurel, 1970)

Enoploteuthis migratory Rancurel, 1970, *Cahiers O.R.S.T.O.M., Océanographique*, 8(4): 3–87 [45]. [Type locality: 0°02'S, 135°48'W, central Pacific Ocean].

Frequent Synonyms: *Enoploteuthis migratory* Rancurel, 1970.

Size: Mantle length to 130 mm.

Geographical Distribution: Very broadly distributed in Indo-Pacific Ocean region, approximately 35°N to 30°S in western Pacific Ocean and 75°E to 90°E in Indo-Pacific Ocean; pantropical to subtropical.

Habitat and Biology: Mesopelagic to lower epipelagic, diel vertical migrator. Prey of lancet fishes and other mesopelagic fishes.

Literature: Rancurel (1970), Tsuchiya (1993).

Enoploteuthis semilineata Alexeyev, 1994

Enoploteuthis semilineata Alexeyev, 1994b, *Ruthenica*, 4(2): 167–171 [167]. [Type locality: 40°10.7'S, 127°48.4'W – 40°03.5'S, 127°36.7'W, eastern South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 90 mm.

Geographical Distribution: Eastern South Pacific Ocean; holotype at 40°S, 127°W.

Habitat and Biology: Presumed diel vertical migrator from mesopelagic to lower epipelagic zones.

Literature: Alexeyev (1994b).

Abralia Gray, 1849

Abralia Gray, 1849, Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia, 164 pp. [50].

Type Species: *Abralia armata* (Quoy and Gaimard, 1832).

Frequent Synonyms: *Enoploion* Pfeffer, 1912; ?*Prodromoteuthis* Pfeffer, 1912; *Stenabralia* Grimpe, 1931; *Arabralia* Nesis, 1982, 1987.

Diagnostic Features: Manus of tentacular club with 1 series of hooks, 2 series of suckers. **Enlarged photophores on tips of arms IV generally absent**; when present, photophores not covered by black chromatophores. Fins terminal. **Buccal crown with typical chromatophores on aboral surfaces**, no other pigmentation present, only occasionally with silvery photophores smaller than the diameter of the arms. **Five to 12 photophores of various sizes on eyeball**. **Right or left arm IV hectocotylized**. Suckers present distally on arms IV. Spermatophore receptacle(s) located under collar, in median pocket at posterior end of nuchal cartilage, or between stellate ganglia. Complex photophores of integument, in life, without red colour filters. Radula with homodont teeth. **Large arm hooks with closed apertures**.

Geographical Distribution: Worldwide in tropical and subtropical waters.

Habitat and Biology: The species principally are epipelagic to mesopelagic. They are members of the midwater fauna of diel vertical migrators that ascend from daytime depths of around 600 m to nighttime depths of usually less than 200 m. Some species may occur at shallow depths when they inhabit waters where the mesopelagic zone intersects slopes of land masses, e.g. of oceanic islands, called the mesopelagic-boundary zone. Species are heavily preyed upon by tunas, billfishes, etc. and by the deeper-hunting odontocete cetaceans.

Remarks: ***Abralia*** is the most speciose genus in the Enoploteuthidae.

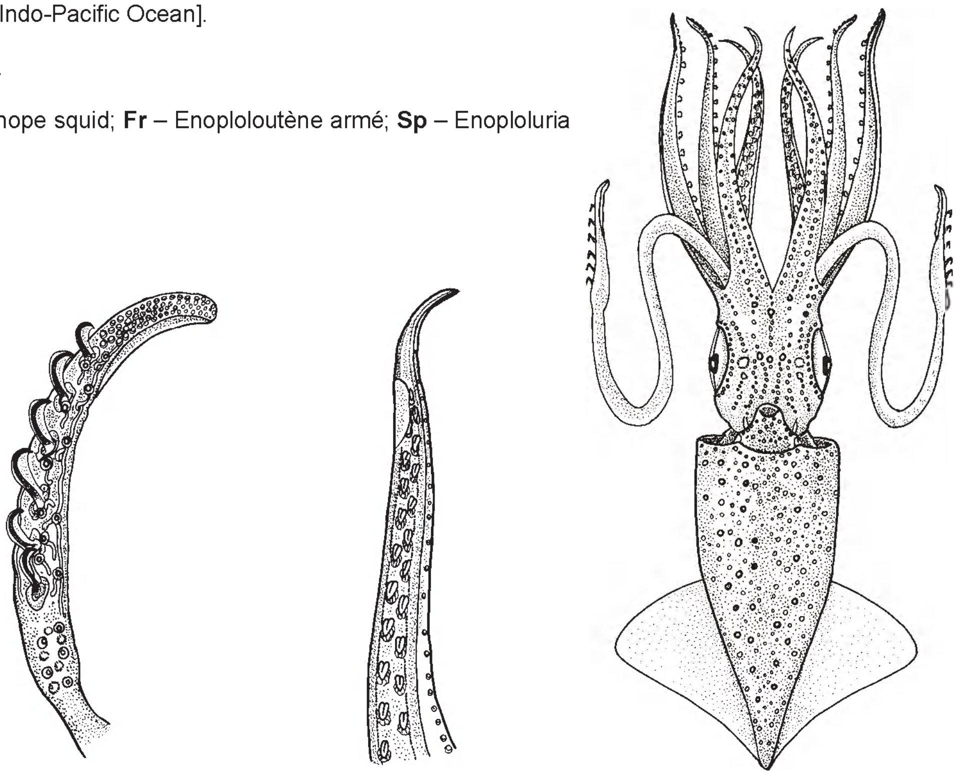
Literature: Roper and Young (1975), Tsuchiya and Okutani (1988), Young *et al.* (1998b), Burgess (1992 [1991], 1998), Young and Tsuchiya (2009a).

Abralia armata (Quoy and Gaimard, 1832) Fig. 217

Onychoteuthis armatus Quoy and Gaimard, 1832, *Voyage de dècouvertes de l'Astrolabe 1826–1829, Zoologie*, 2(1): 1–320 [84]. [Type locality: near Sulawesi (Celebes) Island, Indonesia, Indo-Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Armed enope squid; **Fr** – Enoploloutène armé; **Sp** – Enoploluria armada.



tentacular club hectocotylus ventral view

Fig. 217 ***Abralia armata***

Size: Mantle length to around 20 mm.

Geographical Distribution: Indo-Pacific Ocean: Indonesia, Philippines, Moluccas Islands, South China Sea (Fig. 218).

Literature: Young *et al.* (1998b).

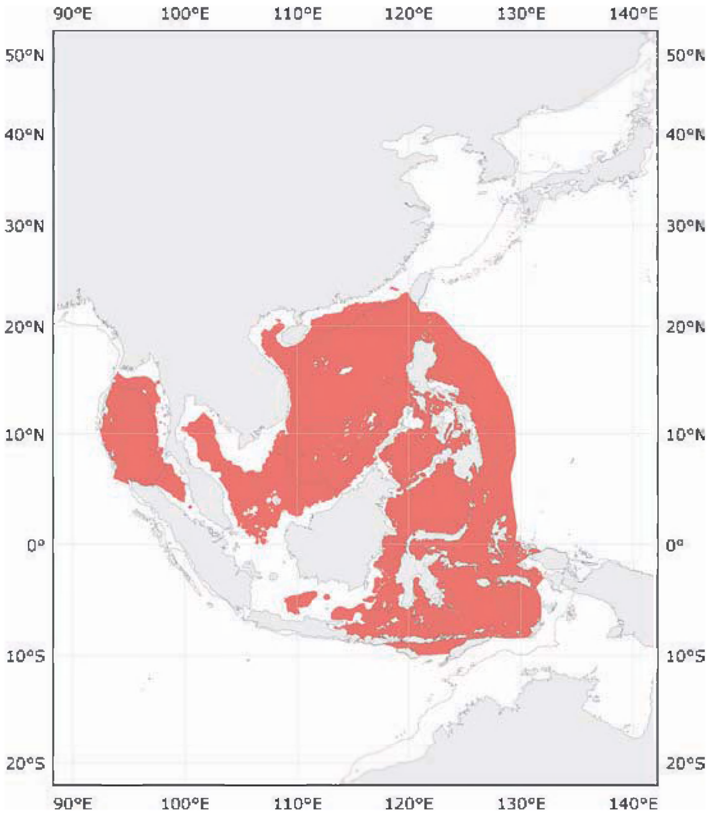


Fig. 218 ***Abralia armata***

🟥 Known distribution

Abralia andamanica Goodrich, 1896

Abralia andamanica Goodrich, 1896, *Transactions of the Linnean Society of London, Zoology*, 7(1): 1–24 [9]. [Type locality: Andaman Sea, eastern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 60 mm.

Geographical Distribution: Indian and western Pacific Oceans: Arabian Sea and Seychelles, Philippines, Indonesia, off Japan to Tasman Sea, East China Sea, South China Sea, Yellow Sea, off Australian North West Shelf.

Habitat and Biology: A mesopelagic-boundary species that ascends from the mesopelagic zone to 100 to 300 m at night. Off Japan it exhibits a multimodal size distribution and spawns in late summer to early winter.

Remarks: This taxon as currently recognized may in fact represent several closely-related species.

Literature: Okutani (1974a), Yamamoto and Okutani (1975), Okutani *et al*. (1987), Okutani (1995).

Abralia astrolineata Berry, 1914

Abralia astrolineata Berry, 1914, *Transactions and Proceedings of the New Zealand Institute*, 46(24): 134–149 [145]. [Type locality: Kermadec Islands, off eastern Australia, western South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Southwestern Pacific Ocean; eastern Australia (off Queensland); off Kermadec Islands.

Habitat and Biology: A presumed mesopelagic-boundary species, with three discrete spawning periods during the year.

Literature: Nesis (1982, 1987).

Abralia astrostricta Berry, 1909

Abralia astrostricta Berry, 1909, *Proceedings of the United States National Museum*, 37(1713): 407–419 [412]. [Type locality: off Oahu Island, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Central and western Pacific Ocean; Hawaiian Islands to Philippine Sea, eastern Australia, off Japan, Kuroshio Current, South China Sea.

Habitat and Biology: This is a widely distributed tropical, subtropical species of the mesopelagic-boundary fauna.

Literature: Tsuchiya (1993), Young (1995).

Abralia dubia (Adam, 1960)

Enoploteuthis dubia Adam, 1960a, *Bulletin of the Sea Fisheries Research Station, Haifa*, 26: 1–26 [12]. [Type locality: Eylath, Gulf of Aqaba, Red Sea, northwestern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Red Sea.

Literature: Young *et al*. (1998b).

Abralia fasciolata Tsuchiya, 1991

Abralia fasciolata Tsuchiya, 1991, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*; 17(2):69–79 [70]. [Type locality: 11°14'06"N, 47°38'12"E, Gulf of Aden, western Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Indian Ocean: Gulf of Aden.

Habitat and Biology: Midwater, mesopelagic to epipelagic at night.

Literature: Young *et al*. (1998b).

Abralia grimpei Voss, 1959

Abralia grimpei Voss, 1959, *Bulletin of Marine Science of the Gulf and Caribbean*, 8(4): 369–389 [375]. [Type locality: 26°25'N, 79°45'W, western Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 27 mm.

Geographical Distribution: Western North Atlantic Ocean, Gulf Stream, Florida; probably Caribbean Sea; tropical, subtropical.

Habitat and Biology: Mesopelagic to epipelagic.

Literature: Young *et al*. (1998b).

Abralia heminuchalis Burgess, 1992

Abralia heminuchalis Burgess, 1992, [1991], *Bulletin of Marine Science*, 49(1–2): 113–136 [120]. [Type locality: 0°44'S, 149°46'W, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Central equatorial Pacific Ocean; from 16°N to 15°S and from 144°W to 168°W.

Literature: Hidaka and Kubodera (2000).

Abralia marisarabica Okutani, 1983

Abralia marisarabica Okutani, 1983b, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 9(4): 161–168 [162]. [Type locality: 24°48'N, 63°20'E, Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 25 mm.

Geographical Distribution: Indian Ocean; Arabian Sea, Seychelles Islands.

Habitat and Biology: Presumed mesopelagic to epipelagic as diel vertical migrator at night.

Literature: Piatkowski and Welsch (1992 [1991]), Chesalin and Zuev (2002b).

Abralia multihamata Sasaki, 1929

Abralia multihamata Sasaki, 1929, *Journal of the College of Agriculture, Hokkaido Imperial University, Supplement*, 20: 357pp. [245]. [Type locality: Akocho, Formosa, Taiwan, western North Pacific Ocean].

Frequent Synonyms: *Abralia (Stenabralia) lucens* Voss, 1963a.

Size: Mantle length to 32 mm.

Geographical Distribution: Far western Pacific Ocean; Taiwan, China; Philippines; northwest Pacific Ocean.

Habitat and Biology: A mesopelagic-boundary species.

Literature: Tsuchiya (1993), Young *et al*. (1998b).

Abralia omiae Hidaka and Kubodera, 2000

Abralia omiae Hidaka and Kubodera, 2000, *Bulletin of Marine Science*, 66(2): 417–443 [419]. [Type locality: 05°00’N, 155°00’E, western tropical Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to about 30 mm.

Geographical Distribution: Western tropical Pacific Ocean; type locality: 05°00’N, 155°00’E.

Literature: Hidaka and Kubodera (2000).

Abralia redfieldi Voss, 1955

Abralia redfieldi Voss, 1955, *Bulletin of Marine Science of the Gulf and Caribbean*, 5(2): 81–115 [99]. [Type locality: off Gun Cay, Bahamas Islands, western North Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 30 mm.

Geographical Distribution: Western Atlantic Ocean, tropical eastern Atlantic Ocean; Nova Scotia (43°N) to Argentina (45°S); most abundant in Bahamas, Bermuda, Greater and Lesser Antilles; western tropical Africa.

Habitat and Biology: This small species is mesopelagic-epipelagic and bathylpelagic, nerito-oceanic in its vertical distribution.

Literature: Cairns (1976), Golub (2001).

Abralia renschi Grimpe, 1931

Abralia renschi Grimpe, 1931, *Zoologischer Anzeiger*, 95(5/8): 149–174 [149]. [Type locality: Sabang Harbour, Sumatra, Indonesia].

Frequent Synonyms: None.

Size: Mantle length to 45 mm.

Geographical Distribution: Indonesian region; off Sumatra, Java, Maldive Islands.

Habitat and Biology: Mesopelagic-epipelagic.

Literature: Young *et al*. (1998b).

Abralia robsoni Grimpe, 1931

Abralia robsoni Grimpe, 1931, *Zoologischer Anzeiger*, 95(5/8): 149–174 [156]. [Type locality: South of Bonomisaki, Japan, western North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 51 mm.

Geographical Distribution: Western Pacific Ocean; off Japan; open ocean.

Habitat and Biology: A mesopelagic to epipelagic diel vertical migrator.

Literature: Tsuchiya and Okutani (1988).

Abralia siedleckyi Lipinski, 1983

Abralia siedleckyi, Lipinski, 1983, Veliger, 25(3): 255–265 [255]. [Type locality: 39°05’08”S, 13°43’E, South Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 33 mm.

Geographical Distribution: Southeastern Atlantic Ocean; off South Africa.

Habitat and Biology: Presumably a mesopelagic-epipelagic species.

Literature: Lipinski (1983), Hidaka and Kubodera (2000).

Abralia similis Okutani and Tsuchiya, 1987

Abralia similis Okutani and Tsuchiya, 1987, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 13(4): 141–150 [141]. [Type locality: 30°03.2’N, 134°03.5’E, western North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 32 mm.

Geographical Distribution: Northwestern Pacific Ocean; Shikoku Basin, Japan, Tonga Islands, (possibly equatorial western Indian Ocean and eastern Pacific Ocean).

Habitat and Biology: Mesopelagic-epipelagic in subtropical waters, e.g. in Kuroshio Current; diel vertical migrations.

Literature: Tsuchiya and Okutani (1988), Hidaka and Kubodera (2000).

Abralia spaercki Grimpe, 1931

Abralia spaercki Grimpe, 1931, *Zoologischer Anzeiger*, 95(5/8): 149–174 [150]. [Type locality: near Amboina, Banda Sea, Indonesia].

Frequent Synonyms: None.

Size: Mantle length to 50 mm.

Geographical Distribution: Indonesia, Philippines, Banda Sea.

Habitat and Biology: Mesopelagic-epipelagic.

Literature: Voss (1963a), Young *et al*. (1998b).

Abralia steindachneri Weindl, 1912

Abralia steindachneri Weindl, 1912, *Anzeiger der Kaiserlichen Akadamie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, 49(17): 270–275 [271]. [Type locality: Shadwan, Red Sea, western Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 55 mm.

Geographical Distribution: Red Sea; Indian Ocean; off eastern Africa, Seychelle Islands, Gulf of Aden.

Habitat and Biology: A mesopelagic boundary species.

Literature: Nesis and Nikitina (1987), Young *et al*. (1998b).

Abralia trigonura Berry, 1913

Abralia trigonura Berry, 1913b, *Proceedings of the United States National Museum*, 45(1996): 563–566 [565]. [Type locality: Pailolo Channel, Hawaiian Islands, central Equatorial Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 37 mm.

Geographical Distribution: Central and western North Pacific Ocean; Hawaiian Islands, off Japan.

Habitat and Biology: Mesopelagic to epipelagic diel vertical migrator. Prey of dolphins.

Literature: Young *et al*. (1979b), Vecchione (1992a [1991]), Bower *et al*. (1999c), Hidaka and Kubodera (2000).

Abralia veranyi (Rüppel, 1844)

Enoploteuthis veranyi Rüppel, 1844, *Giornale del Gabinetto Letterario di Messina*, 5(27–28): 129–135 [131]. [Type locality: off Messina, Sicily, Central Mediterranean Sea].

Frequent Synonyms: *Enoploion eustictum* Pfeffer, 1912.

Diagnostic Features: See general description.

Size: Mantle length to 50 mm.

Geographical Distribution: Mediterranean Sea, off Messina, Italy; Atlantic Ocean. Tropical and subtropical western and eastern Atlantic Ocean, from northeastern United States to the Gulf of Mexico and Suriname; from Mediterranean Sea to Madeira.

Habitat and Biology: At bottom in bathyal and in midwater above slopes, occasionally to surface (night time); absent in the open ocean far from the slopes and slope waters. A mesopelagic to epipelagic diel vertical migrator.

Literature: Berry (1926), Kluchnik and Starobogatov (1978), Herring *et al*. (1992b), Young *et al*. (1998b).

Abraliopsis Joubin, 1896

Plate VII, 40

Abraliopsis Joubin, 1896, *Bulletin de la Société Scientifique et Medicale de l'Quest*, 5(1): 19–35 [20].

Type Species: *Enoploteuthis hoylei* Pfeffer, 1884.

Frequent Synonyms: None.

Diagnostic Features: Manus of club with 2 series of hooks, 1 series of suckers. **Two to 4 (mostly 3) large photophores covered by black chromatophores on tips of arms IV**. Fins terminal. Buccal crown without typical chromatophores, with dark epithelial pigmentation on oral surface. **Eyeball with 5 photophores ventrally, anterior and posterior photophores enlarged**, the 3 remaining photophores small, subequal. **Right or left arm IV hectocotylized**. **Suckers absent from arms IV**. Spermatophore receptacle(s) located under collar or between stellate ganglia. Complex photophores of integument, in life, with red colour filters. Radula with homodont teeth. **Large arm hooks with apertures closed**.

Remarks: ***Abraliopsis*** species occupy similar habitats as ***Abralia*** species, both geographically and vertically. As well, they are heavily preyed upon by epipelagic and mesopelagic top-level predatory fishes and by odontocete cetaceans. Species of

Abraliopsis can be placed into three subgenera (i.e. ***Abraliopsis, Micrabralia, Pfefferiteuthis***) but these may not all be natural groups (Young and Tsuchiya, 2009b).

Literature: Young (1973b), Young *et al*. (1979b), Moreno and Pereira (1998), Young *et al*. (1998b), Young and Tsuchiya (2009b).

Abraliopsis hoylei (Pfeffer, 1884) **(Type Species)** **Fig. 219**

Enoploteuthis hoylei Pfeffer, 1884, *Abhandlung aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 1–30 [17]. [Type locality: Mascarene Islands, southwestern Indian Ocean].

Frequent Synonyms: None.

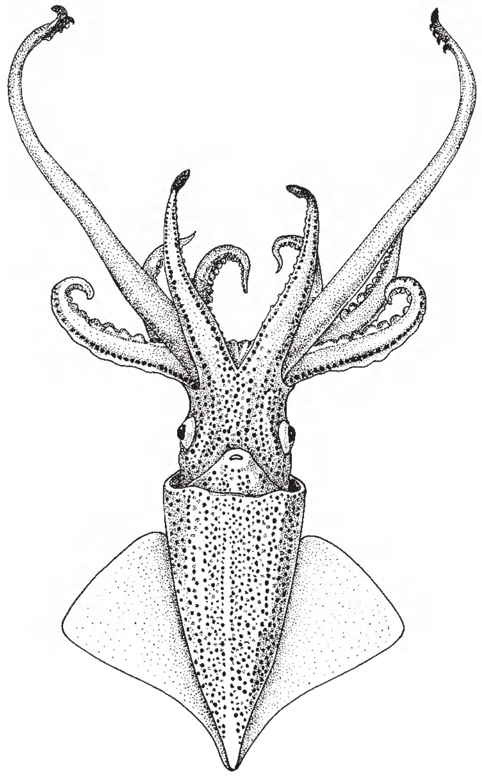
FAO Names: En – Hoyle's enope squid; **Fr** – Enoploloutène de Hoyle; **Sp** – Enoploluria de Hoyle.

Size: Mantle length to 30 mm.

Geographical Distribution: Indian Ocean, Mascarene Islands. Tropical and subtropical Indo-West Pacific Ocean from Hokkaido to the Tasman Sea and from eastern Africa to Hawaii; absent in Arabian Sea and Bay of Bengal (Fig. 220).

Habitat and Biology: Probably diel vertical migrator from mesopelagic zone to epipelagic waters at night.

Literature: Nesis (1974a).



ventral view

Fig. 219 ***Abraliopsis hoylei***

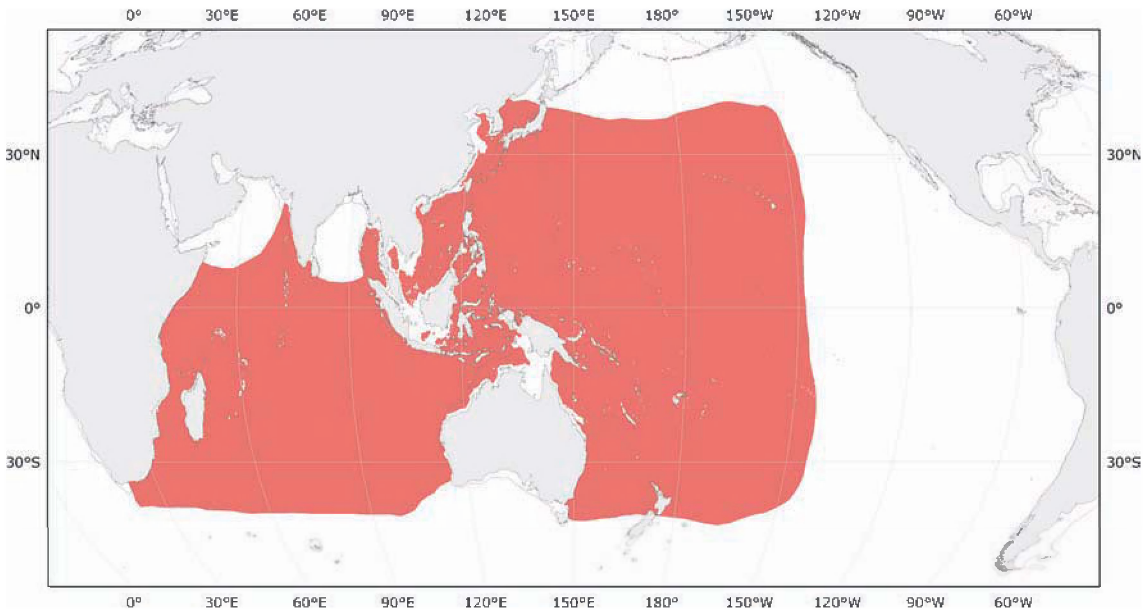


Fig. 220 ***Abraliopsis hoylei***

🟥 Known distribution

Abraliopsis affinis (Pfeffer, 1912)

Abralia (Micrabralia) affinis Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2F(a): 1–815 [160]. [Type locality: eastern temperate North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 40 mm.

Geographical Distribution: Eastern tropical Pacific Ocean, off Mexico south to off Ecuador, approximately from 20°N to 30°S.

Habitat and Biology: A mesopelagic species that migrates to epipelagic zone at night. Prey of hammerhead shark.

Literature: Alexeyev (1994a), Okutani (1995).

Abraliopsis atlantica Nesis, 1982

Abraliopsis atlantica Nesis, 1982, *Light and Food Industry Publishing House*, 358 pp. [172, as footnote]. [Type locality: 01°51'N, 00°31'E, Gulf of Guinea, eastern tropical Atylantic].

Frequent Synonyms: None.

Size: Mantle length to 33 mm.

Geographical Distribution: Eastern tropical Atlantic Ocean, Gulf of Guinea.

Habitat and Biology: Assumed to be mesopelagic to epipelagic as a diel vertical migrator.

Literature: Cairns (1976), Laptikhovsky (1999b).

Abraliopsis chuni Nesis, 1982

Abraliopsis chuni Nesis, 1982, *Light and Food Industry Publishing House*, 358 pp. [172, as footnote]. [Type locality: 01°49'N, 45°29'E, western Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 38 mm.

Geographical Distribution: Western Indian Ocean; tropical Indo-West Pacific Ocean, from eastern Africa to Line Islands.

Habitat and Biology: Presumed to be an equatorial, mesopelagic-epipelagic diel vertical migrator.

Literature: Chun (1910).

Abraliopsis falco Young, 1972

Abraliopsis falco Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 159 pp. [13]. [Type locality: 28°54'N, 118°08'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 46 mm.

Geographical Distribution: Eastern tropical Pacific Ocean; off Baja California to northern Chile from about 35°N to 20°S.

Habitat and Biology: Vertical migrator at night from mesopelagic into epipelagic zone.

Literature: Okutani (1974a, 1995).

Abraliopsis felis McGowan and Okutani, 1968

Abraliopsis felis McGowan and Okutani, 1968, *Veliger*, 11(1): 72–79 [72]. [Type locality: 31°59’N, 122°24’W, Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 45 mm.

Geographical Distribution: Eastern North Pacific Ocean; off west coast North America, 27°N to 43°N; northwest Pacific Ocean off Japan.

Habitat and Biology: Strongly defined vertical migrator from 300 to 600 m (peak 400 to 500 m) during daytime, ascending to the upper 200 m (mean 100 m) at night. A dominant species in the Kuroshio-Oyashio transition zone, northwest Pacific Ocean. Prey of northern elephant seal, Pacific dolphins.

Literature: Young (1972a), Tsuchiya (1993), Mori *et al*. (2002).

Abraliopsis gilchristi (Robson, 1924)

Abralia gilchristi Robson, 1924, *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*, 3: 1–14 [3]. [Type locality: off Cape Town, South Africa, western South Atlantic Ocean].

Frequent Synonyms: *Enoploteuthis neozelanica* Dell, 1959.

Size: Mantle length to 40 mm.

Geographical Distribution: Eastern South Atlantic Ocean; Indian Ocean, off Cape Town; off New Zealand, central South Pacific Ocean (possibly circumglobal in southern subtropical belt).

Habitat and Biology: Probable diel vertical migrator.

Literature: Roeleveld *et al*. (1992), Lipinski (1992).

Abraliopsis lineata (Goodrich, 1896)

Abralia lineata Goodrich, 1896, *Transactions of the Linnean Society of London, Zoology*, 7(1): 1–24 [10]. [Type locality: Andaman Sea and off Ganjam coast, eastern Indian Ocean].

Frequent Synonyms: None.

Size: Mantle length to 27 mm.

Geographical Distribution: Indian Ocean, Andaman Sea; Arabian Sea.

Habitat and Biology: Mesopelagic to epipelagic at night.

Literature: Tsuchiya *et al*. (1991), Young *et al*. (1998b).

Abraliopsis morisii (Verany, 1839)

Onychoteuthis morisi Verany, 1839, *Memorie della Reale Accademia della Science di Torino*, series 2, 1: 99–101 [100]. [Type locality: 39°N, 20°W, eastern Atlantic Ocean].

Frequent Synonyms: *Abraliopsis pfefferi* Joubin, 1896, *Compsoteuthis lonnbergi* Pfeffer, 1900; *Abralia (Compsoteuthis) jattai* Pfeffer, 1912.

Size: Mantle length to 45 mm.

Geographical Distribution: This species is widely distributed in the tropical to warm-temperate eastern and wesern Atlantic Ocean; Gulf of Mexico, Mediterranean Sea.

Habitat and Biology: Inhabits epipelagic and mesopelagic zones; undergoes diel vertical migrations. Prey of giant red shrimp.

Remarks: The name ***Abraliopsis pfefferi*** Joubin, 1896, was used for this species for a while (Nesis, 1982/87). The name ***A. morisii*** was restored by Bello (2005), after the re-examination of the original description of the species given by Verany (1839). Therefore ***A. pfefferi*** Joubin, 1896 is a junior synonym of ***A. morisii*** (Verany, 1839).

Literature: Young *et al*. (1998b), Laptikhovsky (1999b); Bello (2005).

Abraliopsis pacificus Tsuchiya and Okutani, 1990

Abraliopsis pacificus Tsuchiya and Okutani, 1990, *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 16(2): 47–60 [48]. [Type locality: 32°47'18"N, 147° 58'42"E, western North Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 36 mm.

Geographical Distribution: Western North Pacific Basin, off Japan; Shikoku Basin, between latitudes 25°N and 35°N. Hawaiian waters.

Habitat and Biology: Probably a diel vertical migrator.

Literature: Young *et al*. (1998b).

Abraliopsis tui Riddell, 1985

Abraliopsis tui Riddell, 1985, *Fisheries Research Bulletin, New Zealand*, 27: 1–52 [37]. [Type locality: Kermadec Islands, off eastern Australia, western South Pacific Ocean].

Frequent Synonyms: None.

Size: Mantle length to 30 mm.

Geographical Distribution: South Pacific Ocean off New Zealand: 170°E, 20°S to 170°W, 40°S, north and south of the subtropical convergence.

Habitat and Biology: Presumed diel vertical migrator.

Literature: Young *et al*. (1998b).

Watasenia Ishikawa, 1914

Watasenia Ishikawa, 1914, Zoologischer Anzeiger, 43(7): 336 [336].

Type Species: *Watasenia scintillans* (Berry, 1911a).

FAO names: En – Sparkling enope squids.

Diagnostic Features: Manus of club with hooks in 1 series (2 or 3 in number); **1 series of suckers**. **Two to 4 large photophores** covered by black chromatophores **on tips of arms IV**. Fins terminal. Buccal crown without typical chromatophores, with dark epithelial pigmentation on oral surface. **Five photophores on eyeball**. **Hectocotylus on right arm IV with 1 dorsal and 1 ventral flap**. **Suckers absent from arms IV**. Spermatophore receptacles located under collar. Complex photophores of integument, in life, apparently with red colour filters. Radula with homodont teeth. Large arm hooks with closed apertures.

Remarks: Monotypic.

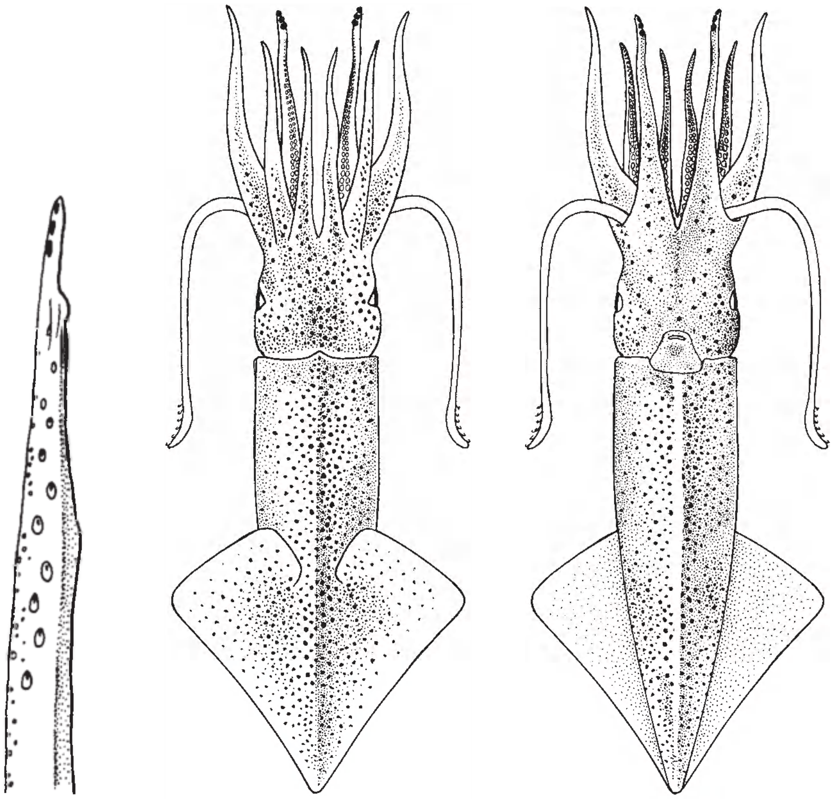
Watasenia scintillans (Berry, 1911)

Fig. 221

Abraliopsis scintillans Berry, 1911a, *Nautilus*, 25(8): 93–94 [93]. [Type locality: Japan, exact locality unknown].

Frequent Synonyms: *Abraliopsis joubini* Watase, 1906; *Abraliopsis scintillans* Berry, 1911a; *Abralia (Compsoteuthis) nishikawae* Pfeffer, 1912; *Abralia japonica* Ishikawa, 1929.

FAO names: En – Sparkling enope squid; **Fr** – Encornet lumiere; **Sp** – Enoploloria centellante.



hectocotylus dorsal view ventral view

Fig. 221 *Watasenia scintillans*

Diagnostic Features: Mantle stocky; elongate, conical posteriorly. Only 2 (3) large hooks on ventral row of manus of club; 4 suckers, no hooks, on dorsal row. Arms with hooks. Mantle covered with numerous, minute photophores on ventral and lateral surfaces, but with ventral midline devoid of photophores. Fins rhomboidal, terminal, about 70 to 75% of mantle length. Minute photophores present in 4 indistinct rows on ventral surface of head; 5 photophores on ventral surface of eyeball, posterior and anterior ones enlarged; 3 (rarely 2 , 4) bulbous black photophores on tips of arms IV. Right arm IV hectocotylized with 1 dorsal and 1 ventral flap. Male has a shorter mantle and fewer mantle photophores than the female.

Size: Small sized squid; maximum mantle length 70 mm in females and 60 mm in males.

Geographical Distribution: Western North Pacific Ocean; Kuroshio-Oyashio transition region; East China Sea, Sea of Japan and southern Sea of Okhotsk; South Kuriles, with occasional occurrence in the North Kuriles, to southern Japan; Japan and Korea; to about 170°E (Fig. 222).

Habitat and Biology: A primarily oceanic luminescent species, that inhabits depths between 100 and 600 m; a mesopelagic-boundary species that undergoes diel vertical migrations of the migrant type in which day and night habitats are clearly separated with peak abundance deeper than 300 m during the day and shallower than 300 m at night. It occurs in the warm core ring and cold water masses, avoiding the warm subtropical water in upper layers of the warm core ring. The species is most abundant in sub-Arctic waters with peak biomass of 32.9 tonnes per sq km and average biomass of 3.2 tonnes per sq km. It spawns in waters close to the shore, e.g. Toyama Bay, Sagami Bay, Suruga Bay, Japan. Spawning occurs year round, with a peak of activity in

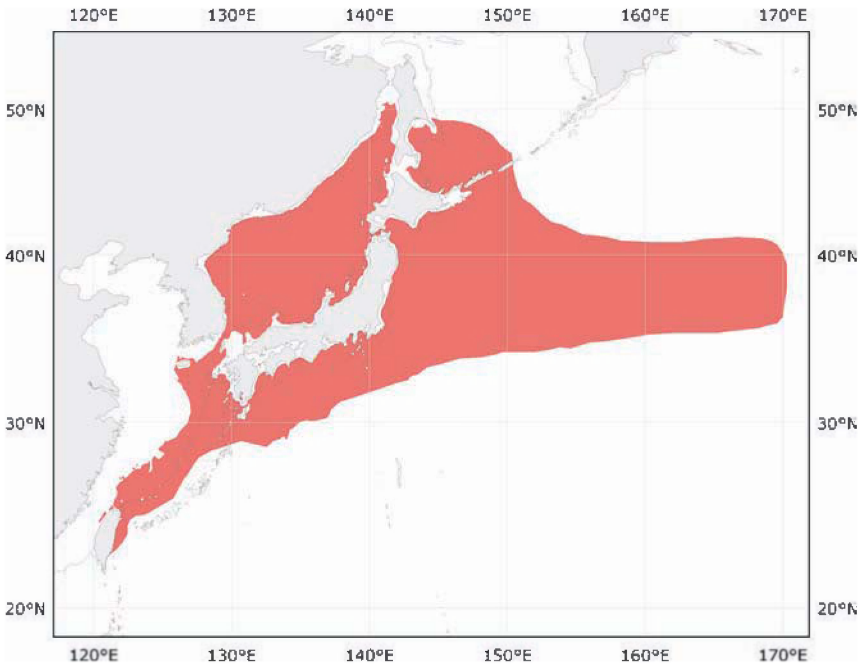


Fig. 222 *Watasenia scintillans*

🟥 Known distribution

spring (April-June). Eggs and juveniles are distributed in the subsurface waters down to 150 m; greatest abundance in the upper 70 m. Post-spawning mortality is complete and the life span is believed not to exceed 1 year. While in inshore waters and bays, ***Watasenia scintillans*** has been observed and photographed during its spectacular luminescent displays of blue greenish light. Diet varies from calanoid copepods in the paralarval stage to planktonic crustaceans (amphipods, copepods, euphausids), fishes and squids during the subadult and adult stages. It is preyed upon by baleen whales and other marine mammals; it constitutes 8% by volume of the diet of the northern Pacific fur seal. The species also is significantly preyed upon by many species of demersal fishes and some sharks.

Interest to Fisheries: The annual catch fluctuates between 800 and 3 700 tonnes over a period of years, without any clear trend. However, recent evidence indicates a relationship between catch abundance and surface water temperature (and associated plankton biomass as an index of food availability) during early spring (April-May) of the same year. The species is taken regularly with set nets in Toyama Bay, Japan, between February and early July (peak April to May), as well as from Sagami Bay and Suruga Bay. During this period it aggregates near the surface, particularly at night. ***Enoploteuthis chunii*** is sympatric with this species in commercial catches.

Local Names: JAPAN: Hotaruika, Matsuika; USA: Japanese firefly squid.

Remarks: Also extensively used in research on bioluminescence.

Literature: Hayashi (1991, 1995a,b), Jivaluk (2001), Okutani (2005), Watanabe *et al*. (2006b), Zuev (2006), Tsuchiya (2007).

2.13 Family GONATIDAE Hoyle, 1886

by Clyde F.E. Roper, Elaina M. Jorgensen, Oleg N. Katugin and Patrizia Jereb

Gonatidae Hoyle, 1886, *Report of the Scientific Results of the Voyage of the HMS Challenger, Zoology*, 16(44): 1–245 [173].

Type Genus: *Gonatus* Gray, 1849.

FAO Names: En – Gonate squids; **Fr** – Gonaleutènes; **Sp** – Gonaluras.

Diagnostic Features: The Gonatidae have a rather **narrow muscular body and medium to large rhomboid or heart-shaped fin**. In some species muscle tissues, particularly mantle, fin and arms, degenerate upon maturation and become watery and flaccid, which is associated with post-spawning egg-brooding, a unique feature among the order Teuthida. The Gonatidae is characterized by a **basic tetraserial armature on the arms**. **Arm tips may have more than 4 series of minute suckers**. **The 2 medial series on arms I to III typically consist of hooks along nearly the entire arm length**, except for the most basal and distal portions of the arms. However, in 1 species, ***Berryteuthis anonychus***, several (usually 5 to 8) small hooks occur at the bases of arms I to III in females, while males have no hooks at all. All members of the family have a **simple, straight funnel-locking cartilage** that may flare slightly at the posterior end; **buccal connectives DDVV**; numerous series of suckers on the clubs: minute, crowded and almost equal-sized on ***Eogonatus tinro*** and ***Berryteuthis anonychus***; larger in the centre and minute along the edges on ***B. magister***; organized in rows with additional hooks on ***Gonatus***. **Tentacles** are equipped **with a well-developed fixing apparatus along the dorsal margin**; this structure covers the proximal edge of the club and may extend well proximately along the club to occupy almost half of the tentacle length in ***B. magister***, for example. The fixing apparatus consists of numerous alternating pads (or knobs) and minute toothless suckers in ***B. magister***, and has evolved into a complex structure of several alternating ridges with knobs and grooves in ***Gonatus*** species. In species of ***Gonatopsis*** the tentacles are present only in the early life stages (from paralarvae to early juveniles), then completely lost by the late juvenile stages. Only 1 species in the family (***Gonatus pyros***) currently is confirmed to have photophores, present as oval patches located on the ventral surface of the eyes. **Most species** of the Gonatidae **do not have a true hectocotylus**; however, males of ***B. magister*** develop a notable modification of suckers in the middle portion of 1 ventral arm upon maturation, which is considered hectocotylization by some authors. Mature males of ***Gonatus*** and ***Gonatopsis***, are known to have a long penis, which is used to transfer spermatophores onto the female's buccal membrane.

Size: Small- to medium- and large-sized squid; maximum mantle length to 550 mm.

Geographical Distribution: The family exhibits a bipolar distribution: the western arctic-boreal region, the boreal North Atlantic Ocean, the boreal (sub-Arctic) North Pacific Ocean (including the cool temperate California Current waters from California to Alaska) and the whole notalian (sub-Antarctic) belt. The vast subtropical and tropical zones of the world's oceans are devoid of gonatid species.

Habitat and Biology: Most species inhabit the upper water levels as paralarvae and juveniles, then they undergo significant ontogenetic descent as adulthood approaches. Adults of species can descend to great depths in the midwaters (mesopelagic) or to the deep-sea floor where they mate and spawn. Paralarvae and juveniles ascend to food-rich epipelagic waters to feed until ontogenetic growth begins. Spent females of ***Gonatus*** and ***Gonatopsis*** *sensu stricto* become degenerate and gelatinous and float, suspended in the meso- and bathypelagic layers or even in the surface waters. Some species also undergo diel vertical migrations during which they descend to the mesopelagic zone during the day, then ascend to the surface layers at night. Gonatid species are extremely important as prey for many fishes (including many commercially valuable species), seabirds, odontocete (toothed) whales and pinnipeds. Several species are fished commercially, most notably ***Berryteuthis magister***, which is harvested by a specialized fishery and as a bycatch during other fisheries (e.g. for walleye pollock, *Atka mackeresl*, etc.). Up to 70 000 tonnes of this species are taken annually on the slope off the Kuril Islands in the Pacific Ocean and in the western Bering Sea by the Russian fishery alone.

Remarks: Species in this family belong to 4 genera, ***Berryteuthis***, ***Eogonatus***, ***Gonatopsis*** and ***Gonatus***. All genera inhabit the North Pacific, and only ***Gonatus*** has expanded its range far beyond the North Pacific Ocean into the Arctic, North Atlantic and southern oceans. All species of the Gonatidae are cold-water forms and are among the most abundant squids in higher latitudes, most especially in the sub-Arctic (boreal) North Pacific Ocean. Of the **19** currently described species in the family, **13** species of gonatids inhabit the sub-Arctic northwestern Pacific Ocean, and the Bering, Okhotsk and Japan seas, **3** species are endemic to the eastern North Pacific, **2** species inhabit the North Atlantic and **1** species dwells in the Southern Ocean. Differentiation occurs among populations of ***Berryteuthis magister*** from different areas, which ultimately led to the disignation of 2 distinguished subspecies, ***B. magister nipponensis*** and ***B. magister shevtsovi***. Therefore, 21 entities are listed and described in this Catalogue.

Local Names: USA: Armhook squids.

Literature: Jefferts (1983), Okutani *et al.* (1988), Arkhipkin and Bizikov (1997), Sweeney and Young (2003k), Katugin (2004), Katugin and Shevtsov (2006), Kubodera *et al.* (2006a,b,c,d), Jorgensen (2007).

Key to the genera of Gonatidae

1a. Tentacles present in adults . . . . → ***2***
1b. Tentacles absent in adults (Fig. 223) . . . . . ***Gonatopsis***

2a. Tentacular club armed with suckers only . . . . → ***3***
2b. Tentacular club armed with suckers and hooks (Fig. 224) . . . . ***Gonatus***

3a. Radula with 5 longitudinal rows of teeth . . . . ***Eogonatus***
3b. Radula with 7 longitudinal rows of teeth . . . ***Berryteuthis***

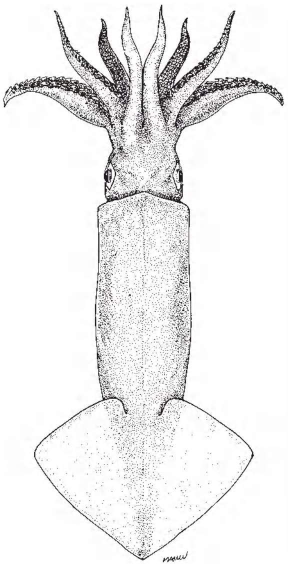

dorsal view

Fig. 223 *Gonatopsis*


tentacular club

Fig. 224 *Gonatus*

Table 3

Ecological Characteristics of Gonatid Squids (from Nesis, 1997, 1999a, 2002; authors' data)

Species	Size	Horizontal Distribution	Spawning Habitat	Diurnal Vertical Migration	Ontogenetic Descent	Gelatinous Degeneration
Berryteuthis anonychus	Small	N P low-boreal	Pelagic	Yes; e	Late	No
Berryteuthis magister	Intermediate/ large	N P panboreal; bottom-associated	Bottom	Yes; (e)m-b	Early	No
Eogonatus tinro	Small	N P upper-boreal	Pelagic/	Yes; e-m-b	Early	Yes
Gonatopsis borealis	Small/ intermediate	N P panboreal	Pelagic/ bottom	Yes; e-m	Late	No
Gonatopsis japonicus	Very large	Nw P panboreal	Pelagic/ bottom?	Yes; e-m	Intermediate	Yes
Gonatopsis makko	Large	Nw P low boreal	Pelagic/ Bottom	Unknown	Unknown	Yes
Gonatopsis octopedatus	Small	Nw P panboreal	Pelagic/ bottom?	Yes; e-m	Early	Yes
Gonatus antarcticus	Intermediate	S O notalian	Pelagic	Yes; e-m-b	Early	Yes
Gonatus berryi	Intermediate	N P panboreal	Pelagic	Yes; m-b	Very late	Yes
Gonatus californiensis	Small	Ne P low-boreal	Pelagic	Yes; (e)m-b	Early?	Yes
Gonatus fabricii	Intermediate	A N A boreal	Pelagic	Yes; e-m-b	Early	Yes
Gonatus kamtschaticus	Very large	N P upper-boreal; nerito-oceanic	Pelagic	Yes; e-m	Intermediate	Yes
Gonatus madokai	Large	N P upper-boreal	Pelagic	Yes; e-m-b	Intermediate	Yes
Gonatus onyx	Small	N P panboreal	Pelagic	Yes; e-m-b	Early	Yes
Gonatus pyros	Small	N P panboreal	Pelagic	Yes; (e)m-b	Early?	Yes
Gonatus steenstrupi	Small/ intermediate	Ne A boreal	Pelagic	Yes; e-m-b	Early?	Yes

Key:

Size: Small: dorsal-mantle length (DML) about 100 to 150 mm; intermediate: DML about 200 to 350 mm; large: DML from 350 to 500 mm; very large: DML larger than 500 mm.

Horizontal Distribution: N P = North Pacific; Nw P = Northwestern Pacific; Ne P = Northeastern Pacific; A N A = Arctic Northwestern Atlantic; Ne A = Northeastern Atlantic; S O = Southern Ocean.

Diurnal Vertical Migration: e = epipelagic; m = mesopelagic; b = bathypelagic.

Gonatus Gray, 1849

Gonatus Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia*, 164 pp. [67].

Type Species: *Gonatus fabricii* Lichtenstein, 1818.

Frequent Synonyms: *Lestoteuthis* Verrill, 1880 (in 1879–1880); *Chiloteuthis* Verrill, 1881 (in 1880–1881).

Diagnostic Features: Tentacular club with at least 1 large central hook on manus and generally with additional hooks (large distally and small proximally) in median line. **Club with distinctive locking (fixing) apparatus** on dorsal border of manus that consists of a series of 4 to 6 large, thick, transverse pads with medial alternating oval pads and suckers; **radula with 5 longitudinal rows of teeth**. **Hooks well developed in 2 medial series on arms** from paralarval or immediate post-paralarval stages. Fins heart-shaped, extend posterior to end of mantle, attenuate into tail supported by cartilaginous rod.

Habitat and Biology: As adults, ***Gonatus*** species are typically mesopelagic and upper bathypelagic; however several species ascend to epipelagic layers at night. They are important prey for odontocete cetaceans, large oceanic and benthic fishes, e.g. gadoids, salmonids, coalfish, redfish.

Interest to Fishesies: ***Gonatus*** species currently do not support any significant commercial fishery, in spite of the good consistency of the flesh and the large size of some species. However, a good potential for future exploitation does exist.

Remarks: Currently the genus consists of 11 species. Eight of these species have been described since 1972 in coincidence with the development of concentrated sampling in deeper waters. Also responsible are the intense sampling and execution of exploratory fishing programmes in high-latitude seas, especially in the northern Pacific Ocean realm.

Literature: Nesis (1997), Katugin (2004), Lindgren *et al.* (2005), Kubodera *et al.* (2006d).

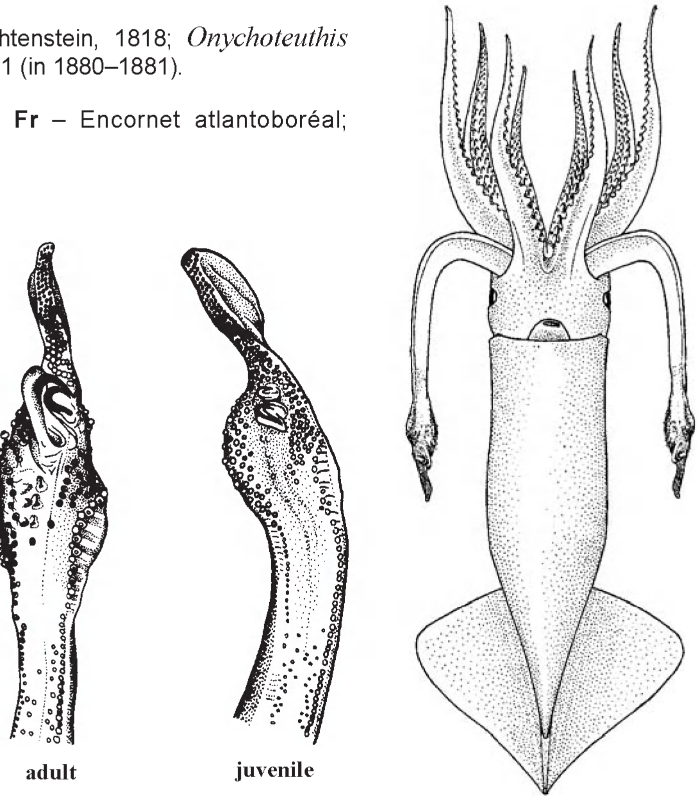
Gonatus fabricii (Lichtenstein, 1818)

Fig. 225

Onychoteuthis fabricii Lichtenstein, 1818, *Isis, oder Encyclopädische Zeitung*, 1818(9): 1591–1592. [1592]. [Type locality: Amerloq Fjord, West Greenland, Davis Strait, North Atlantic Ocean].

Frequent Synonyms: *Onychoteuthis fabricii* Lichtenstein, 1818; *Onychoteuthis amoena* Moller, 1842; *Cheloteuthis rapax* Verrill, 1881 (in 1880–1881).

FAO Names: En – Boreoatlantic gonate squid; **Fr** – Encornet atlantoboréal; **Sp** – Gonalura atlantoboreal.


adult juvenile

tentacular club

ventral view

Fig. 225 *Gonatus fabricii*

Diagnostic Features: Mantle long, slender, conical, slightly wider at midpoint, tapers to a sharp point posteriorly, its muscular part ends at the conus, but a fleshy, tapered column extends posteriorly as the tail. Fins sagittate with anterior lobes free, lateral margins rounded; fin length less than 50% of mantle length, fin width slightly less than the mantle length. **Tentacular clubs slender, small, their length about 12 to 20% of mantle length, with 1 very large, central hook, followed proximally by 3 small hooks and 1 small sucker**, and **distally by 1 moderate-sized sucker**; 9 to 13 transverse series of suckers and hooks on proximal half of arms III, 14 to 17 series of suckers (no hooks) on proximal half of arms IV. Arm hooks develop at about 20 to 40 mm dorsal mantle length, starting in the middle portion.

Size: Maximum mantle length attained is 400 mm.

Geographical Distribution: This boreo-Atlantic squid occurs in offshore arctic and subarctic waters of the northern North Atlantic Ocean from the Newfoundland Basin southward to south of Cape Cod (Georges Bank and various canyons and sea mounts) and northward from the Labrador Sea to Baffin Bay in the western North Atlantic Ocean; around Greenland and eastward to the western Barents Sea and Norway in the eastern North Atlantic Ocean (Fig. 226).

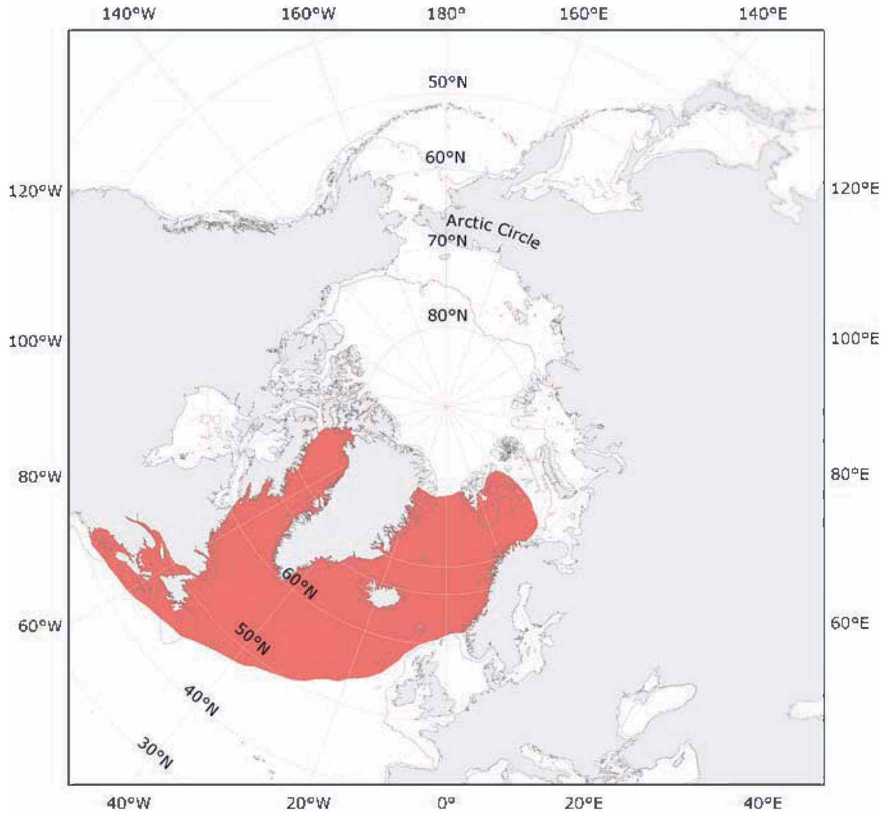


Fig. 226 *Gonatus fabricii*

🟥 Known distribution

Habitat and Biology: ***Gonatus fabricii*** is an oceanic species that occurs between the surface and 500 to 700 m (records to 1 000 m) depth. It is the most abundant squid in the boreal Atlantic waters. Adults are common in midwater layers in arctic and subarctic waters of the North Atlantic Ocean, while juveniles inhabit near-surface waters in the northwestern North Atlantic Ocean. Females produce about 10 000 eggs that are laid in gelatinous masses at great depths. As typical for many gonatid species, maturing and spawning females undergo rapid degradation of tissue of the mantle and arms into a gelatinous consistency; tentacles and arm suckers are lost, and normal, active locomotion is reduced. Egg masses are held in the arms while the embryos develop. After eggs hatch into paralarvae, the female dies. Mating occurs head to head and the spermatophores are deposited on the buccal membrane of females. Spawning seems to extend from mid-April to December with a peak period in late May and June. The incubation period for some species may extend to 6 months. In the Norwegian Sea spawning appears to occur from winter to summer with hatching subsequently from late March to June or July; summer biomass of juveniles in the Norwegian Sea was calculated to be at least 1.5 million tonnes. Juveniles off west Greenland showed average growth rates of 4 to 5.5 mm per month from July to November. The life cycle is about 2 years. Juveniles feed on copepods, euphausiids, hyperiid amphipods, pteropods, and chaetognaths. Once the hooks have developed on juveniles, at a mantle length of about 20 to 40 mm, an important part of the diet is made up of fishes e.g. redfish, hake and small ***Gonatus***; adults can feed on prey larger than themselves. ***Gonatus fabricii*** is preyed upon by the northern bottlenose whale, harp and hooded seals in the Norwegian Sea and extremely heavily by sperm whales off Iceland and in the North Atlantic Ocean. Northern bottlenose whales in the Norwegian Sea annually eat 480 000 tonnes of ***G. fabricii***, while sperm whales consume 365 000 to 520 000 tonnes; total biomass here produced by a 2 year old cohort is about 20 million tonnes. Narwhals feed extensively on ***G. fabricii*** during all feeding seasons and exclusively during the autumn. Also, this species frequently is found in stomachs of other marine mammals, e.g. ringed harp and hooded seals, as well as in coalfish, Greenland halibut, salmon, various gadoids, blue ling, the redfish (*Sebastes marinus*) and others. Atlantic puffins in the Norwegian Sea prey heavily on ***G. fabricii*** in offshore waters in the winter, while northern fulmars prey primarily on this species in autumn through spring. Other predators include thick-billed murres, and ommastrephid squid ***Todarodes sagittatus***.

Interest to Fisheries: This species is believed to have a significant fishery potential if sustainable yields and consumer interest can be developed. ***Gonatus fabricii*** is by far the most abundant "edible" squid in North Atlantic arctic and sub-Arctic waters. Because females undergo significant tissue degradation at maturity, pre-spawning aggregations will need to be targeted. The flesh has a good pre-spawning consistency and the species attains a desirable size. Greenland Eskimos use it as bait in the cod (*Gadus morhua callarias*) and halibut (*Hippoglossus hippoglossus*) hook-and-line fishery and for human food. It is taken as by catch in shrimp trawl and other benthic otter trawl fisheries.

Local Names: GERMANY: Nordische Köder Kalmar.

Literature: Young (1973a), Wiborg (1979b), Kristensen (1980a, b), Bjoerke (1995), Arkhipkin and Bjoerke (1999), Falcon, *et al.* (2000), Piatkowski *et al.* (2001a), Hastie *et al.* (2009).

Gonatus kamtschaticus (Middendorff, 1849)

Fig. 227

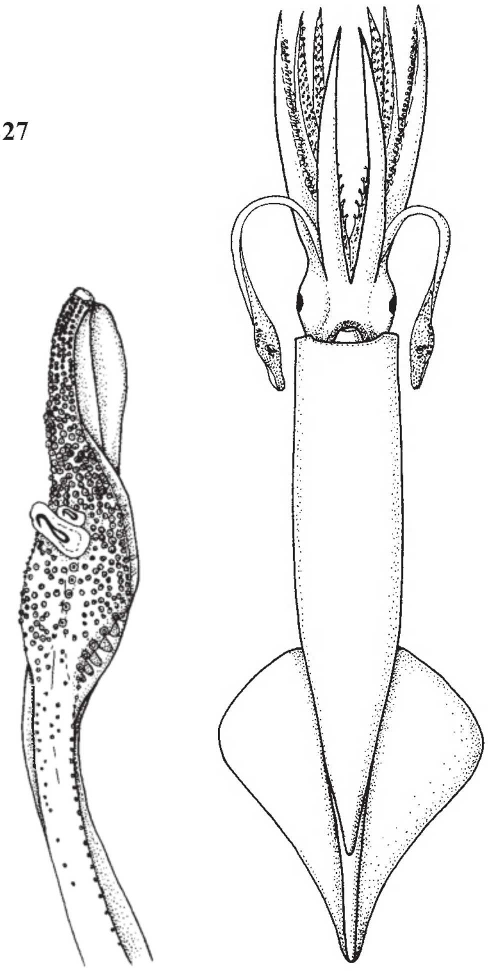
Onychoteuthis kamtschatica Middendorff, 1849, *Memoires de l'Academie Imperiale des Sciences de Saint-Petersbourg*, series 6(6): 329–610 [515]. [Type locality: Schumschu Island, Kuril Islands, Northwest Pacific Ocean].

Frequent Synonyms: *Onychotheutis kamtschatica* Middendorff, 1849 (generic misspelling); *Gonatus middendorffi* Kubodera and Okutani, 1981.

FAO Names: En – Shortarm gonate squid; **Fr** – Encornet bras courts; **Sp** – Gonalura bracicorta.

Diagnostic Features: Mantle long, muscular, very slender, its width from 18% of mantle length in young individuals to 24% of mantle length in maturing individuals, tapers posteriorly to a sharp, long, choroidal tail. **Fins muscular, relatively long** (43 to 52% of mantle length) **and narrow** (their width 40 to 43% of mantle length), sharply pointed posteriorly; fin angle 50° for both fins. Tentacular stalks relatively long; tentacular clubs small, their length less than 13% of mantle length; **manus with a single large central hook, 1 medium-sized distal hook and up to 6 small proximal suckers** (in young specimens), which are modified into hooks as the animal grows. Arms rather short, arms III equal to 50% of mantle length in young animals and to 77% in maturing individuals.

Size: The maximum mantle length attained is 550 mm.



tentacular club **ventral view**

Fig. 227 ***Gonatus kamtschaticus***

Geographical Distribution: This species occurs in the far North Pacific Ocean from the Bering Sea southwest along the Kuril Islands into the southeastern Okhotsk Sea and south to Japan, and eastward along the Aleutian Islands Chain (Fig. 228).

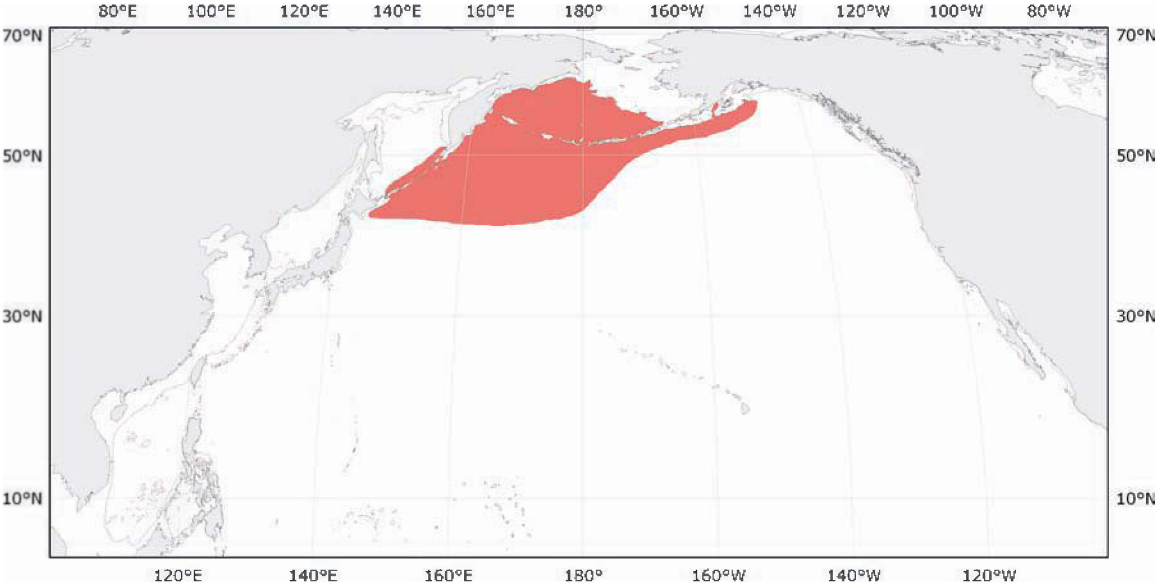


Fig. 228 ***Gonatus kamtschaticus***

🟥 Known distribution

Habitat and Biology: ***Gonatus kamtschaticus*** is an oceanic species that undergoes diel vertical migrations as adults from approximately 400 to 800 m in daytime to less than 200 m at night. The paralarvae occur near the surface at night. Juveniles occur in the upper layers, and do not conduct extensive diel vertical migrations. As the squid grow and mature, they tend to descend to deeper layers, and mature animals of over 300 mm mantle length occur in deep waters along the continental slope. In the Pacific Ocean off the Kuril Islands, the species is most frequently observed in the epipelagic zone throughout the year; in the Okhotsk Sea, animals occur mainly in the meso- and bathypelagic layers from January through June, and mainly in the epipelagic layer from July through December. The species is an important prey item in the diet of sperm whales, northern fur seal, pomfret and Pacific salmon (especially *Oncorhynchus nerka* and *O. kisutch*). Young squids consume mainly crustaceans (*Themisto japonica*, *Primno macropa*, *Thysanoessa longipes*, *T. raschii*), and as they grow they start feeding more intensively upon fish and juvenile gonatid squids.

Interest to Fisheries: This species may have a fishery potential in pre-adult stages, both because of its size and its relatively muscular consistency prior to maturity. However, only juvenile animals are known to swarm in dense aggregations, while maturing adults and especially adults are usually very rare in trawl catches.

Local Names: JAPAN: Kamchatka-Takagiika.

Remarks: After its description in 1849, ***Gonatus kamtschaticus*** was synonymized with ***G fabricii*** by both Steenstrup (1880) and Hoyle (1886). The name was declared nomen dubium by Kubodera and Okutani (1981) when they described ***Gonatus middendorffi***, citing lack of type specimens and subsequent literature on ***G kamtschaticus***. Nesis (1982, 1987, 1997) re-elevated ***G kamtschaticus*** to species status, declaring ***G middendorffi*** a junior synonym.

Literature: Kubodera and Jefferts (1984a,b), Nesis (1997), Shevtsov *et al.* (2004a), Jorgensen (2007), Katugin and Zuev (2007).

Gonatus madokai Kubodera and Okutani, 1977

Fig. 229

Gonatus madokai Kubodera and Okutani, 1977, *Venus*, 36(3): 123–151. [124]. [Type locality: 49°32'N, 168°50'E, Northwest Pacific Ocean].

Frequent Synonyms: None.

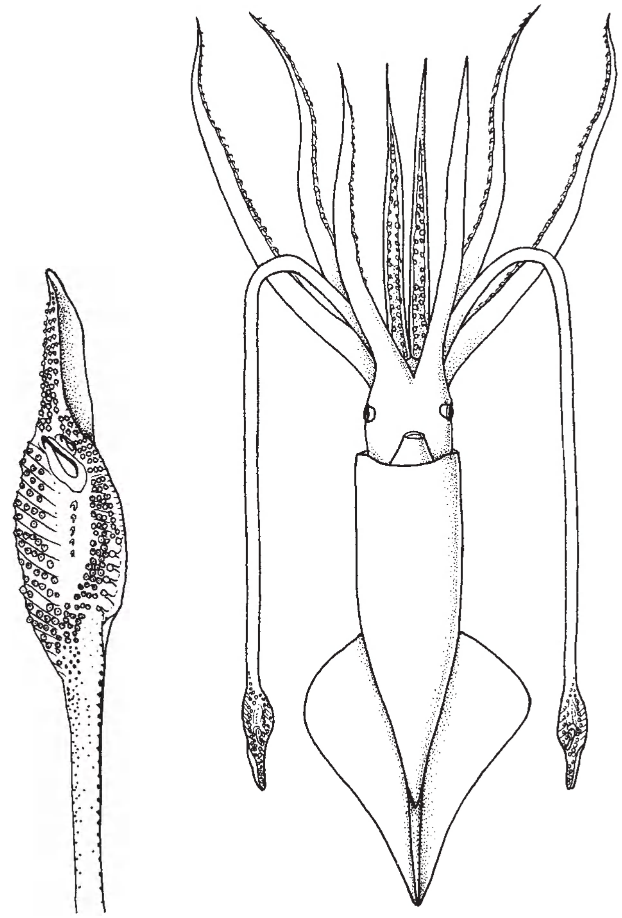
Misidentifications: *Gonatopsis okutanii* (Nesis, 1972b).

FAO Names: En – Madoka's gonate squid; **Fr** – Encornet madokai; **Sp** – Gonalura madokai.

Diagnostic Features: Mantle moderately broad, soft-fleshed, extends posteriorly into a long, pointed tail (20% of mantle length); the posterior part non-muscular posterior to the conus. Fins sagittate, their length 60 to 65% of mantle length, their width 50 to 75% of mantle length. **Tentacular clubs long** (20% of mantle length), with **1 very large central hook, 1 moderate-sized hook distally**, and **4 to 7 very small suckers and hooks proximally** (these develop at greater than 70 mm mantle length). **Arms very long, the longest (III) equal to mantle length**; 11 or 12 transverse series of suckers and hooks on proximal half of arms III; 16 series of suckers proximally on arms IV.

Size: This species attains a maximum mantle length of 470 mm.

Geographical Distribution: ***Gonatus madokai*** is widely distributed in the northern North Pacific Ocean: northern Japan Sea (only 1 reliable record of juveniles off southwestern Sakhalin), Bering Sea (rare), around the Kamchatka Peninsula and the Kuril and Aleutian Islands, the Gulf of Alaska, southward to about 42°N. It is especially abundant in the Okhotsk Sea where it is 1 of the most common of all squids (Fig. 230).



tentacular club **ventral view**

Fig. 229 *Gonatus madokai*

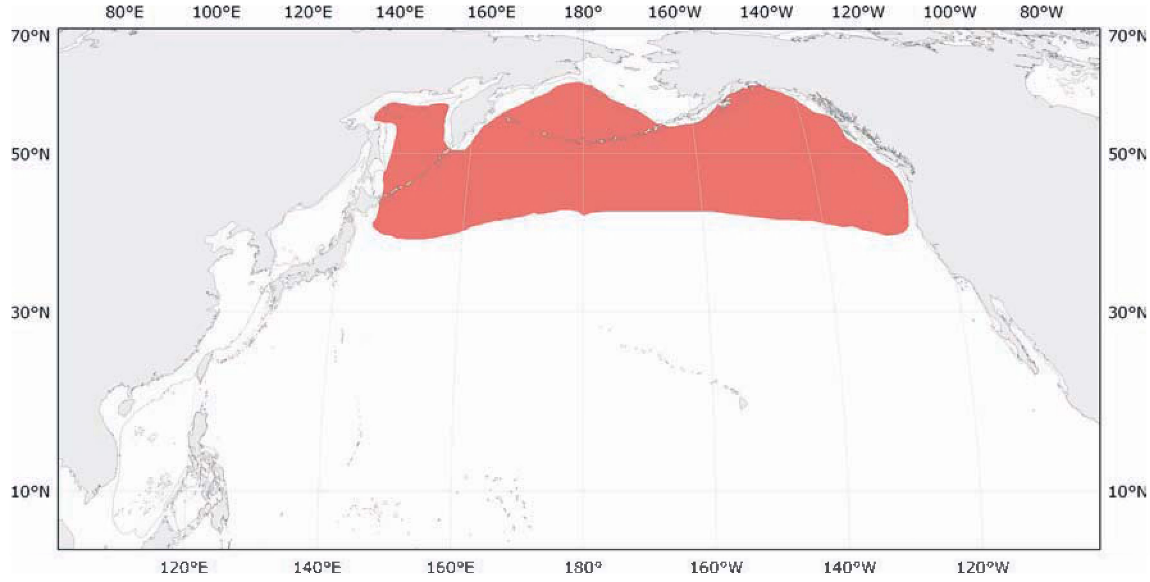


Fig. 230 *Gonatus madokai*

🟥 Known distribution

Habitat and Biology: This large species is an epipelagic to meso-bathypelagic species that descends to mesopelagic depths in daytime (but not exclusively). ***Gonatus madokai*** has been captured to 1 500 m in midwater and possibly as deep as 400 to 3 400 m on the bottom. It has been recorded in association with the Oyashio Current, sub-Arctic Front Zone. The paralarvae are consistently abundant shallower than 300 m in the Okhotsk Sea, where spawning occurs in spring (March to June) and paralarvae are common from June to September. They occur earlier in the season in the Gulf of Alaska. Both diel vertical migration and ontogenetic descent are characteristic. In females, tentacles autotomize during maturation and they break off a short distance from the base, leaving a short but distinctive stem or stump. Muscle tissues become very gelatinous in mature individuals. The life span appears to be at least 2 years. Adult ***G madokai*** consume mainly fish (most commonly *Leuroglossus schmidti*), euphausiids (*Thysanoessa raschii* and *T. longipes*) and juvenile gonatid squid. Juveniles prey predominantly upon amphipods (*Themisto japonica* and *Primno macropa*), and some have had salps and chaetognaths in their stomachs. Adults are heavily preyed upon by toothed whales, walleye pollock (*Theragra chalcogramma*), Pacific salmon, pomfret and northern fur seals.

Interest to Fisheries: While this is a very abundant species, it has no potential for the development of a fishery because, even in the pre-spawning stage, the flesh is watery and jelly-like, which make the squid unacceptable as a food product.

Local Names: JAPAN: Sasaki-Takagiika.

Literature: Kubodera and Jefferts (1984a,b), Katugin and Merzlyakov (2002), Katugin *et al.* (2004b,c), Jorgensen (2007).

Gonatus steenstrupi Kristensen, 1981

Fig. 231

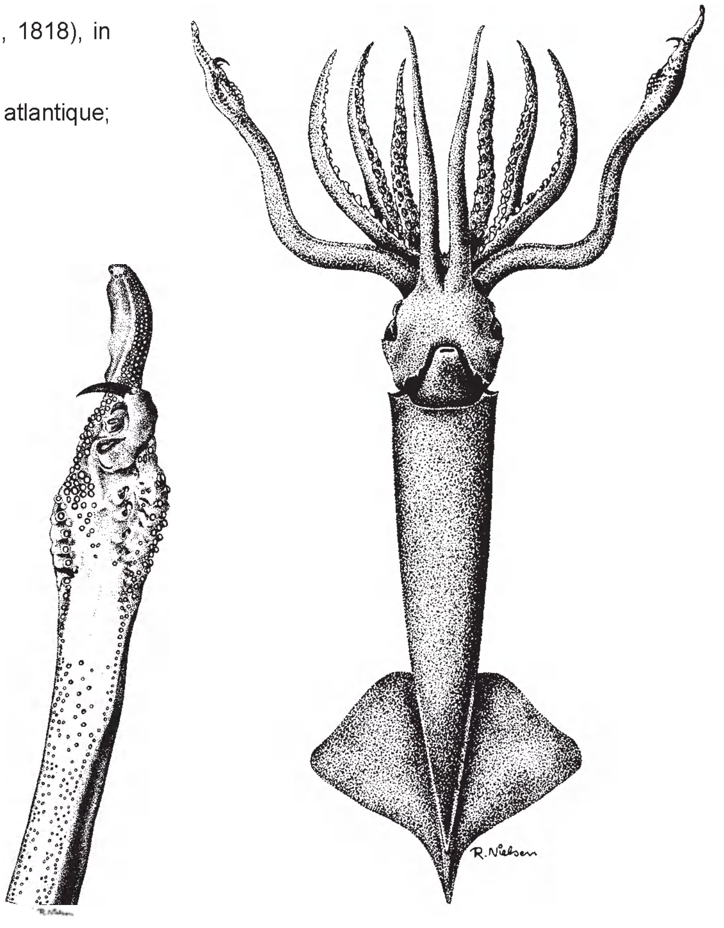
Gonatus steenstrupi Kristensen, 1981, *Steenstrupia*, 7(4): 61–99 [78]. [Type locality: between 53°24' – 51°52' – 8°29'W, Northeast Atlantic Ocean].

Frequent Synonyms: *Gonatus fabricii* (Lichtenstein, 1818), in part.

FAO Names: En – Atlantic gonate squid; **Fr** – Encornet atlantique; **Sp** – Gonalura atlántica.

Diagnostic Features: Mantle long, very slender, thick-walled but muscular; widest at anterior margin then tapers evenly to the posterior pointed tip; muscular part of mantle ends at conus, but a fleshy column extends posteriorly as a short tail. Fins sagittate, their length about 45% of mantle length, their width 52% of mantle length. Tentacles strong and moderately long with tentacular clubs large, expanded, their length about 25 to 36% of mantle length; **1 very large central hook on manus**, with 1 **immediately distal, moderate-sized hook** and **4 or 5 progressively smaller hooks proximal to it** (fifth hook sometimes a sucker). Arms III with 8 or 11 transverse series of 31 to 42 suckers and hooks on proximal half; arms IV with 12 to 14 transverse series of 46 to 57 suckers (no hooks) on proximal half.

Size: The species attains a maximum mantle length of 150 mm, possibly to 190 mm.



tentacular club

ventral view

Fig. 231 *Gonatus steenstrupi*

Geographical Distribution: ***Gonatus steenstrupi*** occurs in the North Atlantic Ocean from 45°N to 63°N. It is widely distributed in the temperate (Bay of Biscay) to boreal (Irminger Sea-East Greenland) waters, east of the Grand Banks of Newfoundland (Fig. 232).

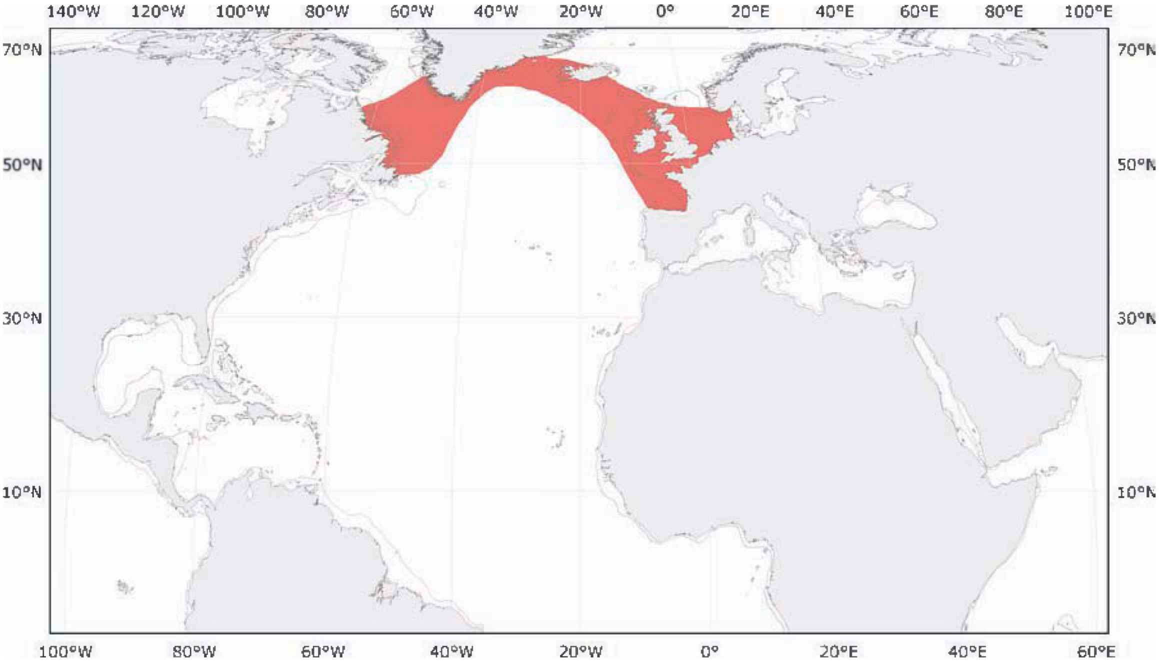


Fig. 232 ***Gonatus steenstrupi***

🟥 Known distribution

Habitat and Biology: This species is an oceanic, mesopelagic species that occurs to 1 000 m depth. Paralarvae up to 20 mm mantle length occur shallower than 200 m, while juveniles larger than 20 mm mantle length occur at depths of 250 to 1 000 m, thus demonstrating a strong ontogenetic descent during development. Young specimens occur only in spring and summer. The species is preyed upon by numerous odontocete cetaceans, e.g. northern bottlenose whale, striped dolphin, Atlantic white-sided dolphin, Risso's dolphin, killer whale, sperm whale.

Interest to Fisheries: Currently no fisheries are directed at this species, but its desirable size and consistency of flesh make it a good potential resource. It is possible that estimates of huge population size and biomass of ***G fabricii*** might also involve a component of ***G steenstrupi***.

Local Names: None.

Remarks: ***Gonatus steenstrupi*** was confused with ***G fabricii*** for decades until it was recognized and separated by Kristensen in 1981. While the distributions of the 2 species overlap considerably, ***G steenstrupi*** occurs slightly more southerly into Bay of Biscay and beyond in offshore waters and around Newfoundland and into the Gulf of St. Lawrence. ***Gonatus fabricii*** extends much further north into high Arctic waters.

Literature: Kristensen (1981), Falcon *et al.* (2000).

Berryteuthis Naef, 1921

Berryteuthis Naef, 1921a, *Mitteilungenaus der Zoologischen Stazion zu Neapel*, (22)16: 527–542 [535].

Type Species: *Berryteuthis magister* (Berry, 1913a).

Frequent Synonyms: *Pfefferiopsis* Ishikawa, 1924; *Berryiteuthis* Grimpe, 1922; *Berryiteuthis* Thiele, 1934.

Diagnostic Features: Tentacular club with suckers only, no hooks; suckers in central part of manus are notably larger than marginal suckers. Fixing apparatus on club consists of suckers and knob-like tubercles, without transverse ridges and grooves. One ventral arm of adult male bears modified suckers, which may serve to transfer spermatophores to female. Radula with 7 longitudinal rows of teeth. Mantle and body firm, muscular. Fins large, rhomboidal, do not extend to posterior end of mantle as a tail; fin length 54 to 56% and fin width 64 to 80% of mantle length.

Remarks: ***Berryteuthis magister*** is the object of a major fishery, the only directed fishery for the Gonatidae, versus those species caught as by catch. Consequently, a large body of research and publications exists for this species.

Literature: Okutani *et al.* (1988), Okutani and Kubodera (1987), Katugin (2004), Kubodera *et al.* (2006a).

Berryteuthis magister (Berry, 1913)

Fig. 233

Gonatus magister Berry, 1913a, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 65: 72–77. [76]. [Type locality: Puget Sound, Washington, Northeast Pacific Ocean].

Frequent Synonyms: *Gonatus magister* Berry, 1913a; *G. septemdentatus* Sasaki, 1915a.

FAO Names: En – Schoolmaster gonate squid; **Fr** – Encornet suçoir; **Sp** – Gonalura magister.

Diagnostic Features: Mantle large, robust, muscular, mantle width 35 to 37% of mantle length. Fins large, rhomboidal, broadly sagittate, thick, straight anterior and posterior margins, relatively long (length up to 55% of mantle length) and broad (width 70 to 80% of mantle length). **Tentacles strong, long** when extended in dead animal, 120 to 160% of mantle length; in live animal they are usually as long as the arms; **tentacular clubs expanded, long, with no hooks but with extremely numerous, long-stemmed minute suckers, that occur in 20 or more transverse series; suckers in central part of manus noticeably larger than others**. Club sucker rings with 20 to 22 sharp teeth. No obvious boundary exists between manus and carpal region, except that the number of transverse series of suckers and sucker size tend to decrease proximally. Arms relatively long, 62 to 67% of mantle length, formula III = II, I, IV. Arms I to III with well-developed hooks in the medial 2 series that emerge at about 75 mm mantle length; hooks in adults occupy all but the distal part of the arms; sucker-hook series number 50 to 55. Arms IV have 4 series of suckers arranged in 60 transverse series. Arm sucker rings with 11 to 18 sharp teeth along distal margin. One ventral arm is modified in males into a hectocotylus-like structure. Seven rows of teeth on radula.

Size: The maximum mantle length of this species is reported to be 430 mm, while its weight can reach to 2.6 kg; normally, however, mantle length is up to 340 mm.

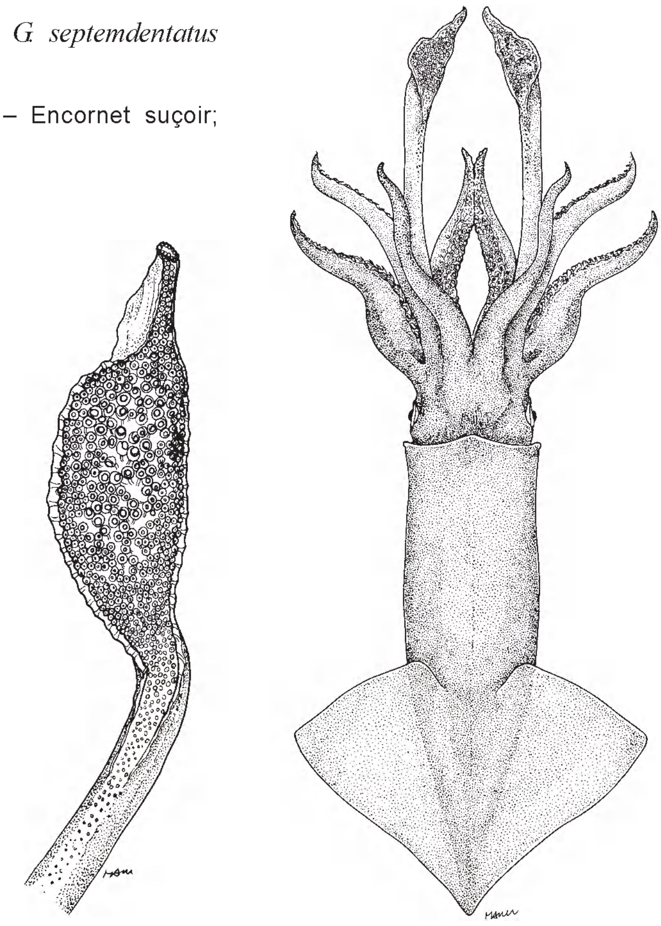

tentacular club dorsal view

Fig. 233 ***Berryteuthis magister***

Geographical Distribution: ***Berryteuthis magister*** is a conspicuous inhabitant of the North Pacific Ocean. It is panboreal and it occurs in the Japan, Okhotsk and Bering seas, along the Kuril, Commander and Aleutian islands, then southward in the eastern North Pacific Ocean as far south as central or southern California waters (Fig. 234).

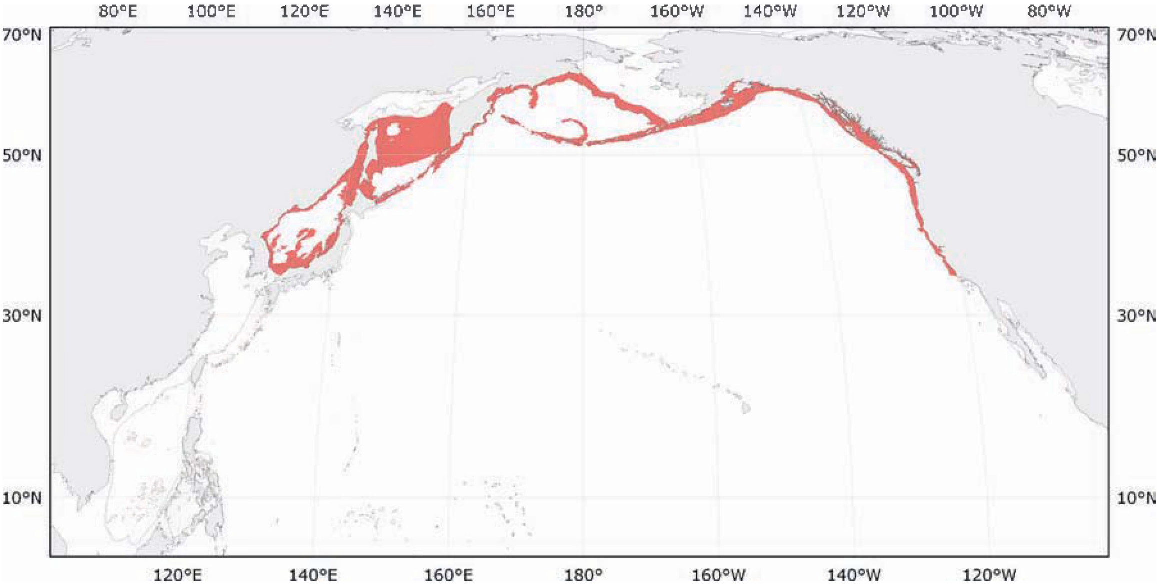


Fig. 234 ***Berryteuthis magister***

🟥 Known distribution

Habitat and Biology: A demersal oceanic pelagic species, ***B. magister*** is recorded from the surface to about 1 500 m depth, but its greatest abundance is near the bottom on the continental slope and in the mesopelagic zone. In the epipelagic zone it occurs occasionally and is much less abundant than most other species of gonatids in the North Pacific Ocean. In spite of extremely high abundance of adults of this species throughout the North Pacific rim, newly hatched/paralarval ***B. magister*** had been reported only once, from about 400 m deep in the Strait of Georgia. Recently, paralarvae have been reported to be common in the epipelagic zone of the slope region of the Gulf of Alaska, where hatchlings with internal yolk sacs were captured at 0 to 200 m in Bongo tows during March. Juveniles with mantle length ranging from 40 to 120 mm regularly occur near the bottom at depths 300 to 450 m in the Bering Sea, and may occur in epi- and mesopelagic waters. However, diel vertical migrations of young ***B. magister*** are much less extensive than, e.g. in ***Gonatopsis borealis***, and even at night, juvenile ***B. magister*** are rarely found in the upper epipelagic waters. Finally, immature squid descend to the benthic habitat where they aggregate and concentrate during the day; at night they disperse into the near-bottom waters, and occasionally into the mesopelagic zone to feed. Because of the extensive geographical range of ***B. magister***, spawning can occur at various locations throughout the year. Aggregations of males and females begin to increase intensely as spawning time approaches. Mating takes place immediately prior to spawning, with only mature stage V females being mated. Penis in ***B. magister*** is rather short, and does not show up out of the mantle edge in mature male; we may suggest that in the absence of distensible penis male uses a modified ventral arm (hectocotylus) to transfer spermatophores into the mantle cavity of the female, where they are attached most frequently to the mantle wall adjacent to the openings of the oviducal glands, or occasionally onto the midgut gland or the gills. Judging from the number of implanted sperm bulbs, most females copulate 2 times, rarely 1 or 3 times. In the Bering Sea, females produce 20 000 to 96 000 eggs (40 000 eggs, on the average), while males produce up to 700 to 1 000 spermatophores in total. In the Japan Sea, where squid are much smaller and produce larger eggs, individual fecundity is only about 4 000 eggs. The incubation period is thought to last for about 6 months. Spawning occurs on the bottom presumably at 400 to 1 000 m, depending on locality. The age estimates for ***B. magister*** vary, depending on aging technique and locality, but most recent analyses favour a 2-year life cycle. The analyses of growth using statoliths and gladii suggest that the 2-year life cycle of ***B. magister*** in the western Bering Sea includes 6 months of embryonic development and 18 months of post-embryonic growth. Several different seasonal groups may exist within a geographic location, apparently related to several spawning events during a year, or different places of origin. Juvenile and maturing squid feed voraciously during their pelagic phases, with younger forms eating euphausiids, hyperiid amphipods and small mesopelagic shrimps, while larger individuals switch to fishes and squids. Cannibalism is common in ***B. magister*** of all sizes and large quantities of squids are consumed, mostly conspecifics. During this feeding phase, the digestive gland ("liver") becomes enormous, up to 25 to 40% of total wet body weight, with enough reserves to supply all energetic needs during final maturation and spawning. During this final benthic stage, feeding activity is very low, then ceases in 92% of mature males and 100% of mature females. The number and variety of predators is enormous and includes, but is not limited to, the following: fishes (walleye pollock, Pacific cod, chinook, chum, coho, pink and sockeye salmon, Pacific pomfret, Greenland turbot, Pacific halibut, sablefish, various grenadiers, liparids, blacksmelts, rockfishes); odontocete cetaceans (Baird's beaked whale, short-finned pilot whale, Dall's porpoise, sperm whale, false killer whale); northern fur seal, thick-billed murre, albatrosses and ***Berryteuthis magister*** itself.

Interest to Fisheries: ***Berryteuthis magister*** is the only species of gonatid squid fished in commercial quantities in the Pacific Ocean and adjacent seas; consequently it has been intensively studied. The commercial fishery production of ***B. magister*** is supported by enormous populations throughout much of its range, but determining actual biomass, either by region or in total, is difficult. Nonetheless, a summary of biomass calculations from different areas (some with different techniques) totals 677 000 tonnes. Of course, annual fluctuations are the norm in squid populations, so this value cannot be used to validate quota expectations. The Russian fishery began in the 1960s off the Commander Islands as by catch in the walleye pollock bottom trawl fishery. By the 1970s and 1980s the fishery included species-directed trawling and was greatly expanded to the northern Kuril Islands and into the Bering Sea, then into the Japan Sea. The total catch of the Russian fishery in 1985 reached approximately 65 700 tonnes; production plummeted in 1986 to 13 000 tonnes, and through the 1990s did not exceed 20 000 tonnes. Russian estimates for a sustainable annual fishery in the western Bering Sea, northwestern Pacific Ocean off the Kuril Islands and in the Russian Exclusive Economic Zone of the Japan Sea, Kita-Yamato Bank, total up to 98 000 tonnes. FAO fisheries statistics report about 49 000 tonnes landed in 2007, for this species. The unique biological features among all gonatid species make ***B. magister*** the best candidate for a significant, sustained fishery: it aggregates on the bottom in the adult stage, following a relatively early-stage ontogenetic descent; it spawns on the bottom; it does not become gelatinous in maturing and spawning stages, consequently, it is accessible to benthic trawling. The meat is judged tasty and it contains high levels of beneficial proteins. Finally, potential is developing for use of the species for valuable biologically active compounds and pharmaceutical preparations, especially from the gonads, digestive gland and optic ganglia.

Local Names: JAPAN: Dosuika; RUSSIA: Commander squid; USA: Commander armhook squid, Red squid.

Remarks: Genetic studies (allozymes using starch and polyacrylamide gel electrophoresis) have shown that differentiation occurs among populations of ***Berryteuthis magister*** from 3 different geographical regions: the Japan Sea, the northwestern Pacific Ocean (including Okhotsk and Bering seas), and the Gulf of Alaska. Genetic differences detected were both temporal and spatial. Subsequently, the form from the Japan Sea has been designated a subspecies of ***B. magister, B. m. shevtsovi*** (see below). In waters around Japan, a subspecies, ***B. m. nipponensis***, has been distinguished based on such external characters as small mantle opening, small fin and less pronounced differences in size between central and marginal club suckers. The more muscular body of this extremely rare form suggests that it is more powerful swimmer than the typical ***B. magister***, whose representatives are quasi-benthic the greater part of their lives.

Literature: Okutani *et al.* (1988), Nesis (1995), Arkhipkin *et al.* (1998a), Katugin (1999, 2000a, 2002), Arkhipkin (2003b), Starovoytov *et al.* (2004), Katugin and Shevtsov (2006), Jorgensen (2007).

Berryteuthis anonychus (Pearcy and Voss, 1963)

Fig. 235

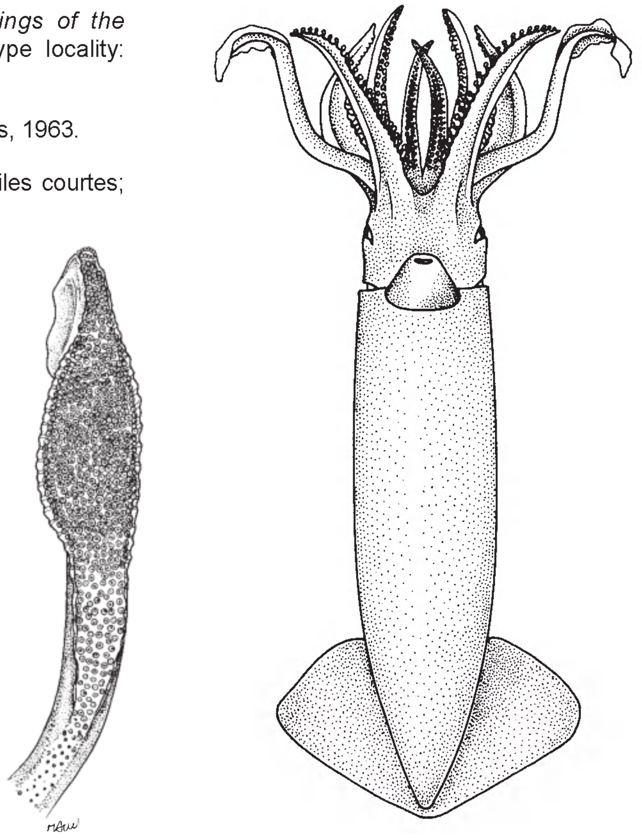
Gonatus anonychus Pearcy and Voss, 1963, *Proceedings of the Biological Society of Washington*, 76: l05–112 [105]. [Type locality: 45°26.8'N, 125°08.1'W, Northeast Pacific Ocean].

Frequent Synonyms: *Gonatus anonychus* Pearcy and Voss, 1963.

FAO Names: En – Smallfin gonate squid; **Fr** – Encornet ailes courtes; **Sp** – Gonalura alicorta.

Diagnostic Features: Mantle muscular, elongate, narrow, with a deep funnel depression on the ventral edge of mantle between the locking cartilages. Fins small, oval, extend to posterior end of mantle in a short gelatinous tail; fins short (length 22 to 27% of mantle length); **narrow** (width 49 to 55% of mantle length). **Tentacular clubs narrow and long** (about one-half of tentacle length), **with numerous minute almost equal-sized suckers in 12 to 15 transverse series**; no hooks. Club sucker rings with 3 or 4 teeth. Arms with 4 transverse series of suckers and very few (about 6 to 8) small hooks in the medial 2 series on the basal part of arms I to III in maturing and mature females; no hooks in males. Radula with 7 longitudinal rows of teeth.

Size: This species attains a maximum mantle length of possibly 150 mm.



tentacular club **ventral view**

Fig. 235 ***Berryteuthis anonychus***

Geographical Distribution: ***Berryteuthis anonychus*** is widely distributed in the North Pacific Ocean, from the Kuril Islands and southeastern Okhotsk Sea to the east, encompassing the Aleutian Islands, the southern Bering Sea and the Gulf of Alaska southward to Oregon (Fig. 236).

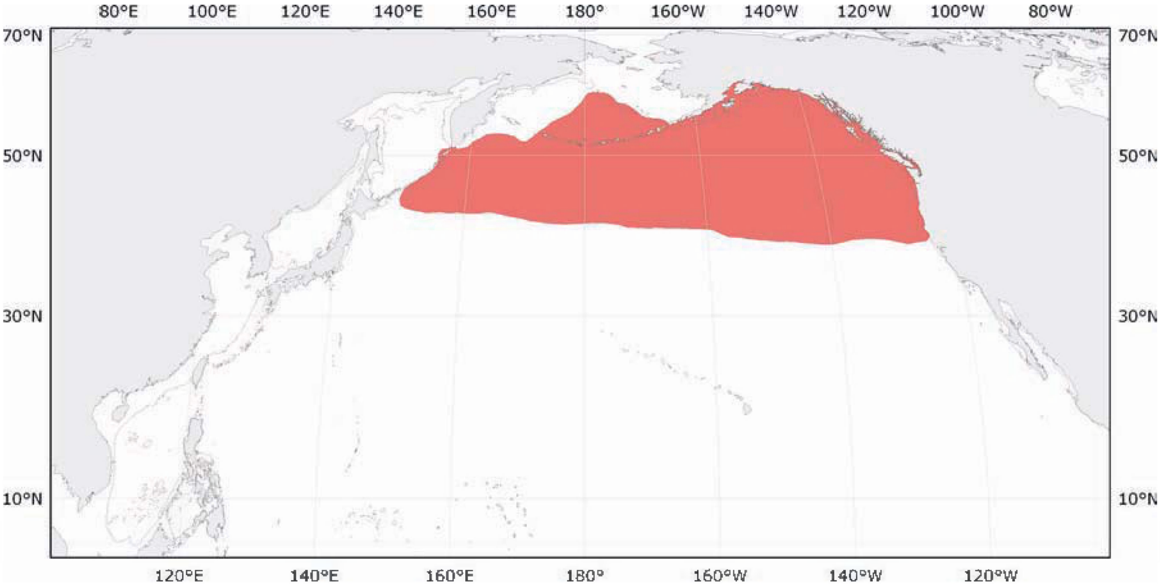


Fig. 236 ***Berryteuthis anonychus***

🟥 Known distribution

Habitat and Biology: ***Berryteuthis anonychus*** is a low-boreal distant-neritic species that occurs from the surface at night to about 1 500 m deep in offshore waters. The exact distribution pattern is unknown. It is most abundant in the Gulf of Alaska and the open sub-Arctic domain to the south and southwest of the Gulf. It is rare south of Oregon and to southern Baja California. The species occurs in open ocean over great depths, but it is most common over the slopes and seamounts, e.g. Eikelberg Ridge, and seamounts Warwich, Miller and Morton. Juveniles are gregarious and broadly dispersed over the northern Pacific Ocean and the southern Bering Sea. While specimens have been reported as deep as 1 000 to 1 500 m, most adults actually are captured in the epipelagic zone, 0 to 200 m; they are concentrated mostly over the seamounts and slopes. No gelatinous degeneration seems to occur at maturity, which begins at 70 to 90 mm mantle length, i.e. at 80 to 90 mm in females and 70 to 80 mm in males. Spawning occurs year-round, with peaks in February to April and again in late June to September; life span is approximately 1 year. The species is a first-order diel vertical migrator in the epipelagic zone; it occurs at 50 to 200 m during the day and at night it ascends to 150 m to the surface. Squids aggregate in areas of oceanic rings (eddies) and vortices where high concentrations of medium- and large-sized zooplankton occur. Food consists mainly of copepods, hyperiid amphipods, pteropods, chaetognaths, and euphausiids. This macroplanktophagous squid in turn is preyed upon by many species of fishes (pomfret, salmonids (pink, coho, chum, sockeye), albacore, lancetfish; neon squid (***Ommastrephes bartramii***); seabirds (murre, short-tailed shearwater, albatross); marine mammals (northern fur seal, fin whale, Dall's porpoise and other odontocete whales).

Interest to Fisheries: Currently the status of any potential fishery is undetermined. However, the firm consistency of the flesh, the convenient size of the species and its dense aggregations in certain oceanic areas seem to indicate a potentially appropriate target species for a fishery.

Local Names: JAPAN: Hime-Dosuika; USA: No-hook armhook squid.

Literature: Pearcy and Voss (1963), Katugin *et al.* (2002), Bower *et al.* (2002), Katugin (2004), Katugin *et al.* (2005), Shimura *et al.* (2006), Jorgensen (2007).

Gonatopsis Sasaki, 1920

Gonatopsis Sasaki, 1920, *Proceedings of the United States National Museum*, 57: 163–203 [198].

Type Species: *Gonatopsis octopedatus* Sasaki, 1920.

Frequent Synonyms: None.

Diagnostic Features: Tentacles absent in individuals larger than juveniles of about 30 mm mantle length. Juveniles smaller than 30 mm mantle length possess small rod-like tentacles about the same size as arms IV; (in ***Gonatopsis borealis*** tentacles disappear at 9 to 20 mm mantle length). **Radula with 5 or 7 longitudinal rows of teeth**. Mantle muscular, becomes flabby, gelatinous in mature and spent females; ***G borealis*** does not degenerate at maturation. Fins heart-shaped with a posterior short or long tail supported by cartilaginous rod, except in ***G borealis***.

Remarks: In 1971, Nesis divided the genus ***Gonatopsis*** into 2 subgenera. ***Boreoteuthis***, with 7 longitudinal rows of teeth on the radula (***Gonatopsis borealis***), and ***Gonatopsis** sensu stricto*, with 5 longitudinal rows of teeth on the radula (***Gonatopsis octopedatus*** and ***G japonicus***). A new species (***Gonatopsis okutanii***) was assigned to ***Gonatopsis** sensu stricto*, since it possessed a 5-rowed radula (Nesis, 1972). In 1973, Nesis suggested that ***Gonatopsis makko*** belongs to the subgenus ***Boreoteuthis***; however, the type specimens from sperm whale stomachs lacked radulas, and it was impossible to determine whether they had 5 or 7 longitudinal rows of teeth (Okutani and Nemoto, 1964). In 1978, Okutani and Satake, based on personal information from Okiyama, reported that ***G makko*** has a 5-toothed radula. Confusion about the systematic status of ***G makko*** remains. In 1997, in one of the latest reviews on the Gonatidae, Nesis used this name as a junior synonym to ***Gonatopsis japonicus***. Recent studies using genetic analyses suggested that ***Boreoteuthis***, which comprises 8-armed gonatids with a 7-toothed radula, might be elevated from subgenus to genus level. However, at the present state of knowledge, and to maintain stability of the generally accepted classification, ***Boreoteuthis*** remains a subgenus in this Catalogue.

Literature: Okiyama (1969, 1970), Kubodera and Jefferts (1984a,b), Shevtsov and Bessmertnaya (1996), Lindgren *et al.* (2005), Kubodera *et al.* (2006c).

Gonatopsis octopedatus Sasaki, 1920

Fig. 237

Gonatopsis octopedatus Sasaki, 1920, *Proceedings of the United States National Museum*, 57: 163–203 [198]. [Type locality: 48°22'30"N, 145°43'30"E, near Cape Patience, Sakhalin, Okhotsk Sea].

Frequent Synonyms: None.

FAO Names: En – Eight-armed gonate squid; **Fr** – Gonaleutène huit-bras; **Sp** – Gonalura ocho-brazos.

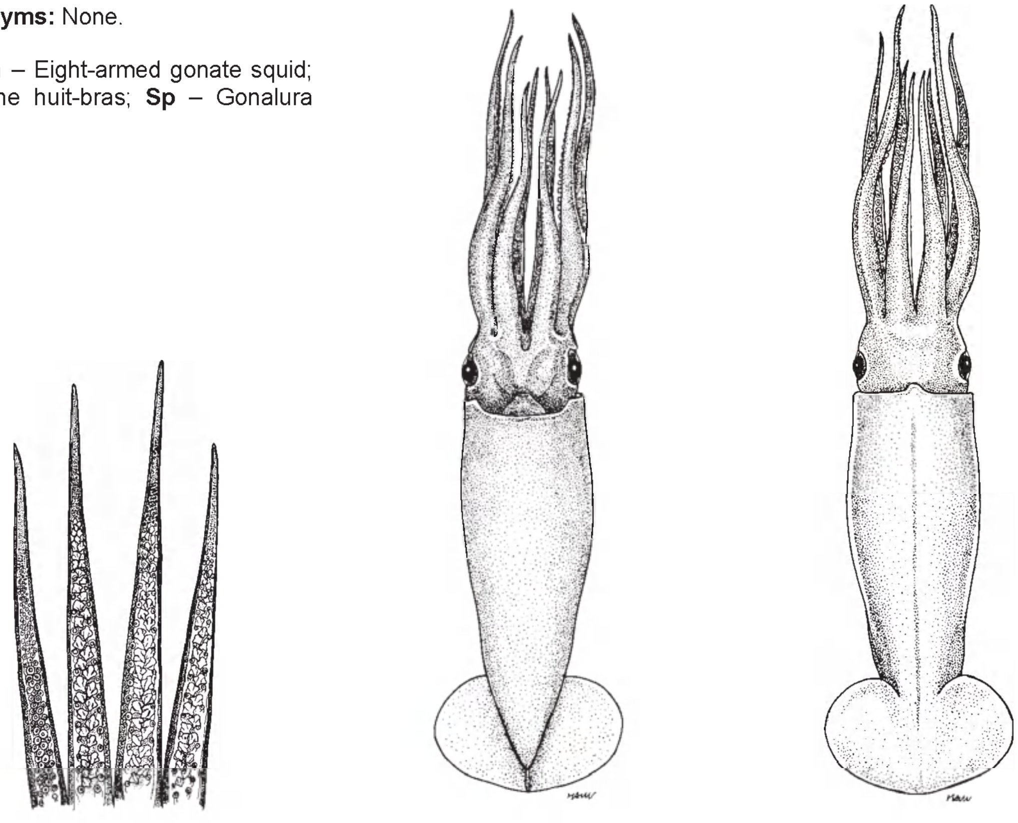

arms ventral view dorsal view

Fig. 237 ***Gonatopsis octopedatus***

Diagnostic Features: See generic section.

Size: Small-sized species that attains a maximum mantle length of 175 mm.

Geographical Distribution: This species occurs in the western North Pacific Ocean (from northeastern Honshu, along the Kuril Islands and Kamchatka), in the Japan Sea, Okhotsk Sea, and central western Bering Sea (Fig. 238).

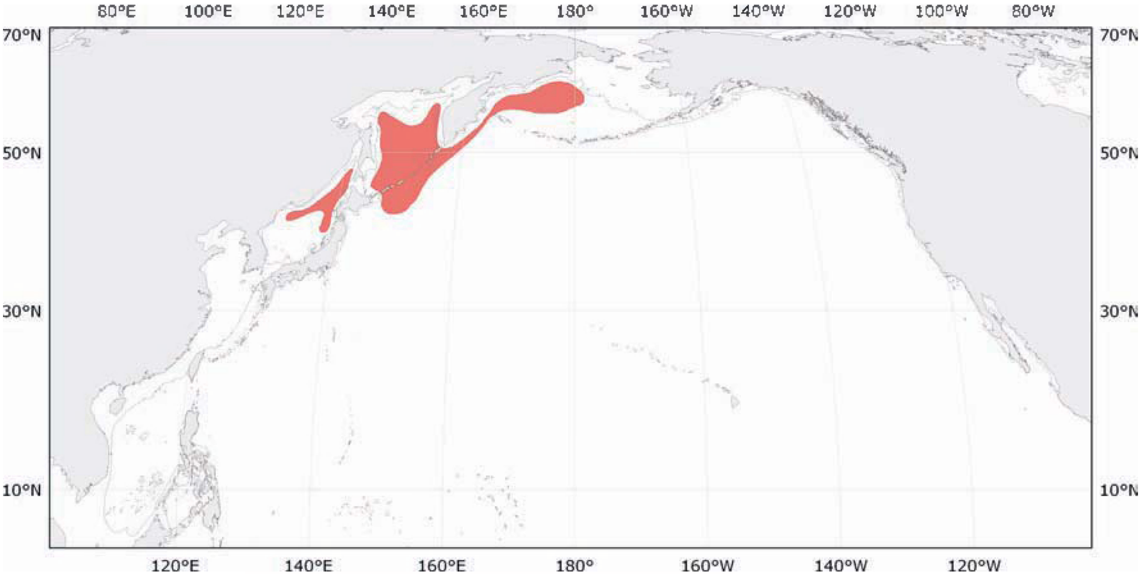


Fig. 238 ***Gonatopsis octopedatus***

🟥 Known distribution

Habitat and Biology: ***Gonatopsis octopedatus*** is a common species that at various times occupies epi-, meso- and bathypelagic zones and descends close to the bottom on the slope. It occurs over a very broad depth range from the surface to 2 000 m. In the Okhotsk and western Bering Sea, the species abundance increases with depth. In the northwestern Japan Sea in winter and spring, it is the most commonly occurring cephalopod species in the pelagic zone down to 1 000 m. Spawning occurs in deep water. This species is known to have the largest ripe eggs among all gonatids, up to 6.5 mm in diameter. Consequently, the individual fecundity is very low, and ranges from 297 to 414 oocytes. Post-paralarvae and juvenile squid occur in the epipelagic zone and conduct diel vertical migrations. Ontogenetic descent occurs early in the life cycle. Maturation starts at about 100 mm mantle length in deep layers, where maturing animals become very gelatinous.

Interest to Fisheries: This species is found in large quantities in the mesopelagic layers over deep-water basins and slope in the Japan and Okhotsk seas, and plays a significant role in trophic structure of local deep-water pelagic communities. However, small size and weak consistency of flesh does not make it a good potential resource for fishery.

Local Names: JAPAN: Tenaga-Takoika.

Remarks: Very large senescent individuals of up to 390 mm mantle length from the Okhotsk Sea, identified as ***Gonatopsis octopedatus***, were most likely another gonatid species (Nesis, 1993a); incorrect species identifications of mature and post-spawning gelatinous gonatids frequently occur due to significant degeneration of their tissues, tentacle autotomy, and significant body damage in trawl nets (loss of fins, arm armature, arm tips and entire arms, breaking into separate pieces, etc.).

Literature: Kubodera and Jefferts (1984b), Okutani *et al.* (1988), Nesis and Nikitina (1996), Katugin (2004), Shevtsov and Mokrin (1998), Hochberg (2006), Katugin and Shevtsov (2006).

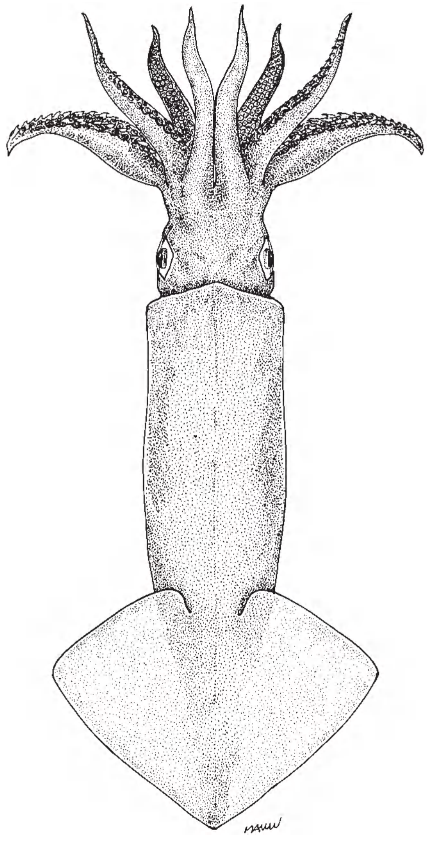
Gonatopsis borealis Sasaki, 1923

Fig. 239

Gonatopsis borealis Sasaki, 1923, *Annotationes Zoologicae Japonenses*, 10: 203–207 [203]. [Type locality: Kushiro, Nemuro, Tokachi; all on eastern Hokkaido, Japan].

Frequent Synonyms: None.

FAO Names: En – Boreopacific gonate squid; **Fr** – Encornet boréopacifique; **Sp** – Gonalura pacificoboreal.



dorsal view

Fig. 239 ***Gonatopsis borealis***

Diagnostic Features: Mantle stout (width 25% of mantle length), thick, muscular; reddish purple coloration. **Fins muscular, relatively short** (40 to 45% of mantle length) and broad (65 to 80% of mantle length), **not attenuate into tail** posteriorly. **Tentacles absent** (present only in larvae and disappear at 12 to 15 mm mantle length). **Arms robust, muscular, short**; length 40 to 50% of mantle length; arms I to III with 2 medial series of hooks and 2 marginal series of suckers; **arm IV with 4 series of suckers, no hooks**. Hooks develop on arms at 35 to 45 mm mantle length. **Radula with 7 rows of teeth**.

Size: The maximum mantle length of this species attains 280 mm in males and 300 mm in females.

Geographical Distribution: ***Gonatopsis borealis*** inhabits the northern Pacific Ocean. It is a panboreal species from northern Japan (37°N to 40°N) throughout the Okhotsk Sea, Bering Sea slope waters, along the Aleutian Islands and Gulf of Alaska, and southward to California, even to Baja California (20°N) (Fig. 240).

Habitat and Biology: An oceanic species, ***G borealis*** is one of the most abundant and widely distributed gonatid species. It occurs in cold temperate waters, where it is extremely eurybathic: it ranges from the surface to mesopelagic depths and even into the bathypelagic zone. It is known to undertake diel vertical migrations and to form increasingly large aggregations between April and early autumn, particularly in the eastern and western parts of the North Pacific Ocean. This species may account for up to 68% of squid catches in the Okhotsk Sea in summer. Biomass estimates reach 278 000 tonnes in the Okhotsk Sea (up to 0.5 million tonnes according to some estimates), 209 000 tonnes in the western Bering Sea, 285 000 tonnes along the western Kamchatka slopes and 100 000 tonnes off the Kuril Islands. ***Gonatopsis borealis*** occurs in epipelagic, mesopelagic and bathypelagic depths from the surface to 1 500 m and is benthic at 200 to 1 375 m, but it is much more abundant in the midwater realm (captured in 95% of midwater tows versus 19% of benthic trawl tows). Maximum abundance occurs at 300 to 500 m, while only single specimens are caught below 1 000 m (consequently probably were caught in much shallower depth while the open nets were hauled back through the zone of abundance). The very pronounced diel vertical migrations involve

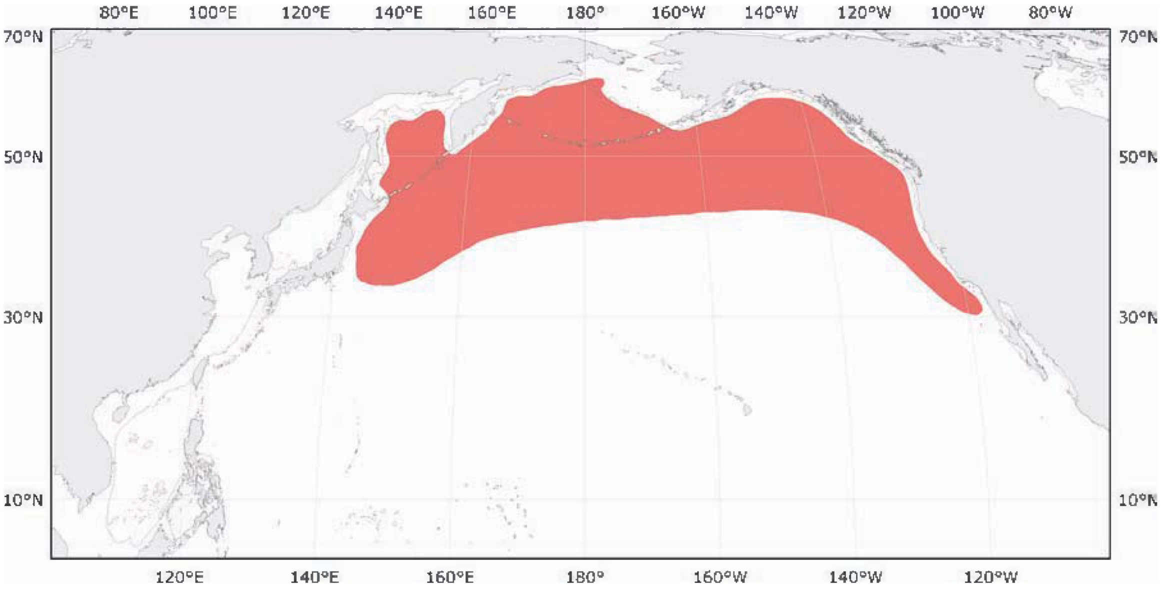


Fig. 240 ***Gonatopsis borealis***

🟥 Known distribution

both adults and young. For example, off California, no specimens occurred during daytime in less than 300 m, even 16 mm mantle length juveniles; 90% of daytime captures were at 400 to 700 m. At night, specimens occurred principally at 100 to 500 m, mostly 300 to 400 m. In the upper epipelagic western Bering Sea in autumn, ***G borealis*** was the most numerous cephalopod species and occurred in 27% of the hauls (in 44% hauls over deep Commander Basin) exclusively during night hours; it appeared that smaller individuals migrated to the surface layers and descended to deeper layers earlier than larger animals, showing possible behavioural adaptation that helps smaller squid to avoid the presence of larger cannibalistic relatives. ***Gonatopsis borealis*** preys on a great variety of pelagic crustaceans (euphausiids, hyperiid amphipods, copepods), fishes (mostly myctophids) and squids. The life span is presumably 1 year or slightly longer. Predators include fishes (e.g. salmonids, walleye pollock, pomfret, albacore, grenadiers); squids (***Berryteuthis magister, G borealis***); seabirds (murres); seals, sea lions, dolphins, toothed whales (sperm, pilot, etc).

Interest to Fisheries: ***Gonatopsis borealis*** (mostly representatives of the large-sized cohort) is captured as bycatch with jigs and in substantial numbers in drift gillnets set for salmonids and the neon squid, ***Ommastrephes bartramii***. It is believed to have some significant fishery potential because of its massive abundance and the consistency of its flesh. Its meat is delicious. However, its role as principal prey for dozens of commercially valuable fishes perhaps is more important at this juncture than a heavily developed fishery.

Local Names: JAPAN: Takoika.

Remarks: In the northwestern Pacific Ocean, 2 populations occur, 1 more northerly, maturing at small size (less than 180 mm mantle length); another one to the south of 45°N to 47°N, maturing at large size (larger than 220 mm mantle length). These populations or size cohorts occur sympatrically along the Kuril Islands.

Literature: Nesis (1972b), Kubodera and Jefferts (1984a, b), Okutani *et al.* (1988), Nesis and Nezlin (1993), Bower and Takagi (2004), Katugin (2004), Shevtsov *et al.* (2004b), Katugin and Zuev (2007), Jorgensen (2007).

Gonatopsis japonicus Okiyama, 1969

Fig. 241

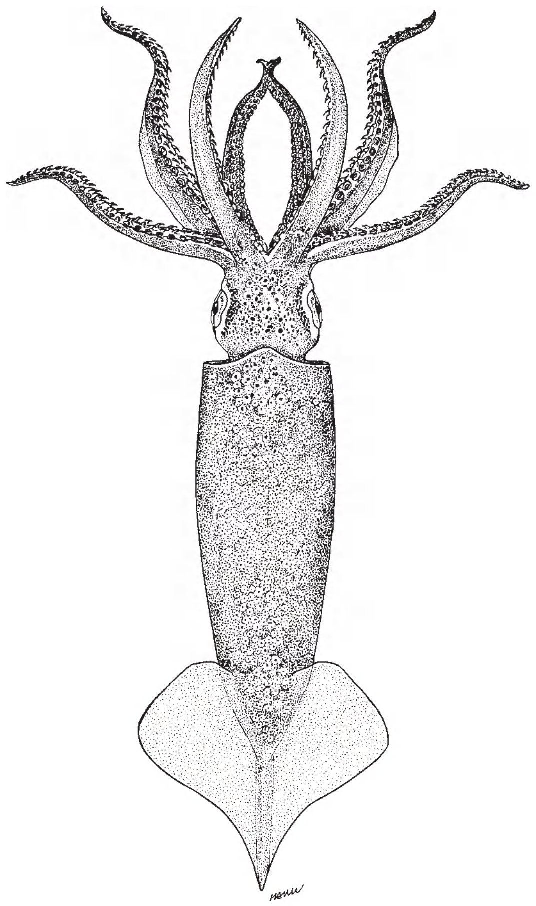
Gonatopsis japonicus Okiyama, 1969, *Publications of the Seto Marine Biological Laboratory*, (17)1: 19–32. [20]. [Type locality: 41°02'N, 138°11'E, Northwest Pacific Ocean].

Frequent Synonyms: *Gonatopsis makko* (Okutani and Nemoto, 1964), in part.

FAO Names: En – Japanese gonate squid; **Fr** – Gonaleutène japonais; **Sp** – Gonalura japonés.

Diagnostic Features: Mantle slender, muscular, fins relatively large and narrow; fin length slightly longer than width, about one-half mantle length. **Tail long, attenuate**, about one-half fin length. Head large, broader than mantle opening. Funnel relatively small, dorsal funnel organ inverted V-shaped. Funnel cartilage lanceolate and slightly curved inward. **Radula with 5 teeth per row**. Arms robust, subequal, the longest about 55% of mantle length. Hooks on arm I-III well developed, 57 to 61 in number. **Tentacles absent in adults**.

Size: The maximum mantle length of this very large gonatid species extends to 620 mm.



dorsal view

Fig. 241 ***Gonatopsis japonicus***

Geographical Distribution: ***Gonatopsis japonicus*** is a northern North Pacific Ocean species that is distributed off eastern Honshu, Japan, in the Japan Sea, in the Okhotsk Sea and along the Kuril Chain north to the central eastern Bering Sea (Fig. 242).

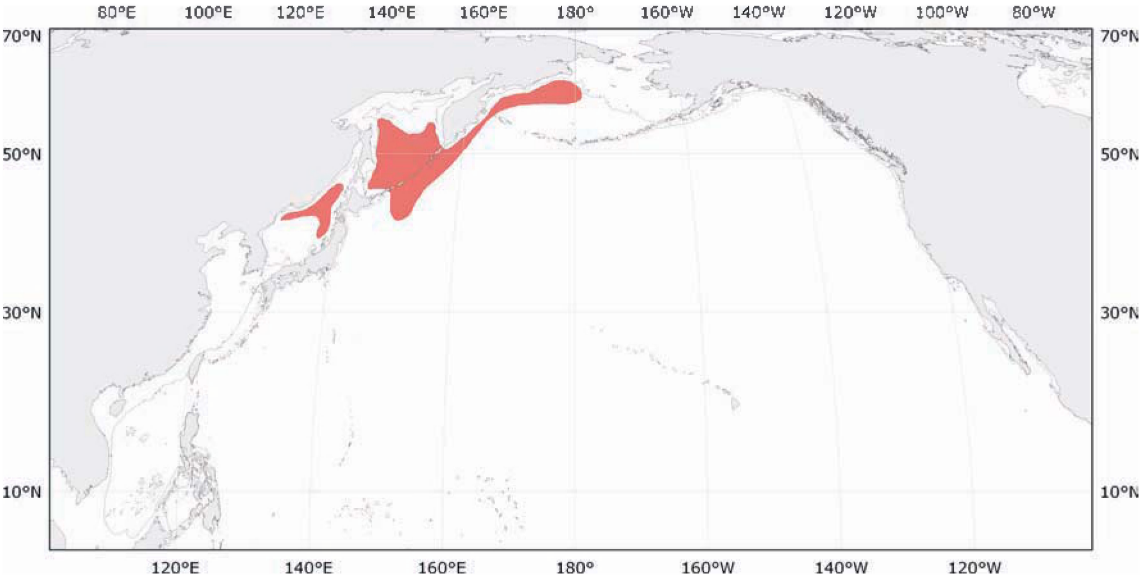


Fig. 242 ***Gonatopsis japonicus***

🟥 Known distribution

Habitat and Biology: This is a panboreal species. It occurs from the epipelagic and down into the meso- and bathypelagic zones, having been captured at pelagic depths from the surface to 1 000 m and on the bottom at 400 to 2 000 m. In the Japan Sea, ***G japonicus*** was most common in the upper 140 m, and its occurrence decreased rapidly with depth. Regular occurrence of juveniles and immature adults in the upper layers suggests that the species is active vertical migrant, and that ontogenetic descend occurs rather late in the life cycle. Most animals captured to date were immature, or at the onset of maturation. In the meso- and bathypelagic Okhotsk Sea, mature and pre-spawning males had mantle lengths from 278 to 478 mm, and immature and maturing females from 398 to 582 mm; the largest animal with mantle length of 620 mm was not dissected. Muscle tissues become gelatinous in mature individuals.

Interest to Fisheries: This species is found in large quantities in the pelagic layers over deep-water basins and slope in the Japan and Okhotsk seas, and plays a significant role in trophic structure of local pelagic communities. Rather weak consistency of flesh, especially in mature animals, does not make it a good potential resource for fishery.

Local Names: JAPAN: Nippon-Takoika.

Remarks: ***Gonatopsis japonicus*** is frequently confused with ***Gonatopsis makko***, particularly, animals from the Japan and Okhotsk seas, mentioned under the name ***G. makko***, belong to ***G japonicus*** (see Remarks for ***Gonatopsis makko***).

Literature: Okutani *et al.* (1988), Okutani *et al.* (1995), Shevtsov and Mokrin (1998), Lindgren *et al.* (2005), Katugin and Shevtsov (2006), Kubodera (2006a), Katugin *et al.* (2008).

Gonatopsis makko Okutani and Nemoto, 1964

Fig. 243

Gonatopsis makko Okutani and Nemoto, 1964, *Scientific Reports of the Whales Research Institute*, Tokyo, 18: 111–121 [113]. [Type locality: from sperm whale stomach, Southern Bering Sea].

Frequent Synonyms: None.

Misidentifations: *Gonatopsis japonicus* Okiyama, 1969.

FAO Names: En – Makko gonate squid; **Fr** – Encornet mako; **Sp** – Gonalura mako.

Diagnostic Features: Mantle elongate, slender, conical, width about 20% of mantle length; **soft and flabby**. **Fins very small, short** (about 33% or less of mantle length); narrow (width from 45 to 50% of mantle length). **Tentacles absent in adults**. Arms I to III very long, robust, attenuate, up to 80% of mantle length. Arm hooks strong in medial 2 series; 2 series of marginal suckers. **Arms IV short, with 4 series of suckers, no hooks**.

Size: This species reaches a maximum mantle length of 350 mm, possibly larger.

Geographical Distribution: ***Gonatopsis makko*** occurs in the eastern North Pacific Ocean, from the northeastern coast of Honshu and the Japan Sea, along the Kuril Chain and eastward to the western Aleutian Islands (Fig. 244).

Habitat and Biology: An oceanic species, ***G makko*** occurs rather frequently in midwater layers and to the bottom (650 to 1 200 m) in the Japan Sea and the northern North Pacific Ocean. It is preyed upon extensively by sperm whales.

Interest to Fisheries: This species is occasionally captured in the mesopelagic zone in the Okhotsk Sea.

Local Names: JAPAN: Makko-Takoika.

Remarks: Some authors consider that ***Gonatopsis makko*** might be the adult of ***Gonatopsis japonicus*** (e.g. Nesis, 1997), but only those specimens from the Japan and Okhotsk Seas. The validity of the name has been questioned by some authors because the species was described based on 3 individuals from sperm whale stomachs; these animals were notably damaged, partly digested and lacked buccal masses with radulas. Therefore, real body proportions and consistency of type specimens could have changed in whale stomachs, and what is more important, it remains uncertain how many rows of radular teeth (5 or 7, a basic systematic character state in the gonatid squid) were in ***G makko*** type specimens.

Literature: Okutani *et al.* (1988), Nesis (1997), Kubodera (2006b).

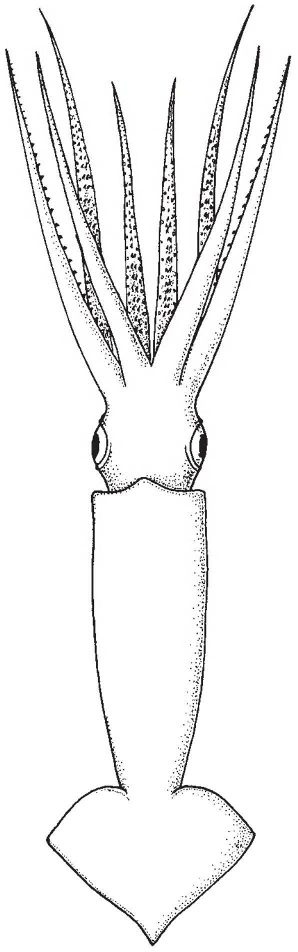


Fig. 243 ***Gonatopsis makko***

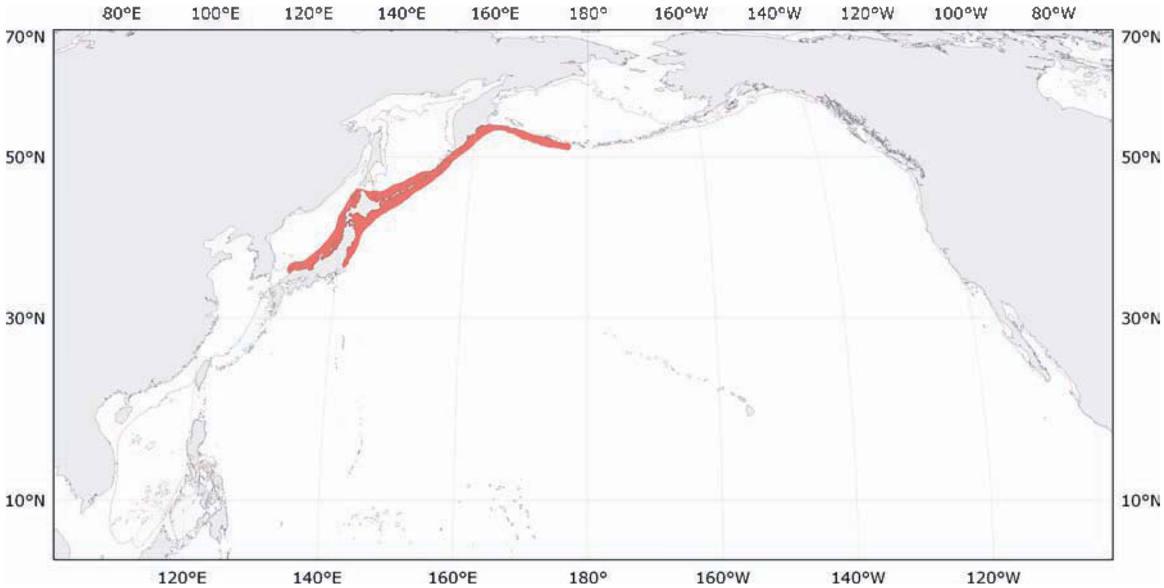


Fig. 244 ***Gonatopsis makko***

🟥 Known distribution

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Gonatus antarcticus Lönnberg, 1898

Gonatus antarcticus Lönnberg, 1898, *Svenska Expeditionen till Magellansländerna*, 2(4): 49–64 [51]. [Type locality: on the beach, Punta Arenas, Chile].

Frequent Synonyms: None.

Size: This species grows to a maximum mantle length of 350 mm.

Geographical Distribution: ***Gonatus antarcticus*** is a notalian circumpolar species in the Southern Hemisphere, reaching Antarctic waters (south of 40°S). It also is distributed around South Georgia and along the Scotia Arc, north to southernmost South Africa, the Cook Strait and Peru (possibly well north on Peru–Chile current).

Habitat and Biology: Paralarvae and juveniles of ***G antarcticus*** live in epipelagic and mesopelagic zones, adults in mesopelagic and bathypelagic zones. It is prey of numerous other species, e.g. white-chinned petrel, Magellanic penguin, king penguin, southern bottlenose whale, black-browed albatross, hake, rattail, southern elephant seal, Patagonian toothfish.

Literature: Okutani and Clarke (1992), Rodhouse *et al.* (1992a), Arkhipkin and Laptikhovsky (2006).

Gonatus berryi Naef, 1923

Gonatus berryi Naef, 1923, *Fauna e Flora de Golfo di Napoli, Monograph*, 35, 1(1) part 2: 149–863 [245]. [Type locality: Monterey Bay, California, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length is 190 mm.

Geographical Distribution: ***Gonatus berryi*** occurs in the North Pacific Ocean, from northern Honshu, eastern Hokkaido, the Bering Sea, through the Aleutian Island chain and the Gulf of Alaska and south to northern Baja California.

Habitat and Biology: A common panboreal meso-bathypelagic species, ***G berryi*** occurs at 400 to 700 m in daytime and at 100 to 700 m (mostly to 500 m) at night. Paralarvae and early juveniles are known from the upper layers in the central and northeastern Pacific Ocean. One specimen has been observed from a deep-diving submersible at 915 m. Diel vertical migrations are not characteristic for this species. ***Gonatus berryi*** undergoes ontogenetic descend to deep waters early in ontogeny. Hooks on arms and tentacular club are developed at very small size, of about 6 to 8 and 12 to 34 mm gladius length, respectively. Muscle tissues become gelatinous in mature individuals. This species is preyed upon by pomfret, swordfish, ***Ommastrephes bartramii***, Dall's porpoise, sperm whale, northern fur seal, and northern elephant seal.

Local Names: JAPAN: Berryi-Tekagiika.

Literature: Young (1972a), Kubodera and Jefferts (1984a, b), Katugin and Shevtsov (2006).

Gonatus californiensis Young, 1972

Gonatus californiensis Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [51]. [Type locality: 33°32'N, 118°24'W, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: This species attains a maximum mantle length of 120 mm.

Geographical Distribution: ***Gonatus californiensis*** seems limited to the eastern North Pacific Ocean from Vancouver Island, Canada, to Baja California, Mexico, and possibly to the Gulf of Panama.

Habitat and Biology: A muscular, low-boreal, pseudo-oceanic, meso-bathypelagic species. No paralarvae of this species have been recorded in the surface layers. A vertical shifter early in ontogeny, ***G californiensis*** may have a total depth range of 100 to 1 200 m with peak abundance at 400 to 700 m in daytime and dispersal to 100 to 500 m at night. This species has been recorded in the diet of sperm whale and beaked whale.

Local Names: JAPAN: California-Tekagiika

Literature: Young (1972a), Okutani *et al.* (1988), Okutani and Clarke (1992).

Gonatus onyx Young, 1972

Gonatus onyx Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [43]. [Type locality: 33°19'N, 118°45'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: ***Gonatus onyx*** reaches a maximum mantle length of 150 mm.

Geographical Distribution: ***Gonatus onyx*** is a North Pacific Ocean panboreal species that is distributed from southern Honshu, Japan, to the southern Okhotsk Sea and Bering Sea, the Aleutian Islands, and Gulf of Alaska, then southward to northern Baja California.

Habitat and Biology: This extremely abundant panboreal species is epipelagic in its paralarval and early juvenile stages, then it becomes mesopelagic to bathypelagic in adult stages. Egg incubation requires from 6 to 9 months. Its daytime distribution shows bimodal peaks at 400 and 800 m, and at nighttime it undergoes diel vertical migration to 100 to 500 m, mostly concentrated at 300 to 500 m. Egg-brooding females, holding egg masses in their arms, have been observed at depths between 1 250 and 2 522 m off California. Egg mass contains about 2 000 to 3 000 ovoid eggs, each 2 to 3 mm in length and 1.8 to 2.1 mm in width. Mantle length of hatchlings ranges from 3.2 to 3.5 mm. Predators include chinook salmon (our data), walleye pollock, pomfret lancetfish, Dall's porpoise, Cuvier's beaked whale.

Literature: Young (1972a), Kubodera and Jefferts (1984a,b), Seibel *et al*. (1997), Seibel *et al*. (2000a, 2005), Katugin and Shevtsov (2006), Jorgensen (2007).

Gonatus oregonensis Jefferts, 1985

Gonatus oregonensis Jefferts, 1985, Veliger, 28(2): 159–174 [167]. [Type locality: off Oregon, USA, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: This species reaches a maximum mantle length of 50 mm.

Geographical Distribution: ***Gonatus oregonensis*** occurs in the eastern North Pacific Ocean off Oregon, USA.

Habitat and Biology: It is confined to the California Current where it occurs shallower than 400 m at night.

Remarks: ***Gonatus oregonensis*** was described based on post-paralarval and juvenile individuals with mantle length ranging from 24 to 46 mm, and has not been recognized since its first description. In his review of the Gonatidae in 1997, Nesis suggested that it is very close to, and may represent a northern subspecies or a form of ***Gonatus californiensis***, from which ***G oregonensis*** is less easily separable (compared to other ***Gonatus*** spp.). Subtle differences between these 2 species are in fin dimensions, in sucker counts on the club and distribution of suckers on the dactylus.

Literature: Okutani *et al*. (1988), Okutani and Clarke (1992), Nesis (1997).

Gonatus pyros Young, 1972

Gonatus pyros Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [49]. [Type locality: 33°37'N, 118°26'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: ***Gonatus pyros*** grows to a maximum mantle length of 130 mm.

Geographical Distribution: ***Gonatus pyros*** is distributed in the eastern North Pacific Ocean from the Bering Sea, Aleutian Islands, and Gulf of Alaska southward to northern Baja California; it is also known from the western North Pacific Ocean off Japan and Kuril Islands.

Habitat and Biology: ***Gonatus pyros*** predominantly is a meso-bathypelagic species. Paralarvae and juveniles rarely occur in epipelagic zone. Juveniles occur by day deeper than 300 to 400 m, mostly at 300 to 700 m; at night they disperse to 100 to 700 m, mostly to 300 to 500 m. The species is a diel vertical migrator. Mature females have mantle length about 130 mm, and undergo gelatinous degeneration; mature eggs are ovoid, 3.0 x 1.7 mm in size. The descent to deep layers presumably begins early in ontogeny. This squid is preyed on by pomfret, salmon, northern fur seal, Dall's porpoise and sperm whale.

Literature: Young (1972a), Okutani *et al*. (1988), Nesis (1997), Katugin and Shevtsov (2006).

Gonatus ursabrunae Jefferts, 1985

Gonatus ursabrunae Jefferts, 1985, *Veliger*, 28(2): 159–174. [160]. [Type locality: South of Alaska Peninsula, Northeast Pacific Ocean].

Frequent Synonyms: None.

Size: Known only from paralarvae and juveniles; maximum reported mantle length 24 mm.

Geographical Distribution: ***Gonatus ursabrunae*** has a narrow distribution in the eastern North Pacific Ocean in the Bering Sea and the Gulf of Alaska; it is confined to the Alaskan gyre.

Remarks: ***Gonatus ursabrunae*** was described based on post-paralarval and juvenile individuals with mantle length ranging from 12 to 24 mm, and has not been recognized since its first description. In his review of the Gonatidae in 1997, Nesis suggested that it is either a species, as yet not recognized in adult stage, or a juvenile form of a known species, probably ***Gonatus kamtschaticus***, from which ***G. ursabrunae*** is separable by its mantle width index and the size at which club hooks develop.

Literature: Kubodera and Jefferts (1984a,b), Okutani *et al*. (1988), Nesis (1997).

Berryteuthis magister nipponensis Okutani and Kubodera, 1987

Berryteuthis magister nipponensis Okutani and Kubodera, *in* Okutani *et al*., 1987, *Cephalopods from Continental Shelf and Slope Around Japan*, 194 pp. [133]. [Type locality: Okirai Bay, Iwate, northeastern Honshu, Japan].

Frequent Synonyms: None.

Size: This subspecies has a reported maximum mangle length of 180 mm.

Geographical Distribution: ***Berryteuthis magister nipponensis*** is recorded only from around Japan: the Japan Sea, off eastern Honshu and southern Hokkaido.

Remarks: According to authors of the original description, this subspecies is distinguishable from the typical ***B. magister*** in having narrower mantle, somewhat smaller fin and less evident size differences between central and marginal club suckers. In addition, they mature at a considerably smaller size.

Literature: Okutani *et al*. (1987), Okutani and Clarke (1992), Katugin (2000a).

Berryteuthis magister shevtsovi Katugin, 2000

Berryteuthis magister shevtsovi Katugin, 2000a, *Veliger*, 43(1): 82–97 [91]. [Type locality: 42°30’N, 113°42’E, Japan Sea western Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length of fully mature females is 320 mm, that of fully mature males is 200 mm; however, smaller size are most common, i.e. 200 mm for females and 170 mm for males.

Geographical Distribution: ***Berryteuthis magister shevtsovi*** lives in the Japan Sea.

Habitat and Biology: This subspecies inhabits bathypelagic waters of very low temperatures. The total depth range for all maturity stages is 50 to 1 200 m, with the peak zone for adults at 300 to 500 m.

Remarks: This subspecies is differentiated on genetic, morphological, distributional, reproductive and ecological characteristics. (See ***B. magister*** section for additional information).

Literature: Katugin (2000a).

Eogonatus Nesis, 1972

Gonatus (Eogonatus) Nesis, 1972b, *Zoologicheskij Zhurnal*, 51(9): 1300–1307 [1300].

Type Species: *Gonatus (Eogonatus) tinro* Nesis, 1972b.

Frequent Synonyms: None.

Diagnostic Features: Tentacles slender, weak. **Tentacular clubs with no hooks, only numerous, very crowded, minute, equal-sized suckers**. The 5 or 6 ridges and grooves of club fixing apparatus are short. **Radula with 5 transverse rows of teeth**. Head enlarged by large, bulbous eyes. **Mantle not muscular**. **Fins ovate, not sagittate**.

Size: Small-sized squid; maximum mantle length 140 mm.

Remarks: This taxon was elevated to generic status because of the absence of any hooks on the tentacular club, combined with 5 rows of teeth on the radula. However, genetic studies using allozymes and mitochondrial DNA suggested that this species is within the ***Gonatus*** s. str. group.

Literature: Nesis (1972b, 1985, 1997), Katugin (2004), Kubodera *et al*. (2006d).

Eogonatus tinro Nesis, 1972

Eogonatus tinro Nesis, 1972b, *Zoologicheskyi Zhurnal*, 51(9): 1300–1307 [1300]. [Typed locality: 58°22.2’N, 174°55’,Bering Sean Northwest Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length recorded for this species is 140 mm.

Geographical Distribution: *Eogonatus tinro* occurs in the northern North Pacific Ocean from northeastern Hokkaido, Japan, the Okhotsk Sea and southern Kuril Islands, to the Bering Sea, the Aleutian Islands, and the Gulf of Alaska, south to British Columbia, Canada.

Habitat and Biology: This species is an upper-boreal, meso-bathypelagic species that undergoes ontogenetic descent and diel vertical migration. It spawns mainly in the summer; paralarvae and juveniles are described.

Local Names: JAPAN: Nise-Tekagiika.

Remarks: Mostly early ontogenetic stages of this species are known. See also Remarks for ***Gonatopsis okutanii***.

Literature: Nesis (1972b), Okutani *et al*. (1988), Katugin and Shevtsov (2006).

Gonatopsis okutanii Nesis, 1972

Gonatopisis okutanii Nesis, 1972b, *Zoologicheskyi Zhurnal*, 51(9): 1300–1307 [1304]. [Type locality: 44°06.4’N, 150°28.2’E, Northwest Pacific Ocean].

Frequent Synonyms: None.

Size: *Gonatopsis okutanii* attains a maximum mantle length of 250 mm.

Geographical Distribution: *Gonatopsis okutanii* occurs in the North Pacific Ocean from the southern Kuril Islands to the northern slope of the Okhotsk Sea, the Bering Sea and the Gulf of Alaska.

Habitat and Biology: This is a mesopelagic, bathypelagic and abyssal species. It has relatively large eggs, and mates presumably “head to head”, then dies after spawning.

Remarks: The validity of this species name has been questioned. Nesis (1997) suggested that it probably is a synonym of ***Gonatus madokai***. However, ***G madokai*** is easily distinguishable from ***Gonatopsis okutanii*** by its much larger fin, longer ventral arms and larger size-at-maturity. Katugin (unpublished) suggest that ***G okutanii*** may represent an adult form of ***Eogonatus tinro***. Usually tentacles of all collected individuals of ***G okutanii*** appear broken at the bases, as in the holotype. However, several individuals of ***G okutanii***, collected by Katugin in the Okhotsk Sea, possessed intact slim tentacles with tentacular clubs like those in ***E. tinro*** (no hooks on the club, only minute suckers, and fixing apparatus with small ridges and grooves). There is one notable difference between these 2 species. In small ***E. tinro***, the ventral arms are almost the same length or slightly longer than the other arms; in ***G okutanii***, the ventral arms are somewhat shorter and thinner than the other arms. However, individuals identified as ***E. tinro*** are usually small juveniles, while those assigned to ***G okutanii*** are much larger adults, and observed differences in relative lengths of arms could be due to their asymmetric growth in ontogeny. Clearly, if this entity possesses tentacles, it does not belong in the genus ***Gonatopsis***.

Literature: Nesis (1972b, 1997), Okutani and Clarke (1992).

2.14 Family HISTIOTEUTHIDAE Verrill, 1881

by Clyde F.E. Roper and Patrizia Jereb

Histioteuthidae Verrill, 1881, *Transactions of the Connecticut Academy of Sciences*, 5(6): 259–446. [431].

Type Genus: *Histioteuthis* d'Orbigny, 1841

FAO Names: En – Jewel squids; **Fr** – Loutènes bijou; **Sp** – Joyelurias

Diagnostic Features: Species are easily distinguished by **numerous** (usually), **anteriorly directed, complex photophores over the surface of the mantle, head and arms, especially on the vental and ventrolateral surfaces**; a broad head, with usually **asymmetrically developed eyes**, the left eye usually considerably larger than the right. Buccal membrane with 6 or 7 buccal lappets; **buccal connectives attach to the dorsal border of arms IV**; straight or slightly curved and slightly broad, simple, funnel-mantle locking elements; **suckers on the tentacular clubs arranged in 5 to 8 irregular series**; suckers on the arms biserial. Gladius with ventrally inrolled, cupped cone at posterior end. **Fins terminal, medium to large, together transversely oval in outline, unite posteriorly with a median notch**. An inner web connects arms and extends to greater than 60% of length of arms. A **hectocotylus is absent in males**, but both arms I have secondary sexual modifications: terminal suckers abruptly reduced in size set on elongate, palisaded pedestals; basal (or all normal) suckers enlarged, with swollen, fleshy collars; arms I often become more elongate, robust. Tentacles long with expanded club; distinct dactylus, manus and carpal adhesive apparatus, with alternating suckers and pads in a single row that extends proximally on the tentacular stalk for 1 to 3 club lengths. Sucker rings on manus are toothed around entire circumference.

Size: Small- to medium-sized squid; maximum mantle length 350 mm.

Geographical Distribution: As a group, the members of the Histioteuthidae occur in all oceans and marine seas of the world.

Habitat and Biology: Members of the cosmopolitan family Histioteuthidae are very broadly distributed throughout the world's oceans and seas in epipelagic (undergo diel vertical migration at night), mesopelagic and bathypelagic, even bathybenthic, habitats. Species range from the tropics to the polar seas. Closing-net data on a few species of ***Histioteuthis*** indicate the strong likelihood that diel vertical migration is common among the family members. For example, in an intensive open-net survey of the eastern Pacific Ocean off California no specimens of ***H. heteropsis*** were captured in the upper 300 m during the day; only 16% of daytime captures were caught at 300 to 500 m, while 62% were caught at 500 to 700 m. In contrast, at night, 69% of ***H. heteropsis*** captured were taken in the upper 400 m, with a peak at 300 to 400 m. The shallowest nighttime capture for specimens larger than 20 mm mantle length was 200 m and most were concentrated at 300 to 400 m. Some species are extremely abundant, and they appear to aggregate in "schools", even at great depths. Some species are quite large and attain mantle lengths of at least 350 mm, but the total length can be 4 to 5 times longer than mantle length. Most species are major components in the diets of sperm whales (up to 62% in some regions), other odontocete cetaceans, pinnipeds; albatrosses, penguins, other seabirds; sharks, tunas, lancetfishes; other squids.

Interest to Fisheries: While there are no large-scale directed fisheries for any species of ***Histioteuthis***, it is possible that a small bycatch interest could develop as commercial fishery trawling probes increasingly deeper, to 1 500 m and beyond. The flesh on the mantle and arms of histioteuthids is firm and thick in adults of pre-spawning condition. At full maturation of both males and females, however, the tissue of the mantle, head and arms begins to soften, and by full spawning and post-spawning stages, the tissues of the mantle, head and arms soften to a semi-gelatinous consistency. A further impediment to development of a consistent fishery would be the suspected ammoniacal composition of the flesh.

Remarks: Following Voss *et al*. (1998a) the family is monotypic and all species are quite easily recognized as members of ***Histioteuthis***. To date, 13 species are recognized, 2 of which have 1 and 3 subspecies, respectively, for a total of 17 currently recognized specific and subspecific entities. The first systematic monograph of the family was by N. Voss (1969). A comprehensive monograph was produced by Voss, Nesis and Rodhouse (1998), to which the reader is referred for detailed aspects of systematics, distribution, morphology, ecology, predation, etc. The family also has been treated on the "Tree of Life" website for Cephalopoda by Young and Vecchione (2000, 2008b,c,d). This site presents valuable information on and comparisons of specific taxonomic characters in tabular form. Most significantly, all subspecies that we list here, have been elevated to species level in ToL, a judgement with which we agree. A valuable adjunct to the contribution by Young and Vecchione is a comprehensive list of nominal genera and species named in the Histioteuthidae, with notations on their status (e.g. validity, synonyms, etc.) by Sweeney and Young (2003l).

The nomenclature and classification used herein is based on Voss *et al*. (1998a). Subsequently, different interpretations have been introduced that depart from the earlier classification (see Young and Vecchione, 2000, 2008h,i,j).

Local Names: USA: Umbrella squids.

Literature: Voss (1969), Voss *et al.* (1992a), Rodhouse *et al.* (1992a,c), Young and Vecchione (2000, 2008h,i,j); Voss *et al.* (1998a), Sweeney and Young (2003l).

Key to the species and subspecies of Histioteuthidae (from Voss *et al.* 1998a)

1a. Median row of tubercles on dorsal surface of mantle and basal portions of arms I–III present . . . . → ***2***

1b. Median row of tubercles on mantle and arms absent . . . . → ***4***

2a. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head, in 8 or 9 longitudinal rows on basal portions of arms IV, in circlet of 19 to 22 around right eye . . . . ***Histioteuthis meleagroteuthis*** **(Atlantic, Pacific, and Indian oceans, tropical-subtropical)**

2b. Photophores of uniformly medium size, arranged in moderately dense pattern on ventral surfaces of mantle and head, in 4 to 6 longitudinal rows on basal portions of arms IV, in circlet of 16 or 17 (rarely 15 or 18) around right eye . . . . → ***3***

3a. Median row of tubercles occupies 19 to 39% of arm length in adults and subadults, 24 to 47% in juveniles of 17 to 38 mm mantle length; numerous photophores in diagonal rows on basal half of arms IV, 5 photophores in first 2 or 3 rows, 4 in subsequent rows . . . . ***Histioteuthis miranda*** **(southern Benguela Current, western Indian Ocean, subtropical waters of Australia-New Zealand)**

3b. Median row of tubercles occupies 46 to 83% of arm length in adults and subadults; 65 to 92% in juveniles of 12 to 22 mm mantle length; numerous photophores in diagonal rows on basal half of arms IV, 6 photophores in first 2 or 3 rows, 5 in subsequent rows. . . . . ***Histioteuthis oceani*** **(equatorial Pacific Ocean and certain adjoining areas of North and South Pacific Oceans, ? tropical Indian Ocean)**

4a. Single, large terminal photophore present on arms I to III or I to IV; inner web connecting basal portions of arms deep: 50% or more of arm length in adults, subadults, and large juveniles . . . . → ***5***

4b. Single, large terminal photophore absent on arms; inner web vestigial to moderate in depth: 30% or less of arm length in adults, subadults, and juveniles . . . . → ***6***

5a. Buccal membrane with 6 lappets and 1 connective to arms IV; segment of inner web absent between right and left junctures of web segments from arms III and IV . . . . ***Histioteuthis bonnellii***[1] **(sub-Arctic, north temperate, and eastern tropical Atlantic Ocean; Mediterranean Sea; Benguela Current; nearly circumglobal in southern half of south subtropical regions)**

5b. Buccal membrane with 7 lappets and 2 connectives to arms IV; segment of inner web present between right and left junctures of web segments from arms III and IV. . . . . ***Histioteuthis macrohista*** **(nearly circumglobal in Southern Subtropical Convergence, Benguela Current)**

6a. Photophores uniformly small, arranged in dense pattern on ventral surfaces of mantle and head, in 8 to 10 longitudinal rows on arms IV, in circlet of about 19 to 21 (range 17 to 23) around right eye . . . . ***Histioteuthis heteropsis*** **(California Current, Peru-Chile Current)**

6b. Photophores large or intermixed large and small, arranged in widely spaced to moderately dense pattern on ventral surfaces of mantle and head, in 3 or 4 longitudinal rows on arms IV, in circlet of 16 to 18 (? rarely 15) around right eye . . . . → ***7***

7a. Photophores large, arranged in widely to moderately widely spaced pattern on anterior one-third to one-half of ventral surface of mantle; circlet around right eye composed of 16 or 17 (rarely 18 or ?15) large photophores. . . . . → ***8***

7b. Photophores intermixed large and small, arranged in moderately dense pattern on ventral surface of mantle; circlet around right eye composed of 17 large and 1 small photophores . . . . → ***15***

8a. Photophores in widely spaced pattern on ventral surface of mantle; dorsal pad of funnel organ with 2 lateral flaps; male genetalia paired; skin conspicuously papillated (exept in small juveniles) . . . . → ***9***

8b. Photophores in moderately widely spaced pattern on ventral surface of mantle; dorsal pad of funnel organ unsculptured; male genetalia single; skin not papillated. . . . . → ***10***

---

[1] Probably comprises more than 1 taxon.

9a. Spermatophore 5 to 6% of mantle length, with single loop in ejaculatory apparatus; large adult males with midportions of arms I with moderately increased robustness, median keel moderately expanded, protective membranes low . . . . ***Histioteuthis hoylei***[2/]
(Pacific and Indian Oceans, tropical-subtropical)

9b. Spermatophore 13 to 21% of mantle length, with numerous loops in ejaculatory apparatus; large adult males with midportions of arms I with greatly increased robustness, median keel greatly expanded, protective membranes high. . . . . ***Histioteuthis arcturi, new combination***[2/]
(Atlantic Ocean, tropical-subtropical)

10a. Terminal group of normal photophores on arms I to IV present, except in mature specimens (? mature male of *Histioteuthis celetaria celetaria* and mature female of *H. celetaria pacifica*), where terminal groups on arms I to III replaced by single, long, narrow, darkly pigmented photophore; denticulate collars of club suckers in ventral marginal rows on manus asymmetrically broadened . . . . ***→ 11***

10b. Terminal group of photophores on arms absent; denticulate collars of club suckers in ventral marginal rows on manus not asymmetrically broadened . . . . ***→ 12***

11a. Suckers in median 2 or 3 rows of club manus slightly enlarged and approximately coequally enlarged; gladius with shoulders of vanes somewhat flaring and angular . . . . . ***Histioteuthis celetaria celetaria***
(Atlantic Ocean, tropical-subtropical)

11b. Suckers of median 3 rows of club manus moderately enlarged to 1½ times ventral marginals (except in small juveniles), decreasing in size from ventral to dorsalmost rows; gladius with shoulders of vanes broadly rounded. . . . . ***Histioteuthis celetaria pacifica***
(Pacific and Indian Oceans, primarily equatorial/tropical)

12a. Four longitudinal rows of photophores on arms IV . . . . ***Histioteuthis corona berryi***
(North Pacific Ocean, subtropical, California Current)

12b. Three longitudinal rows of photophores on arms IV . . . . ***→13***

13a. Sucker rings on arms IV smooth; 20 to 27 teeth on rings of large suckers of club manus . . . . ***Histioteuthis corona inermis***
(northwestern Pacific Ocean, subtropical)

13b. Sucker rings on arms IV with teeth; 30 to 60 teeth on rings of large suckers of club manus. . . . . ***→ 14***

14a. Thirty-three to 38 teeth on rings of large suckers of club manus . . . . ***Histioteuthis corona corona***
(Atlantic Ocean, tropical-north subtropical)

14b. Fifty to 60 teeth on rings of large suckers of club manus . . . . ***Histioteuthis corona cerasina***
(eastern and central equatorial Pacific Ocean, Peru-Chile Current)

15a. Three longitudinal rows of photophores on arms IV (of large organs) . . . . ***Histioteuthis eltaninae***
(sub-Antarctic waters, circumglobal)

15b. Four longitudinal rows of photophores on arms IV (3 rows of large organs, 1 row of small or mixed-size organs) . . . . ***→ 16***

16a. Terminal group of enlarged photophores on arms I to III present; inner web moderately developed, 17 to 30% of longest arm length . . . . ***Histioteuthis atlantica***
(southern Subtropical Convergence and northern half of sub-Antarctic waters, circumglobal)

16b. Terminal group of enlarged photophores on arms absent; inner web vestigial to low, less than 8% of longest arm length . . . . ***Histioteuthis reversa***
(north temperate Atlantic Ocean and fringing sub-Arctic waters,north subtropical, tropical; Mediterranean Sea)

[2/] At present, females and immature males of *Histioteuthis hoylei* and *Histioteuthis arcturi* can be separated confidently only by geographic location.

Histioteuthis d'Orbigny, 1841

Histioteuthis d'Orbigny, 1841, *in* Ferussac and d'Orbigny, 1834–1848, *Histoire Naturelle Générale et Particulière des Cèphalopodes Acètabulifères Vivants et Fossiles*, 1vi and 361pp., 144 pl. [xxxvii].

Type Species: *Histioteuthis bonnellii* (Férussac, 1834).

Frequent Synonyms: *Calliteuthis* Verrill, 1880b; *Histiopsis* Hoyle, 1885a; *Histiothauma* Robson, 1948; *Lolidona* Risso, 1854; *Meleagroteuthis* Pfeffer, 1900; *Stigmatoteuthis* Pfeffer, 1900.

Diagnostic Features: Following Voss *et al.* (1998a) ***Histioteuthis*** is the sole genus in the monotypic family Histioteuthidae. Consequently, the diagnostic characters are the same as those given for the family.

Remarks: Species of ***Histioteuthis*** are extremely important in the diets of many toothed whales and dolphins, as well as fishes, sharks, albatrosses, other sea birds and other squids. Frequently, however, the remains from the stomachs of predators can not be identified to species level, so the food items are identified only to the generic level.

Literature: (see Family Literature) Roper *et al.* (1984), Santos and Haimovici (2002), Okutani (2005).

Histioteuthis bonnellii (Ferussac, 1834) **Species Group** **Fig. 245**

Cranchia bonnellii Ferussac, 1834, *L'Institut, Journal General des Societes et Travaux Scientifiques de la France et de l'Etranger*, 2(77): 355. [355]. [Type locality: off Nice, Mediterranean Sea].

Frequent Synonyms: *Cranchia bonnellii* Ferussac, 1834; *C. bonelliana* Ferussac, 1834; *Histioteuthis bonelliana* d'Orbigny, 1835–1848; *H. rüppelli* Verany, 1846; *Lolidona euphrosina* Risso, 1854; *Histioteuthis collinsi* Verrill, 1879; *H. bonnellii corpuscula* Clarke, 1980.

FAO Names: En – Umbrella squid; **Fr** – Loutène bonnet; **Sp** – Joyeluria membranosa.

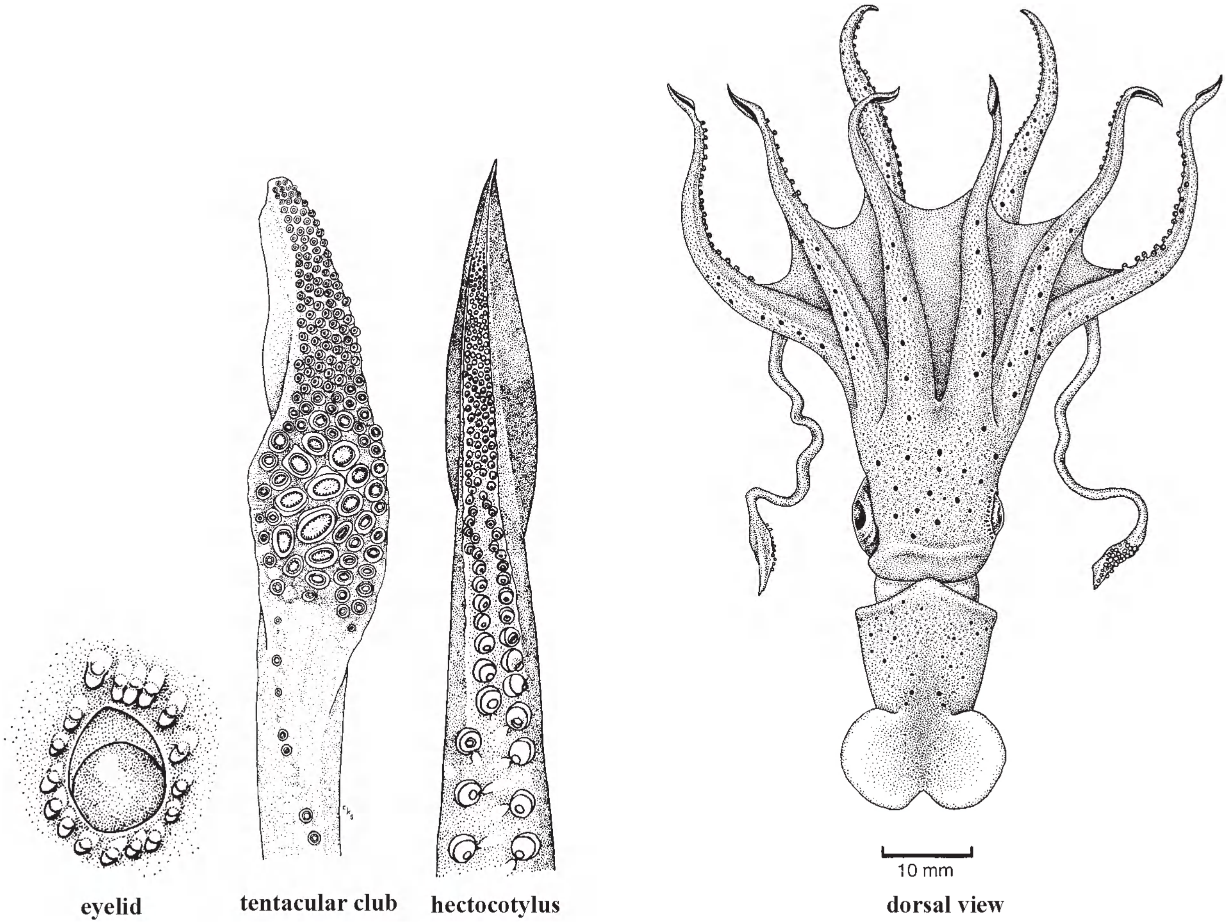


Fig. 245 *Histioteuthis bonnellii*

Diagnostic Features: Mantle conical, relatively short, broad, covered with dark, elongate compound photophores in 7 or 8 diagonal rows on ventral surface (lateral surfaces of mantle and ventral and lateral surfaces of head and arms also covered with these photophores). Fins oval, medium to large, length about 40 to 60% of mantle length, width about 70 to 90% of mantle length. **Head large, with 1 nuchal fold**. **Arms long, 130 to 300% of mantle length, connected with a very broad, deep, maroon-coloured web**; arm formula typically II=III>I=IV. A distinct, single, enlarged, elongate, dark, simple photophore on each arm tip (I to IV). **Buccal membrane 6-membered**. **Seventeen** (rarely 16 or 18) **small, oval photophores** around periphery of right eye-lid.

Size: This species attains a maximum mantle length of 330 mm, reported on a mature female from the sub-Arctic; males also reach about 330 mm mantle length.

Geographical Distribution: This species is very broadly distributed in the North Atlantic Ocean and Mediterranean Sea; from the eastern central North Atlantic Ocean and western Mediterranean, to the southeastern Atlantic Ocean and southwestern Pacific Ocean between Austalia and New Zealand, and the southern Indian Ocean (Fig. 246).

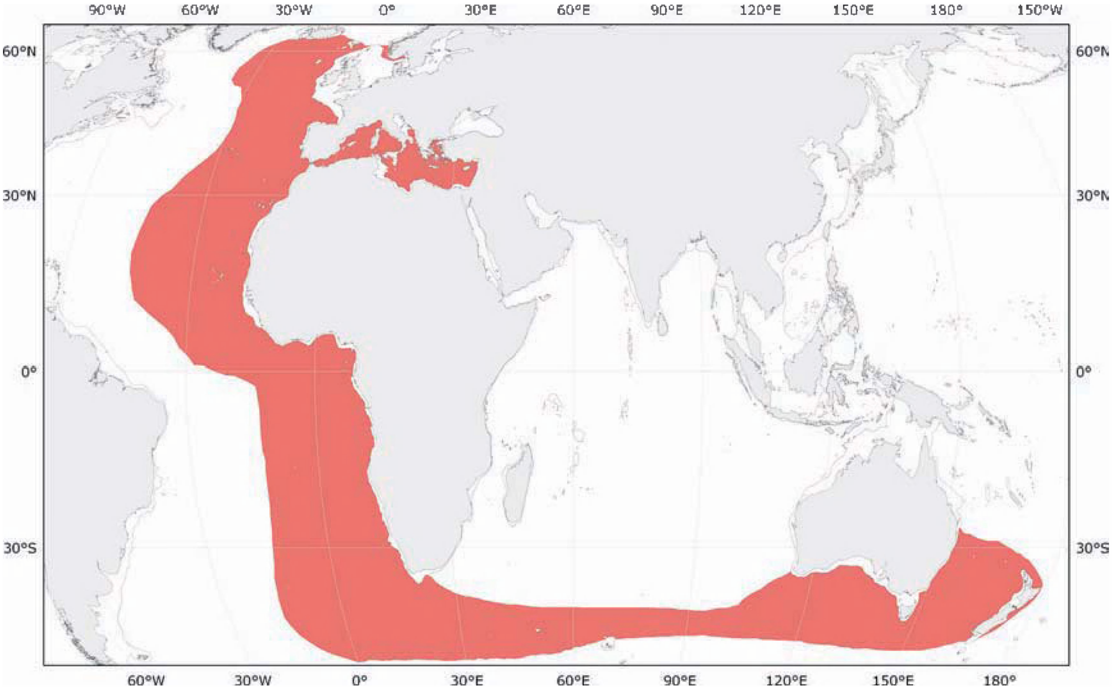


Fig. 246 ***Histioteuthis bonnellii***

🟥 Known distribution

Habitat and Biology: An oceanic species, ***Histioteuthis bonnellii*** is reported to occur usually in depths between 500 and 1 500 m, occasionally to over 2 000 m, sometimes associated with the bottom. Growth seems to be isometric and even juvenile specimens have the proportions of adults. Although they usually are taken singly or in pairs in sampling nets, it is suspected, from evidence in sperm whale stomachs and from very large midwater trawls, that it is a schooling species. Apart from sperm whales and other odontocetes, it is preyed upon by lancetfish (*Alepisaurus ferox*), scabardfish (*Aphanopus carbo*), albacore (*Thunnus alalunga*), swordfish (*Xiphias gladius*), blue shark (*Prionace glauca*).

Interest to Fisheries: The species is believed to have some fishery potential. Important prey for commercially exploited fish species.

Local Names: ITALY: Totano ingioiellato palmato.

Remarks: This is the largest ***Histioteuthis*** species.

Literature: Voss *et al.* (1992a), Tursi *et al.* (1994), Voss *et al.* (1998a), Lefkaditou *et al.* (1999), Quetglas *et al.* (2000), Okutani (2005), Lansdell and Young (2007).

Histioteuthis hoylei (Goodrich, 1896)

Species Group **Fig. 247; Plate VII, 43**

Histiopsis hoylei Goodrich, 1896, *Transactions of the Linnean Society of London, Zoology,* 7(1): 1–24 [15]. [Type locality: Fonseca Bay, West coast of Central America].

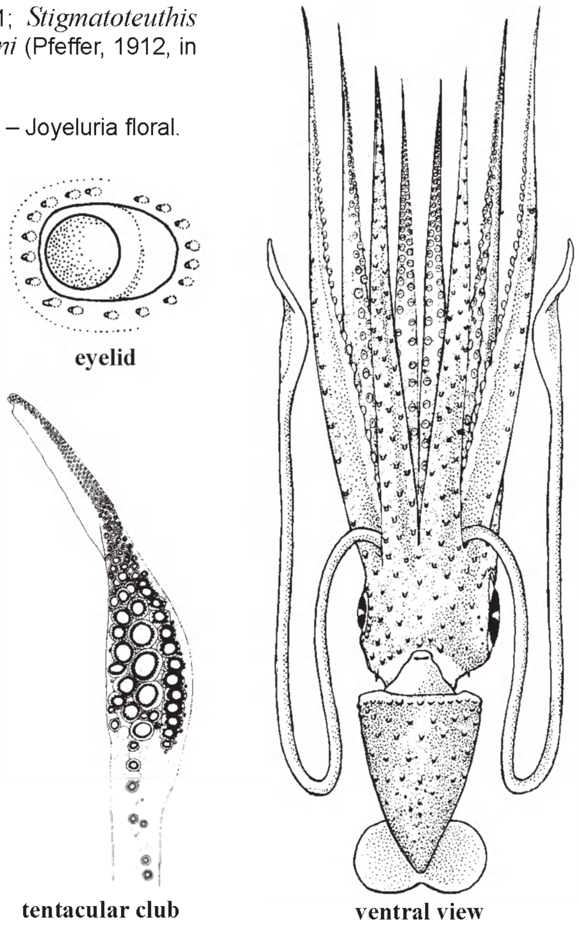
Frequent Synonyms: *Meleagroteuthis hoylei* Pfeffer, 1908a`1; *Stigmatoteuthis chuni* Pfeffer, 1912; *S. dofleini* Pfeffer, 1912; *Histioteuthis dofleini* (Pfeffer, 1912, in part).

FAO Names: En – Flowervase jewell squid; **Fr** – Loutène vase; **Sp** – Joyeluria floral.

Diagnostic Features: Males with paired genitalia. Mantle conical, relatively thick-walled, relatively short, moderately stout; skin of whole body (mantle, head, arms and basal half of fins) covered with thickly spaced, low, fleshy papillae, giving a rough, textured appearance: fins medium-sized, round, length about 30 to 40% of mantle length, width about 45 to 70% of mantle length. Head without nuchal folds. **Arms long, 160 to 250% of mantle length**; **mature males with arms I very elongate, greater than 400% of mantle length**; **no photophores on arm tips**. Ventral and lateral surfaces of mantle, head, arms covered with elongate, compound photophores; widely spaced on ventrum of mantle and arranged in about 6 diagonal rows; photophores progressively decrease in size on posterior two-thirds of mantle. Head large. Web between arms very low, indistinct. **Seventeen large photophores around right eyelid**. Dorsal pad of funnel organ with strong median ridge from apical papilla posteriorly along each lateral arm; expand posteriorly to form 2 broad flaps.

Size: The maximum mantle length attained in females is 240 mm in females, and to 210 mm in males.

Geographical Distribution: ***Histioteuthis hoylei*** (***dofleini***) is widely distributed in the tropical-subtropical waters of the Pacific Ocean between about 45°N and 45°S and in the Indian Ocean between about 10°N and the southern Subtropical Convergence (Fig. 248).


eyelid

tentacular club

ventral view

Fig. 247 ***Histioteuthis hoylei***

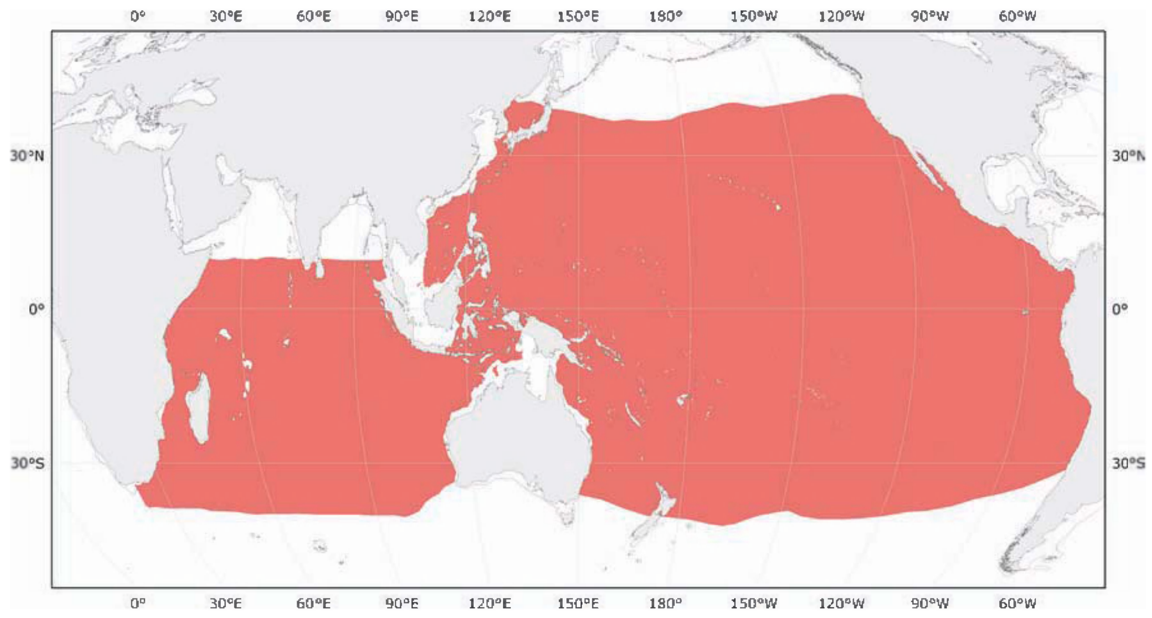


Fig. 248 ***Histioteuthis hoylei***

🟥 Known distribution

Habitat and Biology: Off Hawaii, ***Histioteuthis hoylei*** occurs between depths of 100 and 850 m; in daytime it concentrates at 500 to 700 m (range 355 to 850 m) and at night it vertically migrates to depths of 100 to 500 m with 85% concentrated at 150 to 300 m. In the transitional waters of the northwestern North Pacific Ocean warm core rings and cold water this species is a non-migrant, remaining below 400 m. Analysis of stomach contents from sperm whales off Japan suggests that mature females occur in a dense aggregation adjacent to an isolated oceanic rise. This species is extremely important prey for sperm whales and other odontocete whales, including short-finned pilot whales and Hubb's beaked whale. Other predators include blue sharks in the western North Pacific Ocean. It is reported from the stomachs of swordfish of the west coast of Baja California, Mexico. Analysis of the dimorphic eyes suggests that the large left eye points upward and the small right eye points ventrolaterally when the animal is in its normal oblique, arms downward, position. This enables the squid in its daytime depth of 500 to 700 m, to use its large eye to utilize the dim daylight from above, while the small right eye perceives bioluminescent light from the side and below.

Interest to Fisheries: Undetermined. This species is an important prey for commercial species of fishes.

Local Names: JAPAN: Kuragedako.

Remarks: Voss *et al.* (1992), after the examination of the type of ***Histiopsis hoylei*** Goodrich, 1896, placed all specimens previously known as ***Histioteuthis dofleini*** in the synonyomy of this earlier named species, as ***H. hoylei*** (Goodrich, 1896). Then Voss *et al.* (1998a), recognized that the Atlantic form was different and should be called ***H. arcturi*** (Robson, 1948). Young and Vecchione (2007b) consider members of the Histioteuthidae with paired secondary reproductive organs (penis, spermatophore gland complex, Needham's sac) distinctive and place them in a separate clade. Both ***Histioteuthis hoylei*** and ***H. arcturi*** are placed in this separate clade. The males that originally represented ***H. hoylei*** (Voss *et al.*, 1998a) came from north temperate waters off California and Japan. After the examination of material from off Hawaii, Young and Vecchione (2008i,j) consider the Pacific forms as divided into 2 different species, a temperate north Pacific one, for which they keep the name ***H. dofleini*** and a more southern species, ***H. hoylei***. The same authors then consider the generic name ***Stigmatoteuthis*** Pfeffer 1900 as the valid designated genus name for this separate clade of histioteuthids (see Young and Vecchione, 2008h,i,j).

Literature: Okutani (1974a), Muntz (1976), Voss *et al.* (1992a, 1998a), Nesis (1994), Bower *et al.* (1999c), Okutani (2005), Watanabe *et al.* (2006b), Young and Vecchione (2007b, 2008h,i,j).

Histioteuthis miranda (Berry, 1918) **Species Group** **Fig. 249**

Calliteuthis miranda Berry, 1918, *Biological Results of the Fishing Experiments Carried on by the F.I.S. Endeavor, 1909–1914*, 4(5): 201–298. [221]. [Type locality: 37°54'S, 178°56'E, western South Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Wondrous jewel squid; **Fr** – Loutènes bijou marveilleux; **Sp** – Joyeluria maravillosa.

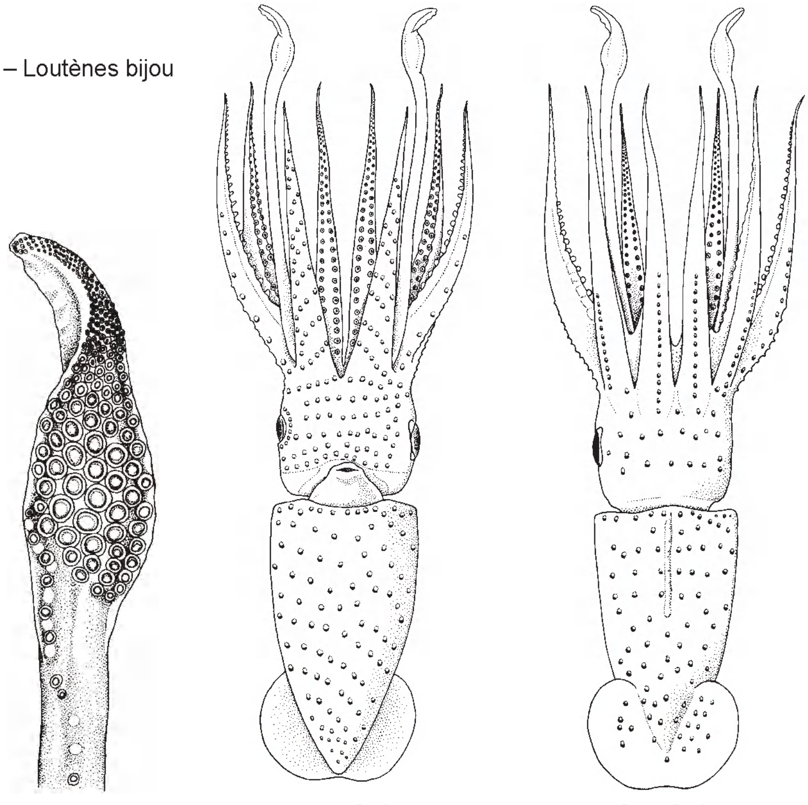

tentacular club ventral view dorsal view

Fig. 249 *Histioteuthis miranda*

Diagnostic Features: Mantle robust, moderately elongate; wall thick; **ridge of low tubercles extends along dorsal midline of mantle** on anterior half, **well developed in medium-sized and large juveniles**, but **hidden beneath mantle tissue in large subadults and adults**. Fins medium-sized, oblong, length about 31 to 44% of mantle length, width about 44 to 57% of mantle length. Head relatively large; 1 nuchal fold present in juveniles, absent in adults. Arms of moderate length, about 100 to 150% of mantle length; arm formula I=II=III>IV. Basal one-third to one-half of arms I to III with median row of low tubercles. Inner web connects basal 16 to 25% of arms I to III; outer web only slightly developed. **Buccal membrane 7-membered**. Tentacles long, 150 to 260% of mantle length. Tentacular club without longitudinal cleft on aboral surface. Suckers on manus closely packed in 6 or 7 series; median suckers enlarged twice the diameter of ventral marginal suckers. Compound photophores numerous, of nearly uniform medium size, moderately widely spaced, arranged in 9 or 10 diagonal rows across ventral mantle; **16 or 17 (rarely 15) moderately large photophores encircle the right eye-lid**. Skin colour a dark grey-blue to purple.

Size: A large- to medium-sized squid. The maximum mantle length of mature females is 270 mm, of mature males is 260 mm.

Geographical Distribution: ***Histioteuthis miranda*** occurs in the Pacific and Indian Oceans but it is absent from the Atlantic Ocean, except off extreme southern South Africa in the Agulhas Current (about 33°S). It occurs in the Indian Ocean southern subtropical waters from southeastern South Africa eastward to Australian/New Zealand waters (Fig. 250).

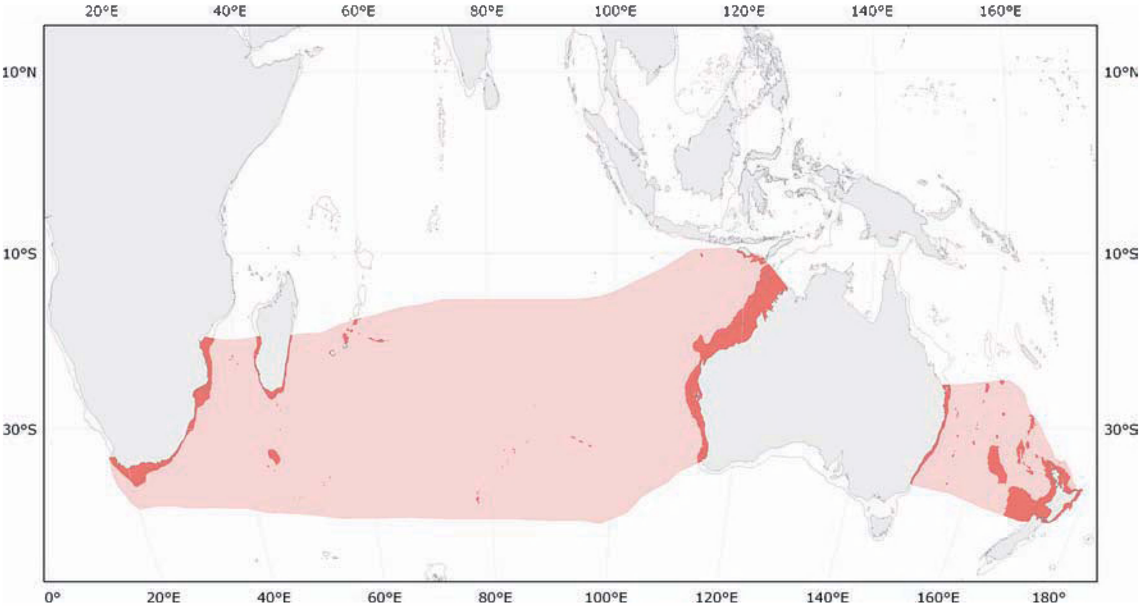


Fig. 250 ***Histioteuthis miranda***

🟥 Known distribution ▨ Probable presence

Habitat and Biology: This species occurs in close association with the slopes of continental masses and their offshore islands and submarine rises. Capture data suggest that this is the most abundant histioteuthid species encountered throughout most of its normal range. It occurs abundantly at 700 to 900 m off South Africa, where a large breeding population is located. It ranges from subsurface waters to at least 1 200 m; ontogenetic descent exists as larger subadults and adults generally are captured deeper than juveniles, 700 to 1 200 m on or close to the bottom; elsewhere subadults and mature males and females were taken both day and night at or near the bottom at 400 to 1 200 m. Many specimens of ***H. miranda*** have been caught frequently in deep-water, bottom-fishing, lobster trawls at 300 to 600 m off the North West Shelf of Australia and the Great Barrier Reef, suggesting an association with the sea floor at some time during their life cycle. This species is preyed upon by swordfish off eastern Australia and by pygmy sperm whale off New Zealand.

Interest to Fisheries: There is no direct interest to fisheries, but the species is important as prey of commercially harvested fishes.

Local Names: None available.

Literature: Clarke (1980), Roeleveld *et al.* (1992), Voss *et al.* (1998a), Dunning and Lu (1998), Okutani (2005).

Histioteuthis reversa (Verrill, 1880) **Species Group** **Fig. 251**

Calliteuthis reversa Verrill, 1880b, *American Journal of Science*, 20(41): 390–403 [393]. [Type locality: 39°53'N, 70°58'W, western North Atlantic Ocean].

Frequent Synonyms: *Stigmatoteuthis verrilli* Pfeffer, 1912; *Calliteuthis reversa mediterranea* Naef, 1921a; *C. r. atlantica* Grimpe, 1922; *C. elongata* Voss and Voss, 1962; *Histioteuthis elongata* (Voss and Voss, 1962).

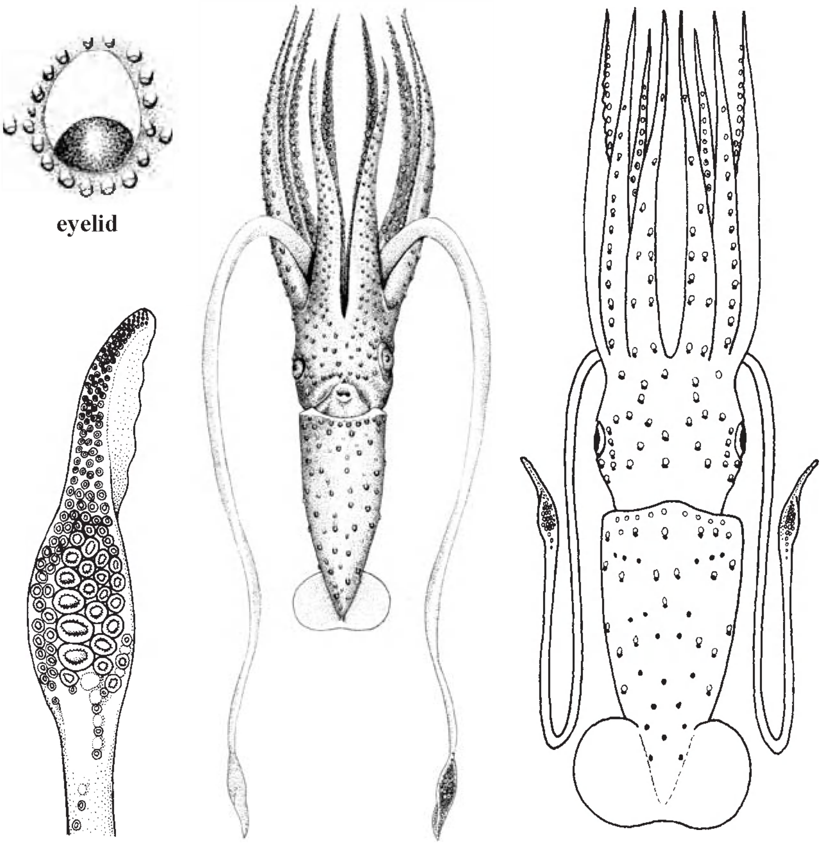
FAO Names: En – Reverse jewell squid; **Fr** – Loutène retournée; **Sp** – Joyeluria invertida.

Diagnostic Features: Mantle **elongate to very elongate**, especially in **mature females**. **Mantle covered** (especially on ventral and lateral surfaces) **with intermixed large and small compound photophores**. Fins medium-sized, rounded; their length about 35 to 50% of mantle length, width about 40 to 60% of mantle length (proportionally smaller in mature females). Head large, wider than mantle (except in mature females). Usually 1 or 2 weak nuchal folds. Arms robust, no distinct photophores on tips; arms of moderate length, about 100 to 150% of mantle length; web between arms vestigial to low. **Eighteen photophores around right eyelid, 17 large and 1 small. Buccal membrane 7-membered**. Tentacles 100 to 200% of mantle length; club with deep longitudinal cleft on aboral surface of manus; manus suckers in about 6 diagonal series, markedly enlarged in median ventral series to 3 to 4 times diameter of ventral marginals.

Size: The maximum mantle length is 200 mm in mature females, smaller in males.

Geographical Distribution: ***Histioteuthis reversa*** is distributed in the Atlantic Ocean and Mediterranean Sea. It is confined to temperate, subtropical and tropical waters including the eastern and western Mediterranean Sea. It extends northward to the sub-Arctic in the Atlantic Ocean to at least 52°N and south into the eastern South Atlantic. Apparently it is excluded from the Gulf of Mexico, Caribbean Sea and South Atlantic Central water mass (Fig. 252).

Habitat and Biology: An oceanic species, ***Histioteuthis reversa*** is taken between the surface and 1 000 m depth with closing nets. Juveniles (up to 15 mm mantle length) occur in the upper 200 m both day and night; all juvenile/subadult sizes were captured in closing nets at 50 to 630 m during the day and 10 to 260 m at night. Consequently, a diel vertical migration is confirmed in this species, following the ontogenetic descent of post-paralarval juveniles. Both closing-net and open net captures, at daytime and night, of mature males and females in mid-water and near the bottom occurred at 500 to 1 000 m; this suggests that maturation immediately prior to spawning occurs in


eyelid

tentacular club

ventral view

dorsal view

Fig. 251 *Histioteuthis reversa*

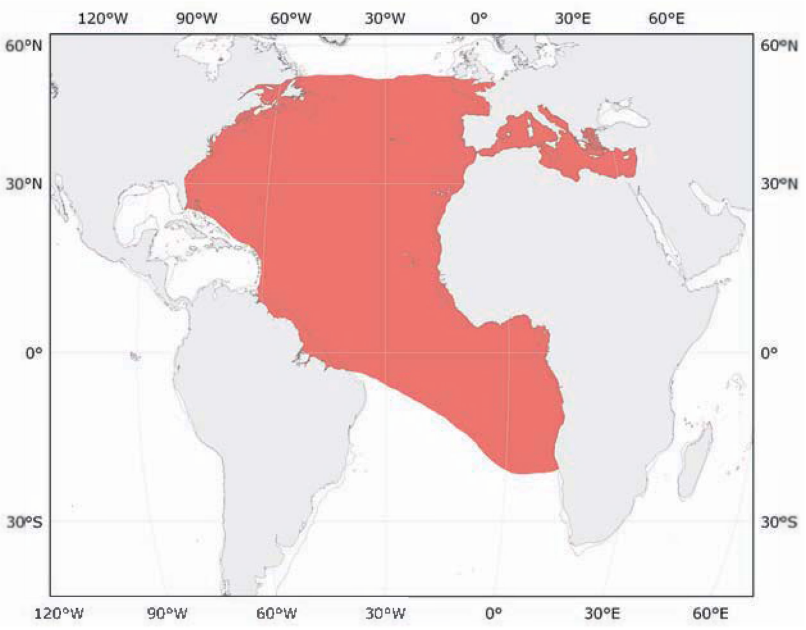


Fig. 252 ***Histioteuthis reversa***

🟥 Known distribution

deep water. Captures of spent (spawning) dead or dying females at the surface suggest that females ascend through the water column to spawn in food-rich surface waters, then die. Specimens from the western North Atlantic were found to have concentrations of persistent organic pollutants and tributyltin, which has implications for trophic level transfer, e.g. to sperm whales and other toothed whales and pelagic predators. The species is preyed upon by sperm whales, pygmy sperm whales, northern bottlenose whales, Risso's dolphins, blue sharks and swordfish.

Interest to Fisheries: Currently no interest to fisheries exists, but this species is important prey for many exploited fish species.

Local Names: ITALY: Totano ingioiellato.

Literature: Voss (1969), Mangold (1974), Lu and Clarke (1975a,b), Voss *et al.* (1992a, 1998a), Lefkaditou *et al.* (1999), Giordano *et al.* (2001), Vecchione and Pohle (2002), Okutani (2005).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Note: The species listed here are presented in the order of their species group, as defined in Voss *et al.* (1998a), but arranged alphabetically.

Histioteuthis arcturi (Robson, 1948)

Stigmatoteuthis arcturi Robson, 1948, *Zoologica*, 33(3): 115–132. [122]. [Type locality: 26°54'N, 51°15'W, south Sargasso Sea, central North Atlantic Ocean, 0–3 000m].

Frequent Synonyms: *Histioteuthis dofleini* (Pfeffer, 1912).

Size: The maximum mantle length is 210 mm in females and 130 mm in males.

Geographical Distribution: ***Histioteuthis arcturi*** occurs in the Atlantic Ocean; it is tropical-subtropical between about 40°N and 30°S, to its southern limit just north of southern Subtropical Convergence. It is very abundant in the Gulf of Mexico, Gulf Stream, Sargasso Sea, central North Atlantic Ocean subtropical waters, the North African Subtropical Sea and sparsely distributed in the South Atlantic Ocean.

Habitat and Biology: Its vertical distribution extends from surface waters to depths below 1 000 m. Shallower living juveniles change to a diel vertical distribution pattern of 450 to 750 m during the day and between the surface and 400 m at night.

Remarks: ***H. arcturi*** has been reported in the literature as ***H. reversa***, until the species was separated into the new combination by Voss *et al.* (1998a).

Literature: Nesis (1974a), Clarke and Lu (1974, 1975), Roper and Young (1975), Voss *et al.* (1998a).

Histioteuthis atlantica (Hoyle, 1885)

Histiopsis atlantica Hoyle, 1885a, *Annals and Magazine of Natural History*, (series 5) 16: 181–203. [201]. [Type locality: Messing [Würzburg Museum], Germany, and no locality [Leipzig Museum], fide Pfeffer (1912: 251)].

Frequent Synonyms: *Histioteuthis cookiana* Dell, 1951.

Size: The maximum mantle length reaches 260 mm in mature males and 150 mm in immature females.

Geographical Distribution: ***Histioteuthis atlantica*** is circumglobal in distribution between about 30°S to 33°S and 50°S, normally in the southern Subtropical Convergence, as well as in the fringes of the subtropical and the sub-Antarctic waters, over oceanic basins, plateaus and shelf areas.

Habitat and Biology: Maximum depth range about 40 to 2 000 m. Juveniles are taken in open nets at 100 to 200 m at night and at 500 to 1 000 m both day and night. Adults and subadults have been captured with open nets between 300 and 2 000 m at night and between 900 to 1 000 m during the day; subadults have been caught on the bottom at night between 700 to 850 m. It is prey of swordfish off eastern Australia.

Literature: Voss *et al.* (1992a), Rodhouse *et al.* (1992a), Voss *et al.* (1998a), Jackson *et al.* (2002), Okutani (2005).

Histioteuthis celetaria celetaria (Voss, 1960)

Calliteuthis celetaria celetaria Voss, 1960, *Fieldiana, Zoology*, 39(40): 419–446. [424]. [Type locality: 32°10'N, 64°45'W, western North Atlantic Ocean [fide Voss (1969: 763)]; originally published incorrectly as 34°45'W].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 260 mm in mature females and 90 mm in mature males.

Geographical Distribution: ***Histioteuthis celetaria celetaria*** lives in the Atlantic Ocean in north subtropical and tropical waters and in the south subtropical region. It is absent from the Gulf of Mexico and the Caribbean Sea, between about 33°N and 19°S.

Habitat and Biology: The vertical distribution is not well established, because so few specimens are available; the species occurs from the upper 40 to 1 000 m.

Literature: Amelekhina *et al.* (1990), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis celetaria pacifica (Voss, 1962)

Calliteuthis celetaria pacifica Voss, 1962a, *Proceedings of the Biological Society of Washington*, 75: 169–176. [174]. [Type locality: Dammi Island, between Jolo and Tawi Tawi, Philippine Islands].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 280 mm in mature males, and 230 mm in immature females.

Geographical Distribution: ***Histioteuthis celetaria pacifica*** occurs in the Pacific and Indian Oceans, primarily associated with tropical and equatorial waters. In Indian Ocean equatorial waters it extends from 8°N to 10°S and in the western part of the southern gyre to 35°S. In Indo-West Pacific Ocean it is very common along the northwest slope and shelf of Australia, northward through the Philippines.

Habitat and Biology: The species occurs throughout the Hawaiian Island chain eastward into the California Current. Most captures of this species are from on or near continental and island slopes and submarine rises. Juveniles occur in the upper 200 m but are capable of descending with growth to increasingly deeper depths, possibly to 1 000 m. Subadult and adult males have been found during day and night in midwaters and near bottom in shelf and slope waters at 250 to 1 000 m.

Literature: Nesis (1977c), Nateewathana (1995), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis corona berryi Voss, 1969

Histioteuthis corona berryi Voss, 1969, *Bulletin of Marine Science*, 19(4): 713–867 [781]. [Type locality: 29°17'N 125°41'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length recorded is 50 mm; all known specimens are juveniles.

Geographical Distribution: ***Histioteuthis corona berryi*** occurs exclusively in the eastern Pacific Ocean, between 26°N and 37°N, 115°W and 138°W in the California Current and the fringing waters to the westward.

Habitat and Biology: This may be a species that is more normally found in subtropical waters to the west of the California Current. Its vertical range is 300 to 800 m.

Literature: Jefferts (1983), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis corona cerasina Nesis, 1971

Plate VII, 41

Histioteuthis corona cerasina Nesis, 1971, *Zoologicheskij Zhurnal*, 50(10): 1463–1471. [1463]. [Type locality: 00°01’S, 84°59’W, eastern Central Pacific Ocean].

Frequent Synonyms: None.

Size: The species is known only from juveniles, the largest of which is 57 mm mantle length.

Geographical Distribution: ***Histioteuthis corona cerasina*** occurs in the eastern Pacific Ocean; it is concentrated in the equatorial waters and Peru-Chile Current between 00° and 24°S, 70°W and 85°W, but records indicate its extension to at least 155°W in equatorial waters.

Habitat and Biology: The species is caught in the open ocean and in the vicinity of submarine ridges and continental slopes. Open nets have caught early juveniles in the upper 300 m (to the surface) and late juveniles at 200 to 1 000 m at night and 500 to 1 500 m in the daytime.

Literature: Nesis (1971), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis corona corona (Voss and Voss, 1962)

Calliteuthis corona Voss and Voss, 1962, *Bulletin of Marine Science of the Gulf and Caribbean*, 12(2): 169–200. [191]. [Type locality: 29°10’N, 88°00’W, Gulf of Mexico, western Central Atlantic Ocean].

Frequent Synonyms: None.

Size: A maximum mantle length of 190 mm is reported in mature males and 170 mm in immature females.

Geographical Distribution: ***Histioteuthis corona corona*** is limited to the Atlantic Ocean exclusively. Principally it occurs from tropical and north subtropical waters in the Gulf of Mexico and Caribbean Sea and in the eastern Atlantic Ocean, in the tropical waters from the Azores, the Gulf of Guinea to well off South Africa; the Gulf Stream distributes it well into the northern and eastern Atlantic Ocean.

Habitat and Biology: The vertical distribution of this subspecies extends from the upper 100 m to in excess of 1 500 m.

Literature: Clarke and Lu (1974, 1975), Arkhipkin and Shchetinnikov (1989), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis corona inermis (Taki, 1964)

Calliteuthis inermis Taki, 1964, *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*, 5(2): 297–343 [297]. [Type locality: off Kambara, Suruga Bay, Japan].

Frequent Synonyms: None.

Size: This species is known only from juveniles, the largest of which is 53 mm mantle length.

Geographical Distribution: ***Histioteuthis corona inermis*** lives in the northwestern North Pacific Ocean off the east coast of Japan between 33°N and 35°N in Tosa, Suruga and Sagami Bays and off the Kii Peninsula.

Habitat and Biology: This species has been collected at depths of about 420 to 600 m. It is a non-vertical migrator at depths below 400 m where it is restricted to warm core ring waters in the northwestern North Pacific Ocean. It is prey of odontocete whales and blue sharks.

Literature: Okutani *et al.* (1987), Voss *et al.* (1998a), Okutani (2005), Watanabe *et al.* (2006b)

Histioteuthis eltaninae Voss, 1969

Histioteuthis eltaninae Voss, 1969, *Bulletin of Marine Science*, 19(4): 713–867. [755]. [Type locality: 40°05'S, 149°55'W, South Pacific Ocean].

Frequent Synonyms: None.

Size: This small species attains a maximum mantle length of 110 mm.

Geographical Distribution: ***Histioteuthis eltaninae*** is circumglobal in sub-Antarctic waters. Its normal northern boundary is the southern Subtropical Convergence and its normal southern boundary is the Antarctic Polar Front; a few captures have been made around the Antarctic Peninsula and Scotia Sea. It also has been taken in the East Australian Current to about 33°S, and in the northeastern Tasman Sea.

Habitat and Biology: While the species occurs over oceanic basins, its greatest abundance occurs in the higher-productivity waters associated with submarine ridges and continental shelves. It occurs from the upper 100 m to in excess of 1 000 m, perhaps to 2 000 m. It is a dominant prey of southern elephant seals.

Literature: Nesis (1974a), Rodhouse *et al.* (1992a), Rodhouse and Piatkowski (1995), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis heteropsis (Berry, 1913)

Calliteuthis (Meleagroteuthis) heteropsis Berry, 1913a, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 65: 72–77. [75]. [Type locality: off Santa Barbara, California, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length is 90 mm in males and 130 mm in females.

Geographical Distribution: ***Histioteuthis heteropsis*** occurs in the eastern Pacific Ocean, including transitional waters of the California Current and the Chile-Peru Current. It is considered to be an eastern Pacific Ocean transitional species.

Habitat and Biology: The known vertical distribution of this species is derived from open nets off California and indicates daytime depths of 300 to 800 m with 62% of the specimens at 500 to 700 m. At night, 69% of the specimens were taken at 0 to 400 m, with a peak at 300 to 400 m. The species clearly undergoes a diel vertical migration of 300 to 400 m in extent. ***Histioteuthis heteropsis*** is prey for swordfish off northern Baja California and for hammerhead sharks in the southern part of the Gulf of California (24°N).

Literature: Young (1972a), Voss *et al.* (1998a), Seibel *et al.* (2004), Okutani (2005).

Histioteuthis macrohista Voss, 1969

Histioteuthis macrohista Voss, 1969, *Bulletin of Marine Science*, 19(4): 713–867. [845]. [Type locality: 45°10'S, 160°10'E, Tasman Sea].

Frequent Synonyms: None.

Size: The maximum mantle length is 65 mm in females and 55 mm in males.

Geographical Distribution: ***Histioteuthis macrohista*** is broadly distributed in the Atlantic, Indian and western Pacific Oceans; it occurs primarily in fringing and transitional waters of the southern Subtropical Convergence between about 33°S and 47°S (where it is sympatric with ***H. atlantica***). It is absent from the eastern Pacific waters.

Habitat and Biology: This species occurs close to continental slopes as well as oceanic basins. The vertical distribution of the species extends between the surface 100 m to over 1 000 m; both juveniles and subadults have been caught over the entire known vertical range at night, so a diel vertical migration is not confirmed. It is prey of swordfish off eastern Australia and pygmy sperm whales off New Zealand.

Literature: Lipinski and Turoboyski (1983), Roeleveld *et al.* (1992), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis meleagroteuthis (Chun, 1910)

Calliteuthis meleagroteuthis Chun, 1910, *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition dem Dampfer Valdivia, 1898–1899*, 18: 1–401. [170]. [Type locality: 35°45'S, 176°20'E, western South Pacific Ocean].

Frequent Synonyms: *Meleagroteuthis separata* Sasaki, 1915b; *Histioteuthis bruuni* Voss, 1969.

Size: The maximum recorded mantle length is 114 mm in mature females and 102 mm in mature males.

Geographical Distribution: ***Histioteuthis meleagroteuthis*** has a circumglobal distribution in tropical and subtropical waters between approximately 35°N to 45°N and 45°S. The southern limit of occurrence is sharply defined by the southern Subtropical Convergence; the species does not normally inhabit the convergence transition waters. It is widespread in the tropical and subtropical Atlantic Ocean, but it does not occur in the Caribbean Sea or the Gulf of Mexico. It is a pan-Pacific Ocean species with many records concentrated in New Zealand and Australian warm waters, northward through the islands to southern Japan. Records in the Indian Ocean are scattered from about 65°E to the tip of South Africa.

Habitat and Biology: The species, throughout its range, appears to reach greatest abundance in the zones of higher productivity, particularly those waters associated with bottom slopes and submarine rises. The vertical distribution extends from the surface to in excess of 1 000 m. Closing nets have recorded juveniles at 210 to 300 m in daytime, with larger subadults at 610 to 700 m. At night juveniles were captured at 100 to 360 m. Open nets have captured specimens to 1 950 m in midwaters and to 1 250 m near the bottom. It is preyed upon by the deep sea shark, *Galeus melastomus* on the continental slope.

Literature: Okutani (1974a), Muntz (1976), Voss *et al.* (1998a), Okutani (2005).

Histioteuthis oceani (Robson, 1948)

Histiothauma oceani Robson, 1948, *Zoologica*, 33(3): 115–132. [123]. [Type locality: 2°33'S, 89°44'W, eastern Central Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 70 mm, (possibly 100 mm). The species is known from only 19 specimens.

Geographical Distribution: ***Histioteuthis oceani*** occurs in the Pacific Ocean. It exhibits a broad equatorial distribution from the Galapagos Islands northward to the Hawaiian Islands, then westward to the Indo-West Pacific Ocean off New Guinea and the Philippines.

Habitat and Biology: The species occurs around islands, above submarine rises and in the open ocean.

Literature: Young (1978), Voss *et al.* (1998a), Okutani (2005).

2.15 Family JOUBINITEUTHIDAE Naef, 1922

by Clyde F.E. Roper and Patrizia Jereb

Joubiniteuthidae Naef, 1922, *Die Fossilen Tintenfische*, 322 pp. [299].

Type Genus: *Joubiniteuthis* Berry, 1920.

FAO Names: En – Joubin's squids; **Fr** – Loutènes de Joubin; **Sp** – Lurias de Joubin.

Diagnostic Features: Arm pairs I to III extremely long, thin, greater than 2 times the mantle length, very small suckers in 6 transverse series; **arms I to III joined by a low web**. Ventral arms (IV) short (length one-third of, or less, than length of arms I to III) with suckers in 4 transverse series. Tentacles in juveniles shorter and much thinner than arms I to III, thread-like; **tentacular clubs laterally compressed**; **bear minute suckers in 5 to 12 transverse series**; protective membranes present only in distal half of club; **no fixing apparatus** (carpus); adult tentacles fully reduced. **Buccal membrane with 7 lappets**; buccal connectives attach to ventral borders of arms IV. **Head narrow, eyes small, neck long**. Mantle long, narrow, posterior conical; semigelatinous. Tail long (longer than the mantle) and very slender, needle-like; it is comprised of the conus which is elongate with ventral fusion, covered only by soft, thickened integument. **Fins** relatively **very small, ovoid, width nearly equal to length**. Funnel-locking apparatus with oval depression, without tragus or antitragus. Buccal connectives attached to ventral borders of arms IV. **Hectocotylus absent**. **Photophores absent**.

Size: Small-sized squid; maximum mantle length to 105 mm.

Geographical Distribution: Circumglobal, in tropical and subtropical waters.

Habitat and Biology: A mesopelagic to bathypelagic, rarely encountered, squid. Little is known about the biology of this squid.

Remarks: This monotypic family contains a single species.

Literature: Young and Roper (1969b), Nesis (1982, 1987), Sweeney and Young (2003m), Young (2008a).

Joubiniteuthis Berry, 1920

Joubiniteuthis Berry, 1920b, *Biological Bulletin*, 38(3): 141–169 [152].

Type Species: *Joubiniteuthis portieri* (Joubin, 1916).

Frequent Synonyms: *Valdemaria* Joubin, 1931.

Diagnostic Features: The same as given for the family.

Joubiniteuthis portieri (Joubin, 1916)

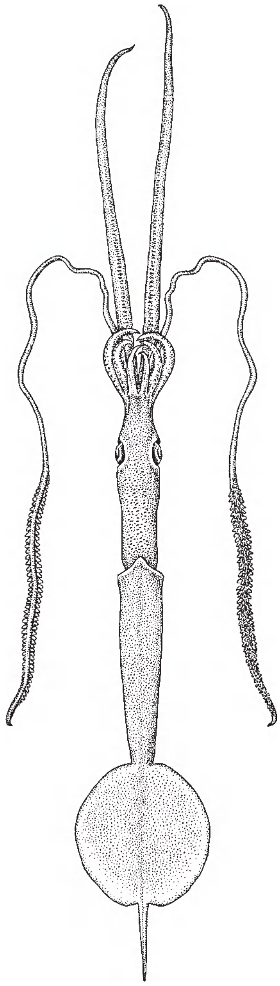
Fig. 253; Plate VII, 42

Chiroteuthis portieri Joubin, 1916, *Bulletin de l'Institut Océanographique, Monaco*, 317: 1–10. [1]. [Type locality: 29°03'N, 16°08'30"W, eastern Central Atlantic Ocean].

Frequent Synonyms: *Valdemaria danae* Joubin, 1931.

FAO Names: En – Joubin's squid; **Fr** – Loutène de Joubin; **Sp** – Luria de Joubin.

Diagnostic Features: The features are the same as those given for the family. Paralarvae with semi-transparent, spindle-shaped mantle, very small leaf-like fins, needle-like tail longer than mantle, possibly a small secondary fin at posterior one-third point of needle-like tail. Neck short without septa. Arm-crown pillar absent. Arms and tentacles proportionally very short at mantle length less than 10 mm; tentacles short and thick, club very short, 4 transverse series of suckers at 6 to 9 mm mantle length, 8 series at 18 mm mantle length. The thick tentacles, long arms and very long tail are characteristic in adults.



dorsal view

Fig. 253 ***Joubiniteuthis portieri***

Size: Mantle length of mature male 105 mm; tail length an additional 155 mm.

Geographical Distribution: Cosmopolitan in tropical and subtropical, even temperate waters; Atlantic Ocean, 40°N to 30°S, including Caribbean Sea; Pacific Ocean, Hawaii, Japan, eastern Australia, Tasman Sea, New Zealand (Fig. 254).

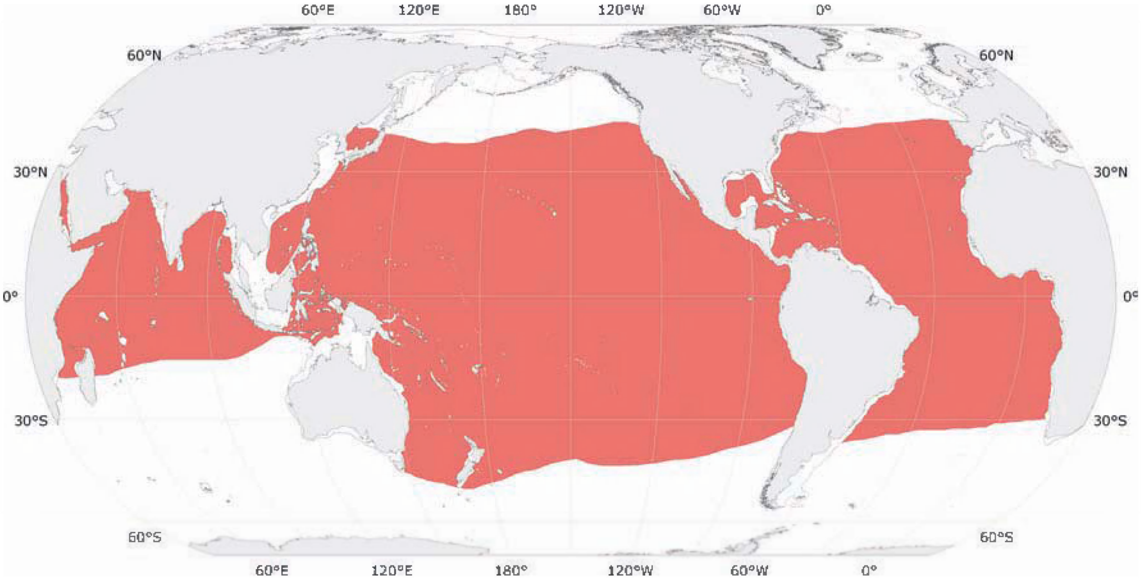


Fig. 254 ***Joubiniteuthis portieri***

🟥 Known distribution

Habitat and Biology: Males are fully mature at 105 mm mantle length; females clearly developing but immature at 85 mm mantle length, with paired nidamental glands. Depths of capture in open nets range from 300 to 500 m at night (1 at 3 500 m) and 800 to 2 500 m during daytime: this clearly is a meso- to bathypelagic species. Specimens are reported as prey of lancetfish, blue shark and sperm whale.

Interest to Fisheries: None.

Remarks: This is a very rare species with only a few dozen specimens known.

Literature: Young and Roper (1969b), Nesis (1999b), Seibel *et al*. (2000b), Vecchione (2002), Vecchione *et al*. (2002).

2.16. Family LEPIDOTEUTHIDAE Pfeffer, 1912

by Clyde F.E. Roper and Patrizia Jereb

Lepidoteuthidae Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2: 1–815. [535].

Type Genus: *Lepidoteuthis* Joubin, 1895:

FAO Names: En – Soft-scaled squids; **Fr** – Loutènes écaille-doux; **Sp** – Lurias escamuda blandas.

Diagnostic Features: Distinct dermal cushions (formerly called “scales”) present on the mantle; mantle of paralarvae and juveniles covered with small papillae, the precursors to dermal cushions; **dermal cushions are relatively large, diamond- to hexagonal-shaped structures** that cover the whole circumference of the mantle except on the posteroventral part under the posterior half of the fins; they **resemble scales of some fishes in outline and in overlapping arrangement,** but they lack any form of solid bony structure; the cushions overlap tightly, like roofing tiles, and are at least 10 by 12 mm in dimension in adults; the internal structure is highly vacuolate with loose connective tissue forming the “walls” of the chambers; dermal cushions occur only on the mantle, not on fins, funnel, head nor arms; papillae in juveniles each have 2 to 4 minute “cartilaginous” points or tips. **Buccal connectives attach to the ventral borders of arms IV; funnel- locking cartilage a straight, simple groove, deeper anteriorly**. Suckers biserial on the arms with long, sharply-pointed teeth on distal half of inner ring; a few (6 to 8) suckers occur on the small, slightly expanded tentacular clubs of paralarvae and juveniles; tentacles present but weakly developed in young, absent in subadults and adults (from about 85 mm mantle length). **Fins large, terminal, not lobed or scaled, together are oval shaped** with the long axis longitudinal with the mantle. The posterior end of the mantle bulges slightly. The gladius is very thin, narrow; posteriorly it consists of a dorsal, axial, cartilaginous rod enveloped by a very elongate chitinous conus. Arms on adults thickened, subequal in length. **Photophores absent**. **Hectocotylus absent**. Males have a pair of very enlarged, saber-like hooks near the base of arms II.

Size: Large-sized squid; maximum mantle length to 1 m.

Remarks: The family is monotypic, although for a period of time 2 other genera, ***Pholidoteuthis*** and ***Tetronychoteuthis***, were included on the basis of shared, curious dermal cushions, so-called “scales”. Subsequent analyses have proven that these genera are not related at the familial level based on several important non-shared characters (Clarke 1980; Roper and Lu, 1989; Nesis and Nikitina, 1990; O’Shea *et al*. 2007).

Literature: Roper and Lu (1989), Nesis and Nikitina (1990), Sweeney and Young (2003n), O’Shea *et al*. 2007, Young and Vecchione (2008c).

Lepidoteuthis Joubin, 1895

Lepidoteuthis Joubin, 1895b, *Compte Rendu des Sèances de l’Acadèmie des Sciences*, 121: 1172–1174 [1172].

Type Species: *Lepidoteuthis grimaldii* Joubin, 1895.

Frequent Synonyms: *Enoptroteuthis* Berry, 1920.

Diagnostic Features: The diagnostic features are the same as given in the family.

Lepidoteuthis grimaldii Joubin, 1895

Fig. 255

Lepidoteuthis grimaldii Joubin, 1895b, *Compte Rendu des Sèances de l’Acadèmie des Sciences*, 121: 1172–1174. [1172]. [Type locality: 38°34’;45”N, 29°37’W, near Teceira, Azores Islands, central North Atlantic Ocean (from sperm whale stomach)].

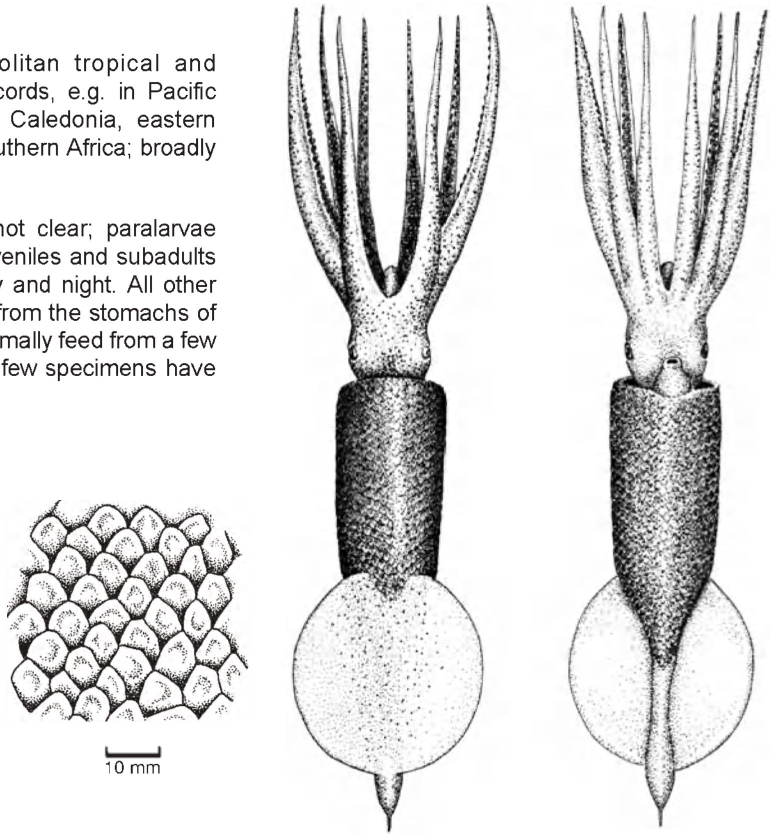
Frequent Synonyms: *Enoptroteuthis spinicauda* Berry, 1920a.

FAO names: En – Grimaldi's soft-scaled squid; **Fr** – Loutène écaille-doux de Grimaldi; **Sp** – Luria escamuda blanda de Grimaldi.

Size: Mantle length to 1 m.

Geographical Distribution: A cosmopolitan tropical and subtropical species with broadly disjunct records, e.g. in Pacific Ocean from Hawaii, Honshu, Japan, New Caledonia, eastern Australia, Tasman Sea; western Australia, southern Africa; broadly in Atlantic Ocean (Fig. 256).

Habitat and Biology: Vertical distribution not clear; paralarvae have been taken in upper 100 m at night; juveniles and subadults have been taken in open nets to 700 m day and night. All other records of larger subadults and adults come from the stomachs of predatory deep sea fishes and whales that normally feed from a few hundred metres to 2 000 m. While relatively few specimens have been studied, some information is available on its biology. ***Lepidoteuthis grimaldii*** is a mesopelagic to bathypelagic, benthic-bathyal species. It is preyed upon by sperm whales, lancetfish (*Alepisauris*), yellowfin tuna, scabbard fish, dolphins, pilot whales, deep-sea sharks. Paralarvae attain the relatively large size of 10 mm mantle length or larger prior to becoming juveniles. The large, thick tentacles of paralarvae have small, compact clubs with 6 to 8 suckers in 2 transverse series, some very small, others very much larger; tentacles are lost by the early subadult stage. The unusual dermal cushions with very numerous internal vacuoles might function as a buoyancy mechanism if the vacuoles contain a lightweight fluid such as ammonium chloride.



dermal cushions **dorsal view** **ventral view**

Fig. 255 ***Lepidoteuthis grimaldii***

Interest to Fisheries: None currently, but it attains a large size (1 m mantle length) and its mantle musculature is relatively firm, not gelatinous. Its deep-sea habitat and apparently low population density would be deterrent factors in developing a fishery.

Literature: Clarke and Maul (1962), Roper and Young (1975), Nesis (1982, 1987), Roper and Lu (1990), Nesis and Nikitina (1990), Young (1992 [1991]), Vecchione and Pohle (2002), Okutani (2005), Young and Vecchione (2008c).

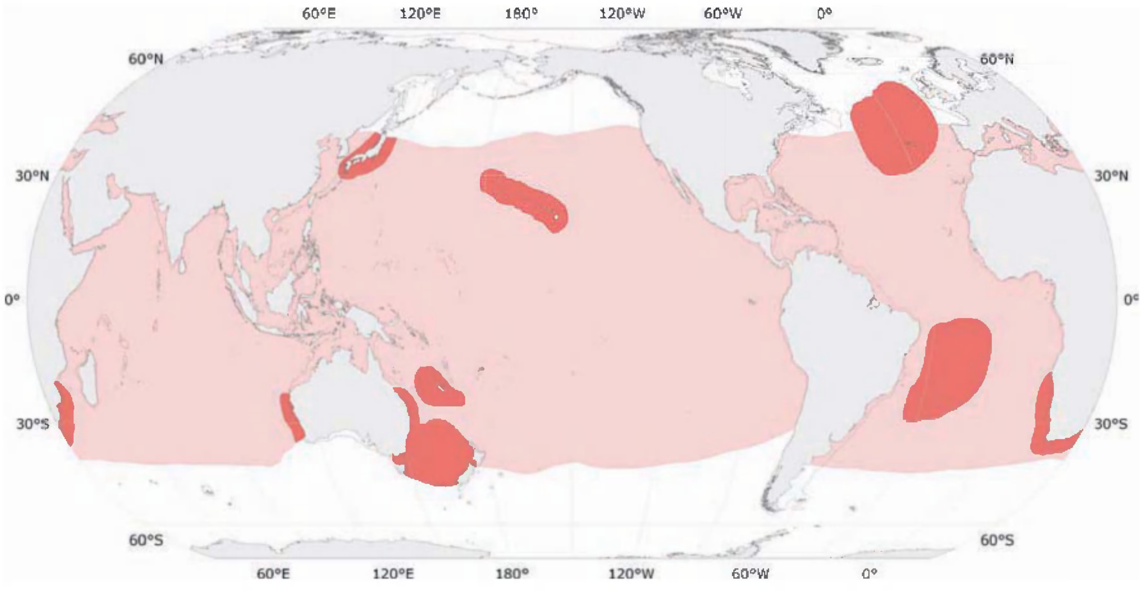


Fig. 256 ***Lepidoteuthis grimaldii***

🟥 Known distribution 🟥 Probable presence

2.17 Family LYCOTEUTHIDAE Pfeffer, 1908

by Clyde F.E. Roper and Patrizia Jereb

Lycoteuthidae Pfeffer, 1908a, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 25: 287–295 [287].

Type Genus: *Lycoteuthis* Pfeffer, 1900.

FAO Names: En – Firefly squids; **Fr** – Encornets luciole; **Sp** – Luciernalurias.

Diagnostic Features: Suckers only present on arms (in 2 series) **and clubs** (in 4 transvere series); **hooks absent**. Carpal-locking apparatus with few suckers and knobs, often compact, in circular arrangement. Fins broad, rhomboidal, occasionally posteriorly extended into a tail. **Four or 5 oval photophores** on ventral surface of eyeball. **Visceral photophores: anal, branchial, abdominal and postero-abdominal organs**. Spherical **photophores embedded in tentacular stalks**. Buccal membrane with 8 lappets and supports; connectives to arms IV attach to dorsal margins. Spermatangia attach to modified tissue in nuchal region. Funnel-locking apparatus a straight, simple groove. Gladius with conus and elongate conus field.

Size: Mostly small-, rarely medium-sized squids; maximum recorded mantle length 194 mm.

Geographical Distribution: Circumglobal, mostly in tropical and subtropical waters, but not known from the North Pacific Ocean.

Habitat and Biology: These muscular squids with conical mantles occupy mesopelagic to bathyal/mesopelagic depths during the day and migrate into near-surface waters at night. They possess a large variety of luminous organs. Strong sexual dimorphism in general morphology occurs in some species.

Interest to Fisheries: One of the species may be of interest as a commercial fishery.

Remarks: Two subfamilies are recognized, the Lycoteuthinae and the Lampadioteuthinae. The Lampadioteuthinae is monotypic, and the only genus contains a single species, ***Lampadioteuthis megaleia***; the Lycoteuthinae consists of 3 genera; 1 is monotypic (***Selenoteuthis***) while the other 2 contain 2 species each.

Literature: Voss (1962c), Roper and Young (1975), Vecchione and Young (1999a), Arocha (2003), Sweeney and Young (2003p).

Key to the subfamilies of Lycoteuthidae

1a. Five photophores on ventral surface of eyeball, all evenly spaced and aligned in a row; 2 photophores on tentacular stalk; abdominal photophores present; hectocotylus absent; paired penes may be present; rostrum on gladius absent . . . . **Lycoteuthinae**

1b. Four photophores on eyeball arranged in a complex pattern; 4 photophores on tentacular stalk, 1 at base; abdominal photophores absent; hectocotylus present; paired penes absent; rostrum on gladius present . . . . **Lampadioteuthinae**

Subfamily **LYCOTEUTHINAE** Pfeffer, 1908

Lycoteuthinae Pfeffer, 1908a, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 25: 287–295 [287].

Type Genus: *Lycoteuthis* Pfeffer, 1900.

Key to genera of Lycoteuthinae

1a. Arms III greatly elongate, filiform, much longer than mantle; suckers absent distally . . . . ***Nematolampas***

1b. Arms III not elongate, not longer than mantle; suckers present distally . . . . → **2**

2a. One large, spherical photophore embedded at posterior trip of mantle in males and females; spherical photophore on tip of arms II and III in males . . . . ***Selenoteuthis***

2b. No large, spherical photophore at posterior tip of mantle in males and females; spherical photophores absent on tips of arms II and III in males . . . . ***Lycoteuthis***

Lycoteuthis Pfeffer, 1900

Plate VIII, 44

Lycoteuthis Pfeffer, 1900, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2): 147–198.

Type Species: *Lycoteuthis lorigera* (Steenstrup, 1875).

Frequent Synonyms: *Thaumatolampas* Chun, 1903b; *Asthenoteuthion* Pfeffer, 1912; *Leptodontoteuthis* Robson, 1926a; *Oregoniateuthis* Voss, 1956.

Lycoteuthis lorigera (Steenstrup, 1875)

Fig. 257

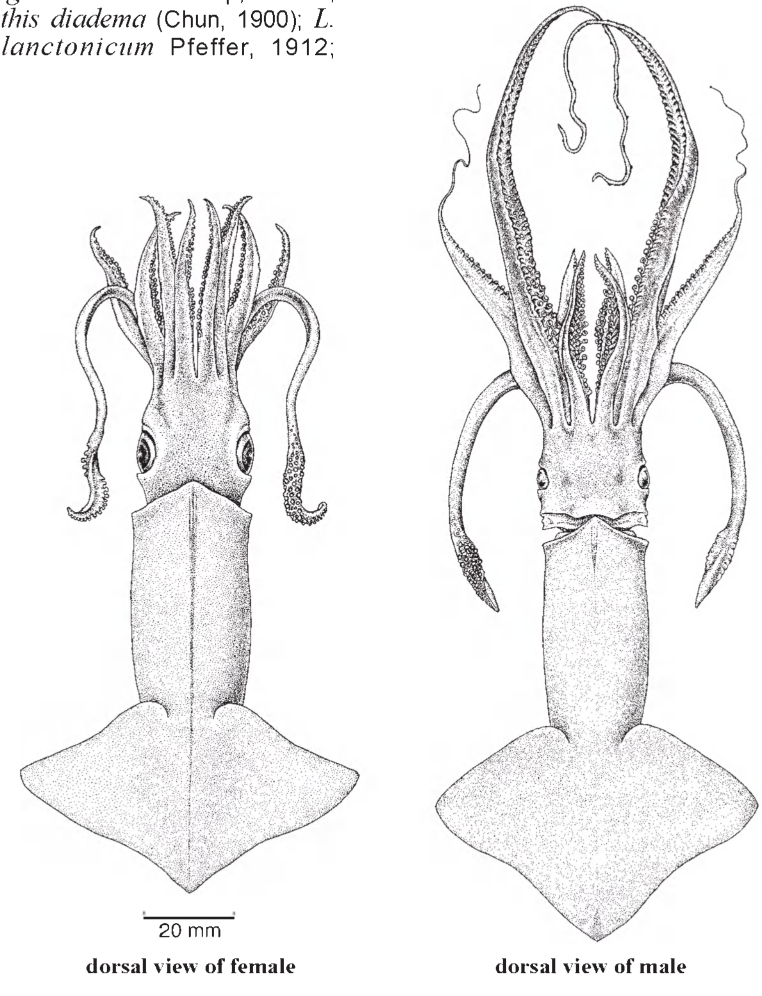
Onychoteuthis lorigera Steenstrup, 1875, *Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 10(7): 465–482. [473], 2 pl. [Type locality: 31°21'S, 15°58'E eastern South Atlantic Ocean].

Frequent Synonyms: ?*Onychoteuthis longimanus* Steenstrup, 1857a; *Enoploteuthis diadema* Chun, 1900; *Lycoteuthis diadema* (Chun, 1900); *L. jattai* Pfeffer, 1900; *Asthenoteuthion planctonicum* Pfeffer, 1912; *Leptodontoteuthis inermis* Robson, 1926a.

FAO Names: En – Crowned firefly squid; **Fr** – Encornet luciole couronné; **Sp** – Luciernaluria coronada.

Diagnostic Features: Arms II greatly elongated in males, with a series of regularly spaced photophores on the aboral surface. **Three abdominal photophores present**. Males with additional photophores on arms III, head and mantle. **Male genitalia paired**.

Size: Mantle length maximum to about 190 mm in males.



dorsal view of female dorsal view of male

Fig. 257 *Lycoteuthis lorigera*

Geographical Distribution: Circumglobal in southern, subtropical and notalian zones (Fig. 258).

Habitat and Biology: Bathyal- and mesopelagic over slopes and seamounts. Females are smaller than males, around 110 mm mantle length maximum. The only mature male aged was estimated to have 386 growth increments on the statoliths. Paired spermatophoric and terminal organs (penes) in males are both functioning.

Interest to Fisheries: While no commercial fishery currently exists, ***Lycoteuthis lorigera*** (referred to as ***L. diadema***), was found to be sufficiently abundant in the Benguela ecosystem to support a fishery.

Remarks: The long-used name for this species, familiar to most teuthologists even currently, was ***Lycoteuthis diadema*** (Chun, 1900). This species was designated a junior synonym to ***L. lorigera*** (Steenstrup, 1875) by Villaneuva and Sanchez (1993: 31). Consequently the combination ***L. diadema*** can no longer be used. Females of this species are, presently, indistinguishable from those of ***L. springeri***. It has been suggested that the very elongated and modified arms II and III in males may play a role in spermatophore transfer during mating (Villanueva and Sanchez, 1993; Hoving *et al*., 2007).

Literature: Voss (1962c), Nesis (1982, 1987), Lipinski (1992), Villanueva and Sanchez (1993), Alekseyev (1994a), Vecchione and Young (1999b), Hoving *et al*. (2007).

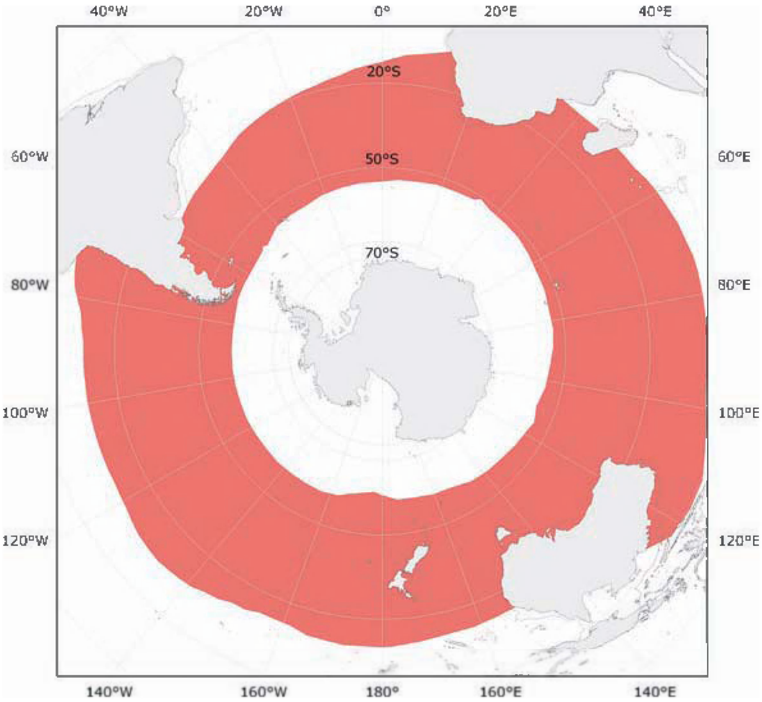


Fig. 258 ***Lycoteuthis lorigera***

🟥 Known distribution

Lycoteuthis springeri (Voss, 1956)

Oregoniateuthis springeri Voss, 1956, *Bulletin of Marine Science of the Gulf and Caribbean*, 6(2): 85–178 [120, fig. 7b–f]. [Type locality: 29°11.5'N, 88°07.5'W, Gulf of Mexico, western Central Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length to 97 mm.

Geographical Distribution: Gulf of Mexico.

Habitat and Biology: Bathyal to mesopelagic.

Literature: Vecchione and Young (1999a).

Nematolampas Berry, 1913

Nematolampas Berry, 1913c, *Biological Bulletin*, 25(3): 208–212 [208].

Type Species: *Nematolampas regalis* Berry, 1913.

Nematolampas regalis Berry, 1913 **Fig. 259**

Nematolampas regalis Berry, 1913, *Biological Bulletin*, 25(3): 208–212. [208]. [Type locality: Sunday Island, Kermadec Islands, southwestern South Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Regal firefly squid; **Fr** – Encornet luciole royal; **Sp** – Lucernaluria real.

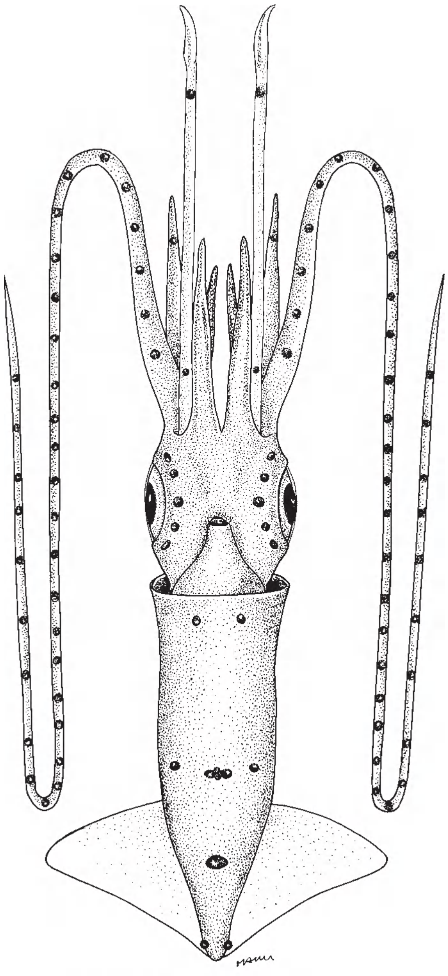
Diagnostic Features: Arms III greatly elongated in males, with thread-like distal portions, devoid of suckers. Arms II normal. Arms III with numerous photophores embedded, in linear series. **Males genitalia single**.

Size: Mantle length to 30 mm.

Geographical Distribution: Kermadec Islands, southwestern South Pacific Ocean (Fig. 260).

Remarks: This species is known from only 3 specimens, 1 washed ashore on the beach; 2 trawled from 48 m.

Literature: Vecchione and Young (1999c), Arocha (2003).



ventral view of male

Fig. 259 ***Nematolampas regalis***

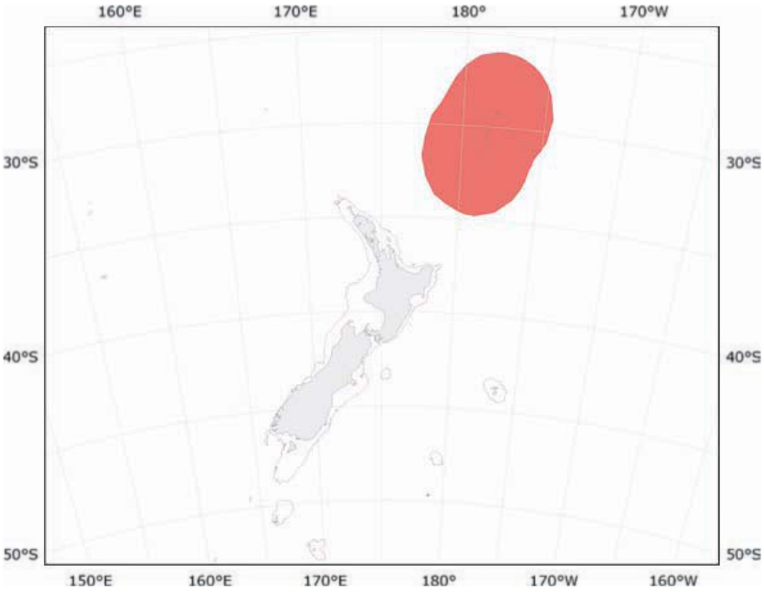


Fig. 260 ***Nematolampas regalis***

🟥 Known distribution

Nematolampas venezuelensis Arocha, 2003

Nematolampas venezuelensis Arocha, 2003, *Bulletin of Marine Science*, 72: 941–953. [941]. [Type locality: 10°55'N, 67°57'W, northeast of Golfo Triste, Venezuela, western Central Atlantic Ocean].

Size: The mantle length reaches about 30 mm.

Geographical Distribution: Tropical North Atlantic Ocean.

Literature: Arocha (2003).

Selenoteuthis Voss, 1959

Selenoteuthis Voss, 1959, *Bulletin of Marine Science of the Gulf and Caribbean*, 8(4): 369–389 [370].

Type Species: *Selenoteuthis scintillans* Voss, 1959.

Selenoteuthis scintillans Voss, 1959

Fig. 261

Selenoteuthis scintillans Voss, 1959, *Bulletin of Marine Science of the Gulf and Caribbean*, 8(4): 369–389 [370, figs. 1a–e]. [Type locality: 26°22'N, 76°10'W, western Central Atlantic Ocean]

Frequent Synonyms: None.

FAO Names: En – Shining firefly squid; **Fr** – Encornet luciole scintillant; **Sp** – Lucernaluria centelleante.

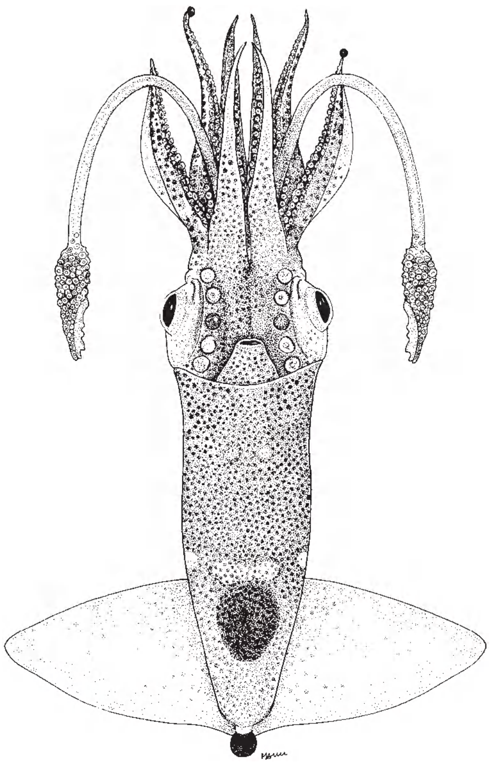
Diagnostic Features: One enlarged photophore present at the tip of the tail, larger in males. Five ventral ocular photophores in a straight line; **3 photophores on tentacles**: at the base of the tentacle, at midpoint and at the base of the carpus. A peculiar, spherical organ present on each arm II and III in males. **Male genitalia paired**.

Size: Mantle length to 45 mm.

Geographical Distribution: Tropical and subtropical western and eastern North Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Fig. 262).

Habitat and Biology: Mesopelagic in daytime, vertical migrator to epipelagic at night.

Literature: Voss (1962c), Lea (1985), Voss and Stephen (1992), Vecchione (2008i).



ventral view of male

Fig. 261 ***Selenoteuthis scintillans***

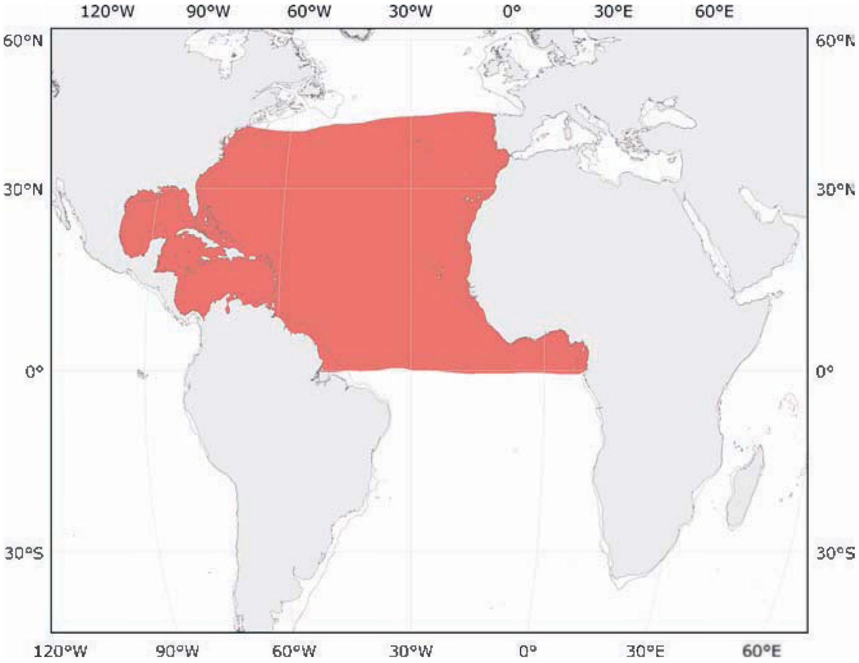


Fig. 262 ***Selenoteuthis scintillans***

🟥 Known distribution

Subfamily **LAMPADIOTEUTHINAE** Berry, 1916

Lampadioteuthinae Berry, 1916, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68: 45–66 [51].

Type Genus: *Lampadioteuthis* Berry 1916.

Lampadioteuthis Berry, 1916

Lampadioteuthis Berry, 1916, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68: 45–66 [52].

Type Species: *Lampadioteuthis megaleia* Berry, 1916

Lampadioteuthis megaleia Berry, 1916

Fig. 263

Lampadioteuthis megaleia Berry, 1916, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68: 45–66 [52, figs 4–14, pl 8]. [Type locality: Sunday Island, Kermadec Islands, southwestern Pacific Ocean]

Frequent Synonyms: None.

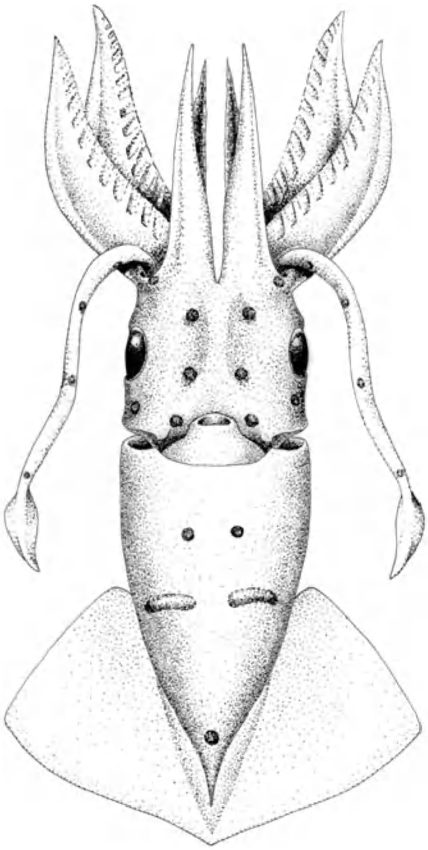
FAO Names: En – Wonderful firefly squid; **Fr** – Encornet luciole marveilleux; **Sp** – Lucernaluria maravillosa.

Diagnostic Features: Four ocular photophores present: 3 ventral in a line, 1 lateral. **One stalked photophore at the base of each tentacle**. Right ventral arm hectocotylized in males, with an enlarged protective membrane at midpoint. **Five visceral photophores present**: 2 anal, circular, 2 branchial, transversely elongate, 1 postero-abdominal, circular. Numerous functional chromatophores present; external skin overlying photophores with violet pigment.

Size: Mantle length to 40 mm.

Geographical Distribution: Subtropical North Atlantic Ocean; Gulf Stream and northern zone of Sargasso Sea; southwestern Pacific Ocean. Upper mesopelagic to epipelagic (Fig. 264).

Literature: Voss (1962c), Nesis (1982, 1987), Guerra (1992), Young and Vecchione (2008b).



ventral view of male

Fig. 263 ***Lampadioteuthis megaleia***

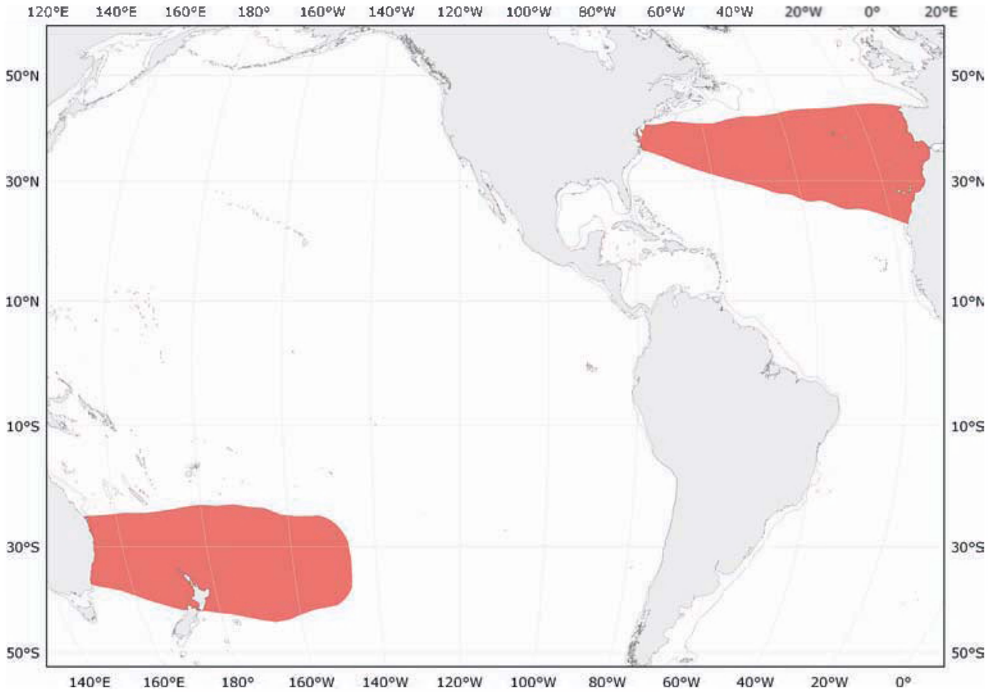


Fig. 264 ***Lampadioteuthis megaleia***

🟥 Known distribution

2.18 Family MAGNAPINNIDAE Vecchione and Young, 1998

by Clyde F.E. Roper and Patrizia Jereb

Magnapinnidae Vecchione and Young, 1998, *South African Journal of Marine Science*, 20: 429–437 [430].

Type Genus: *Magnapinna* Vecchione and Young 1998: 430.

FAO Names: En – Bigfin squids; **Fr** – Encornets ailé; **Sp** – Lurias aladas.

Diagnostic Features: Mantle proportionally very small, plump, thinly muscled. **Fins terminal, extremely large, heart-shaped, 3 to 3.3 times longer than the functional mantle**, even longer than entire squid from functional mantle tip to tips of arms and tentacles; width nearly equal to length. **Tentacles short, thick, robust**, with fleshy trabecular membranes; keels and carpal-locking apparatus absent; tentacular club suckers very small, arranged in about 8 transverse series, except fewer at the base; dentition unknown; **distal tips of tentacles very thin, pointed, vermiform, devoid of suckers**. **Arms short**; basal portion thick, crowded with suckers in series of 2, 3 or 4, but **distally become abruptly vermiform, devoid of suckers**. Funnel-locking cartilage oval, with deep depression anteriorly; tragus and antitragus absent. Buccal connectives attach to ventral margins of Arms IV. Photophores absent (apparently). Ink sac small, with patch of reflective tissue on ventral surface.

Size: Only juveniles, paralarvae and damaged specimens none to date.

Geographical Distribution: The known specimens were captured in the eastern North Pacific Ocean, in tropical to subtropical waters and in the North Atlantic Ocean (Gulf of Mexico and Azores Islands).

Interest to Fisheries: None.

Remarks: This remarkable family is monogeneric, known only from a few specimens from the Pacific and Atlantic oceans. The Pacific specimens were caught roughly in a line between offshore California to off the Hawaiian Islands, eastern North Pacific Ocean. One juvenile and the paralarva were caught in plankton nets that fished 0 to 200 m and 0 to 300 m, respectively, while the second juvenile was taken from the stomach of a lancet fish, *Alepisaurus ferox*, a lower epipelagic to upper mesopelagic species. The specimens from the North Atlantic also were young, immature squids. In addition, sightings of a very unusual deep-sea squid have been reported, based on observations, photos and videos taken from submersibles and ROV's (remotely operated vehicles). While none of the animals were captured, the authors of the report tentatively identified them as possibly the adults of Magnapinnidae (Vecchione *et al*., 2001). Remarkably, no specimens of this size or appearance have ever been captured in deep-sea trawls. Observations were made at depths of 1 940 to 4 734 m, and the size of the largest specimen was estimated to be 7 m total length. These observations came from the western Atlantic Ocean off Brazil, eastern Atlantic Ocean off Africa, Gulf of Mexico, Indian Ocean, and central Pacific Ocean. They suggest the famly is circumglobal. The Magnapinnidae belongs to the chiroteuthid group of families.

Literature: Vecchione and Young (1998), Guerra *et al*. (2002b), Sweeney and Young (2003q), Vecchione and Young (2006).

Magnapinna Vecchione and Young, 1998

Magnapinna Vecchione and Young, 1998, *South African Journal of Marine Science*, 20: 429–437 [430], figs 1–4.

Type Species: *Magnapinna pacifica* Vecchione and Young, 1998.

Frequent Synonyms: None.

Remarks: Currently 5 species are recognized, 1 from the Pacific Ocean and 4 from the Atlantic Ocean. However, only 3 species have been completely described and named: ***Magnapinna pacifica*** (from the Pacific Ocean), ***M. atlantica*** and ***M. talismani*** (from the Atlantic Ocean). Two other potential species have been recognized from the Atlantic, but the specimens are too incomplete to enable full descriptions and names (Vecchione and Young, 2006).

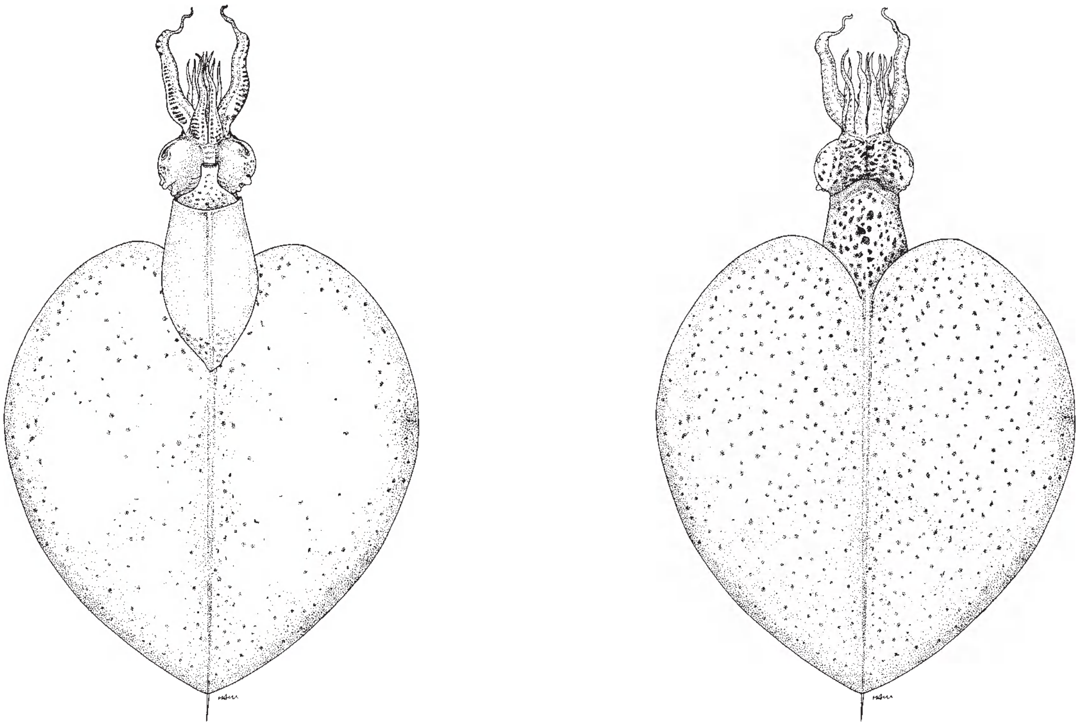
Magnapinna pacifica Vecchione and Young, 1998

Fig. 265

Magnapinna pacifica Vecchione and Young, 1998, *South African Journal of Marine Science*, 20: 429–437 [430]. [Type locality: 33°49'N, 121°51'W, western North Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Pacific bigfin squid; **Fr** – Encornet ailé du Pacifique; **Sp** – Luria alada del Pacífico.



ventral view **dorsal view**

Fig. 265 ***Magnapinna pacifica***

Size: Mantle length including huge fin and gladius tip, 53 mm. Only 2 juveniles and 1 paralarva are known.

Geographical Distribution: The species occurs in the eastern to central North Pacific Ocean in subtropical to tropical waters (Fig. 266).

Literature: Vecchione and Young (1998), Vecchione and Young (2006).

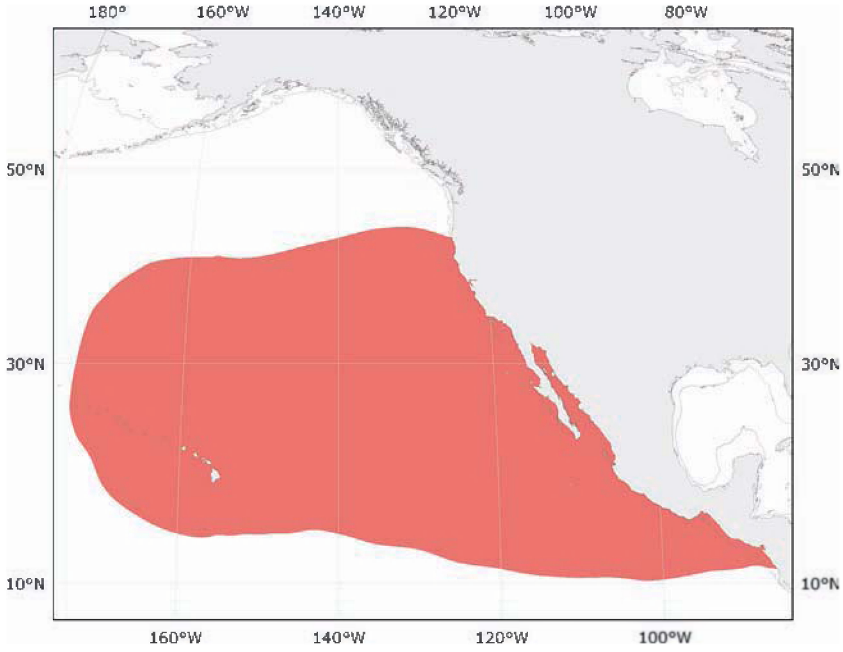


Fig. 266 ***Magnapinna pacifica***

🟥 Known distribution

Magnapinna atlantica Vecchione and Young, 2006

Magnapinna atlantica Vecchione and Young, 2006, *Proceedings of the Biological Society of Washington*, 119(3): 365–372 [367], figs 1–3,4f. [Type locality: 27°09'N, 86°07'W, Gulf of Mexico, western Equatorial Atlantic Ocean].

Frequent Synonyms: None.

Size: Mantle length of the 2 known specimens is 53 and 59 mm.

Geographical Distribution: North Atlantic: Gulf of Mexico, mid-Atlantic Ridge.

Literature: Vecchione and Young (2006).

Magnapinna talismani (Fischer and Joubin, 1907)

Mastigoteuthis talismani Fischer and Joubin, 1907, *Expéditions scientifiques du Travailleur et du Talisman – Céphalopodes*, 8: 313–353 [342]. [Type locality: 34°46'N, 36°11'W, Azores Islands, eastern Atlantic Ocean].

Frequent Synonyms: *Mastigoteuthis talismani* Fischer and Joubin, 1907.

Size: Mantle length 61 mm.

Geographical Distribution: Known from a single specimen taken from south of the Azores, North Atlantic Ocean.

Remarks: ***Magnapinna talismani*** was originally described from a single damaged specimen that came from south of the Azores, North Atlantic, very near the capture site of ***M. atlantica*** and the specimens belonging to the unnamed ***Magnapinna*** species. The identy of ***M. talismani*** is uncertain, and the poor condition of the holotype which has lost most species-level characters makes comparisons with other species difficult. However, several features suggest that it is not conspecific with ***M. atlantica*** Vecchione and Young (2006). Thus ***M. talismani*** was originally placed in the genus ***Chiroteuthopsis*** which is a junior synonym of ***Mastigoteuthis***, and was placed in ***Magnapinna*** by Vecchione and Young (2006).

Literature: Vecchione and Young (2006).

2.19 Family MASTIGOTEUTHIDAE Verrill, 1881

by Clyde F.E. Roper and Patrizia Jereb

Mastigoteuthidae Verrill, 1881a, *Transactions of the Connecticut Academy of Sciences*, 5(6): 259–446 [430].

Type Genus: *Mastigoteuthis* Verrill, 1881.

FAO Names: En – Whiplash squids; **Fr** – Loutènes filamentoux; **Sp** – Flageloluria.

Diagnostic Features: Mantle weakly muscular to semigelatinous; anterior portion cylindrical, posterior part tapered, conical. **Fins very large**, with half or more of their length posterior to the muscular part of the mantle; oval to round, heart- or diamond-shaped, usually longer than 50% of mantle length. **Ventral arms very elongate, thickest of all arms**, possess expanded lateral membranes; **arm suckers biserial, no arm hooks**. **Tentacles vermiform, extremely long, slender, whip-like, weakly muscled** (often lost during capture); transverse muscles used to rapidly extend/deploy tentacles, e.g. for prey capture, are nearly absent; clubs not expanded or only slightly expanded; **club elongate with very numerous (often thousands) small to microscopic suckers** arranged in many irregular series (usually more than 15, even more than 30 in some species); **club without keels or locking (fixing) apparatus**. Buccal membrane with seven lappets; buccal connectives attach to ventral borders of arms IV. **Funnel-locking apparatus ear-shaped or oval with various knobs** (tragus, antitragus) that affect the shape of the depression in the funnel component in different species; mantle component with nose-shaped or L-shaped ridges. Gladius narrow, with long conus that forms a needle-like tail spike that extends posterior to terminus of fins. **Coloration an overall reddish to maroon cutaneous pigmentation**, much of which not incorporated in chromatophores but dispersed in other integumental cells; many typical chromatophores usually present, but their mobility is uncertain. Photophores variously present in most species: some species with numerous minute, round cutaneous organs embedded in ventral surface of mantle, head and arms; 1 on the anteroventral edge of eyelid; some with only eyelid photophores and 1 (***Mastigoteuthis hjorti***) with 2 photophores on ventral surface of eyeball.

Size: Medium to large-sized squids, maximum mantle length to 1 m.

Habitat and Biology: Deep sea pelagic or benthopelagic squids. Paralarvae do not exhibit a high degree of sudden (breakpoint) morphological change during early ontogeny; tentacle length increases disproportionately rapidly as a support for the “dangling tentacle” feeding technique observed *in situ* on adult ***Mastigoteuthis hjorti*** and presumed for juveniles. Observations from submersibles recorded mastigoteuthid squids in close proximity to the bottom, oriented vertically with head down and tentacles extended to the sediment, presumably to capture copepods and other small plankton of the epibenthic zooplankton; position was maintained by gentle undulations of the very large fins. The tentacles are supported proximally by the tentacular sheath of arms IV and are held apart in the “tuning fork” posture. Additional observations from submersibles at 700 to 1 000 m support hypotheses that the large fins provide propulsion. Tentacular suckers have a weak release-mechanism (they adhere like fly paper to anything they touch) and retain a sensory function; these morphologies enable the species to forage in the relatively food-rich zone on and immediately above the bottom. Closing net captures of ***Mastigoteuthis*** species have helped to define their diel vertical distributions: in general, minor diel vertical shifting occurs. Observations from submersibles, as well as morphological and histological examination of the giant nerve fibers in the mantle indicate the absence of a strong, rapid jet propulsion capability. Tissues of the mantle, head and especially the large ventral arms are vesiculate and contain ammonium ions in the tissue fluid, providing near-neutral buoyancy; the positive buoyancy of the anterior portion is overcome by complex rhythmic wave-like undulations of the fins to maintain the head-down posture during feeding.

Interest to Fisheries: No direct interest to fisheries exists for any of the species. However, Mastigoteuthids are occasional or important prey species for numerous oceanic predators, among them the following: lancetfish, swordfish, blue shark and cetaceans, such as, for example, sperm whales, dwarf sperm whale, long-finned pilot whale, southern bottlenose whale, Hubb’s beaked whale.

Remarks: The Mastigoteuthidae is among the most taxonomically confused of all deep-sea squid families, principally because many characters are based on the structures frequently lost during capture, e.g. tentacles and skin photophores. Further, the family includes many poorly known species, some described only from one or very few, often badly damaged, specimens, or from paralarvae.

Several genera and subgenera have been erected for various entities of mastigoteuthids, and the systematics of the family has been in a state of flux for many years. In recent times, Salcedo-Vargas and Okutani (1994) proposed a generic and subgeneric classification based on actual or presumed morphological characteristics. Considerable modification of this classification subsequently was proposed by Salcedo-Vargas (1997) and former subgeneric names were dropped. Extensive systematic and nomenclatural studies on the family and new findings are due to Vecchione *et al.* (2007a) and Young *et al.* (2008a, b). Phylogenetic data also are available for a few species and genetic studies are in progress (e.g. Young *et al.*, pers.comm.).

In the absence of a comprehensive systematic monograph and waiting until our knowledge has increased to the point where a full phylogenetic study can be made, we agree with Vecchione *et al.* (2007a) on the fact that modifying the classification within the family currently is premature. Consequently, in this Catalogue we consider the family Mastigoteuthidae to be monogeneric, with the single genus ***Mastigoteuthis***, comprised of 13 valid nominal species; other species, of doubtful validity or uncertain status, are listed at the end of the section. All nominal genera and species are listed by Sweeney and Young (2003r).

Among the characters most frequently used to distinguish species are ramifications of the familial characters. These include, but are not limited to: variations in arm IV dimensions; tentacular club relative length and degree of expansion, numbers of suckers in transverse series, size and dentition of inner and outer sucker rings, presence of enlarged central club sucker and the proportion of tentacle club length they occupy; number and configuration of knobs on funnel-locking apparatus (including tragus and antitragus), depth of depression in funnel component of locking apparatus; presence/absence of photophores, their number, configuration, distribution and size on integument of mantle, head, arms; presence/absence, size and shape of photophores on anteroventral eyelid; presence/absence, numbers, configuration of photophores on ventral surface of eye ball; arm sucker dentition; presence/absence of integumentary tubercles on mantle; relative fin length to mantle length; relative fin width to fin length, relative length of “tail spike” to mantle length .

Because so many of the nominal species are poorly known, it is not possible to provide a key to the species of Mastigoteuthidae. Instead, a breakdown into species and groups of species that share a few characters is given (Vecchione *et al*., 2007a).

Species groups

1. ***Mastigoteuthis agassizii*** group: ***M. agassizii***, ***M. dentata***, ***M. psychyrophila***

Characteristics:

a. Numerous, small but easily seen integumental photophores.

b. Broadly spaced chromatophores.

2. ***Mastigoteuthis cordiformis***

Characteristics:

a. No photophores.

b. Club with very large suckers (about 0.5 mm diameter) at proximal end.

c. Skin tubercles present.

3. ***Mastigoteuthis danae***

Characteristics:

a. Large integumentary tubercles in advanced paralarvae.

b. Fins longer than wide.

4. ***Mastigoteuthis glaukopis*** group: ***M. glaukopis***, ***M. atlantica***, ***M. famelica***

Characteristics:

a. Large eyelid photophore present.

b. No other photophores present.

5. ***Mastigoteuthis hjorti***

Characteristics:

a. Two photophores on each eyeball.

b. Very large fins (fin length about 90% of mantle length).

6. ***Mastigoteuthis magna*** group: ***M. magna***, ***M. microlucens***

Characteristics:

a. Flask-shaped funnel-locking apparatus.

b. Very small (ca. 0.05 mm diameter) tentacular club suckers.

7. ***Mastigoteuthis pyrodes***

Characteristics:

a. Numerous, small, but easily seen integumental photophores and a much larger photophore on each eyelid.

b. Funnel-locking apparatus broad, without antitragus and with undercut posterior margin and tragus.

c. Large club suckers (about 0.3 mm diameter).

8. ***Mastigoteuthis tyroi***

Characteristics:

a. Clubs expanded in paralarval stage.

b. Integumentary tubercles present in paralarval stage.

Literature: Roper and Lu (1990), Vecchione and Roper (1992 [1991]), Salcedo-Vargas and Okutani (1994), Salcedo-Vargas (1995), Salcedo-Vargas and Young (1996), Roper and Vecchione (1997), Salcedo-Vargas (1997), Sweeney and Young (2003r), Vecchione *et al*. (2002, 2007a).

Mastigoteuthis Verrill, 1881 **Plate VIII, 45**

Mastigoteuthis Verrill, 1881b, Bulletin of the Museum of Comparative Zoology, 8(5): 99-116. [100].

Type species: *Mastigoteuthis agassizii* Verrill, 1881 [100].

Frequent synonyms: *Chirtoteuthopsis* Pfeffer, 1900; *Echinoteuthis* Joubin, 1933; *Idioteuthis* Salcedo-Vargas and Okutani, 1994 (uncertain status).

Mastigoteuthis agassizii Verrill, 1881 **Fig. 267**

Mastigoteuthis agassizii Verrill, 1881b, *Bulletin of the Museum of Comparative Zoology*, 8(5): 99–116 [100]. [Type locality: 33°35'N, 76°00'W and 34°28'N, 75°22'W, western North Atlantic Ocean].

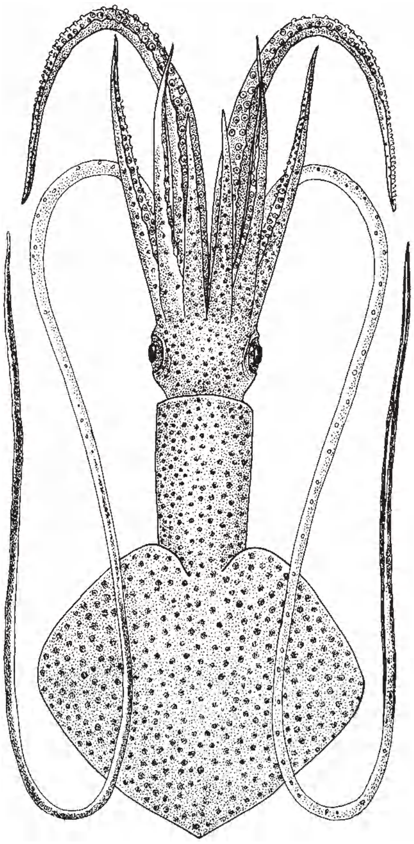
FAO Names: En – Agassizi's whiplash squid; **Fr** – Loutène filamentoux de Agassizi; **Sp** – Flageloluria de Agassizi.

Size: Maximum mantle length reaches 100 mm.

Geographical Distribution: Central North Atlantic ocean (Fig. 268).

Remarks: This species may have 2 forms, a north temperate/boreal form and a tropical form that cannot be separated with any certainty at present (Vecchione and Young 2007a). The type locality of ***Mastigoteuthis agassizii*** (about 34°N) in warm temperate waters off the eastern United States is a region where the boreal and tropical forms of ***M. agassizii*** could overlap. Two other names are available for the temperate/boreal form if it proves to be distinct: ***M. grimaldii*** described by Joubin (1895b) from a damaged 38 mm mantle length squid taken near the Azores at 39°43'N, 33°22'W and ***M. schmidti*** described by Degner (1925) from a 46 mm mantle length squid in excellent condition taken from the Bay of Biscay at 46°30'N, 07°00'W. One name is available for the tropical form if it proves to be distinct: ***M. flammea*** described by Chun (1910) from 2 small squid (27 and 35 mm ML) captured in the eastern tropical Atlantic (0°25'N, 7°0'E and 1°14'N, 2°10'W), both of which had lost their tentacles.

Literature: Shea and Vecchione (2006), Vecchione and Young (2007a), Young and Vecchione (2007c).



dorsal view

Fig. 267 *Mastigoteuthis agassizii*

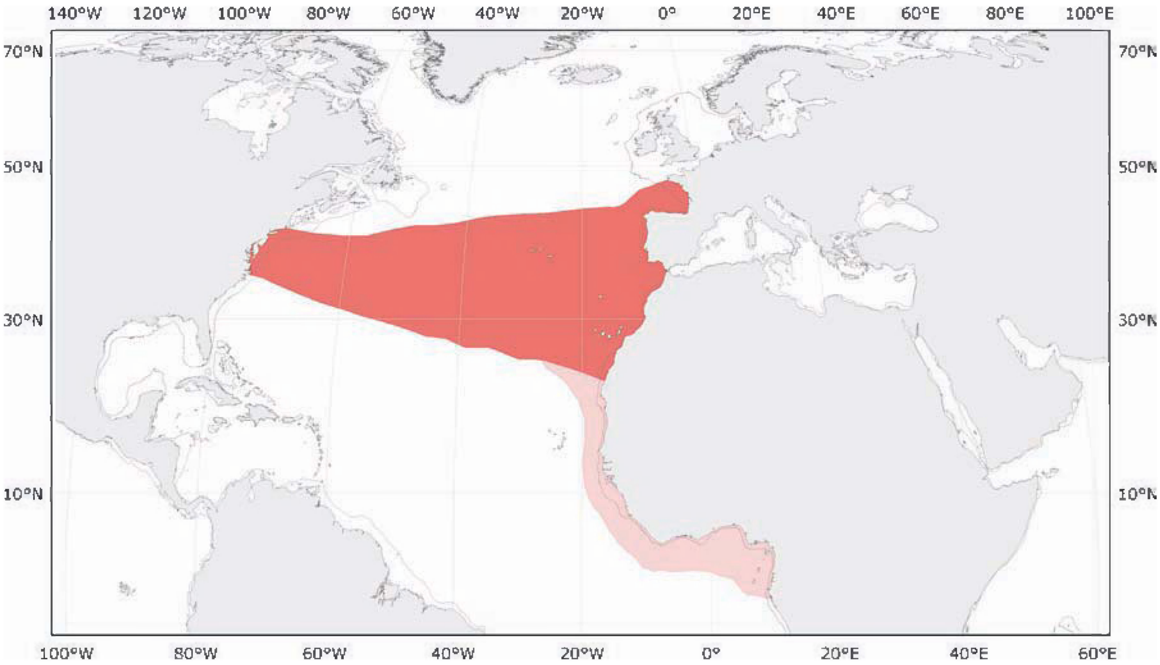


Fig. 268 *Mastigoteuthis agassizii*

🟥 Known distribution ▨ Probable presence

SPECIES ACCOUNTS

The species listed here are those defined in Vecchione *et al.* (2007a); since these authors list species groups as well as single species, the 13 named species are arranged alphabetically here.

Mastigoteuthis atlantica Joubin, 1933

Mastigoteuthis atlantica Joubin, 1933, *Annales de l'Institut Océanographique*, 13(1): 1–49 [20]. [Type locality: 46°28'N, 08°01'W, near the Bay of Biscay, eastern North Atlantic Ocean].

Size: Maximum mantle length reaches 120 mm.

Geographical Distribution: This species occurs in the eastern North and South Atlantic Ocean.

Literature: Guerra (1992), Vecchione and Young (2007b).

Mastigoteuthis cordiformis Chun, 1908

Mastigoteuthis cordiformis Chun, 1908, *Zoologischer Anzeiger*, 33(2): 86–89 [88]. [Type locality: 0°15'N, 98°08'E, off Nias Island, Sumatra, Indonesia, eastern Indian Ocean].

Size: Maximum mantle length known to reach 700 mm. (Unpublished reports record it to 1 m or more).

Geographical Distribution: Broadly distributed on the continental slope in the Indo-West Pacific, Indonesia, the Philippines, southern Japanese waters and of the Northwest Slope, Australia, the Tasman Sea and New Zealand waters.

Habitat and Biology: This wide-ranging species lives in tropical and subtropical waters to depths of 1 000 m and undergoes diel vertical migration.

Literature: Roper and Lu (1990), Dunning (1998g), Young and Vecchione (2008d,e).

Mastigoteuthis danae (Joubin, 1933)

Echinoteuthis danae (Joubin, 1933), *Annales de l'Institut Océanographique*, 13(1): 1–49 [13]. [Type locality: 34°40'N, 33°16'W, southwest of the Azores Islands, eastern North Atlantic Ocean].

Size: Maximum mantle length known to 30 mm.

Geographical Distribution: Eastern central North Atlantic Ocean in subtropical waters. Other localities near the Antilles and east of the Canary Islands.

Remarks: Known only from a few paralarval and juvenile specimens.

Literature: Vecchione and Young (2007c).

Mastigoteuthis dentata Hoyle, 1904

Mastigoteuthis dentata Hoyle, 1904, *Bulletin of the Museum of Comparative Zoology*, 43(1): 1–72 [34]. [Type locality: 07°21'N, 79°35'W off Cape Mala, Panama, Gulf of Panama, eastern North Pacific Ocean].

Size: Maximum mantle length known to reach 72 mm.

Geographical Distribution: Tropical eastern and western North and South Pacific Ocean, waters off Panama and the Galapagos Islands. Indian Ocean from southern Africa.

Literature: Young and Vecchione (2007c).

Mastigoteuthis famelica (Berry, 1909)

Chiroteuthis famelica Berry, 1909, *Proceedings of the United States National Museum*, 37(1713): 407–419 [414]. [Type locality: off Kauai Island, Hawaiian Islands, central North Pacific Ocean].

Size: Maximum mantle length reported is in excess of 300 mm.

Geographical Distribution: Restricted to the central North Pacific Ocean.

Habitat and Biology: The species occupies the zone of about 675 m to 800 m, both day and night.

Literature: Roper and Young (1975), Young (2008b).

Mastigoteuthis glaukopis Chun, 1908

Mastigoteuthis glaukopis Chun, 1908, *Zoologischer Anzeiger*, 33(2): 86–89 [88]. [Type locality: 04°63'N [sic], 48°37'E, Arabian Sea, Indian Ocean].

Size: Maximum mantle length known to reach 100 mm.

Geographical Distribution: The distribution of the species seems very disjunct. It has been reported from the western North Pacific Ocean off Japan, the northwestern Indian Ocean, Arabian Sea off Somalia, southwestern Indian Ocean, southeastern South Atlantic Ocean, off South Africa and eastern North Atlantic Ocean off Spain and Portugal.

Literature: Kubodera (*in* Okutani) (2000), Young and Vecchione (2007d).

Mastigoteuthis hjorti Chun, 1913

Plate VIII, 46

Mastigoteuthis hjorti Chun, 1913, *Report on the Scientific Results of the Michael Sars North Atlantic Deep-sea Expedition 1910*, 3(1): 1–28 [8]. [Type locality: 31°24'N, 34°47'W in the open tropical central North Atlantic Ocean].

Size: Maximum mantle length reaches 100 mm.

Geographical Distribution: Very broadly distributed, possibly as a tropical-subtropical circumglobal species with northern limits of about 40°N and southern boundaries undetermined. It occurs in the North Atlantic Ocean from eastern regions of the Gulf of Mexico, northward to Bermuda and to the Gulf of Maine, in the western North Atlantic Ocean, and in the eastern Atlantic Ocean, off South Africa, the central Pacific Ocean and the Indian Ocean.

Literature: Rancurel (1973a), Roper and Lu (1990), Vecchione and Roper (1992 [1991]), Nesis (1999b), Vecchione and Young (2007d).

Mastigoteuthis magna Joubin, 1913

Mastigoteuthis magna Joubin, 1913, *Bulletin de l'Institut Océanographique, Monaco*, 275: 1–11 [2]. [Type locality: 31°44.5'N, 42°39'W, in the mid-North Atlantic Ocean].

Size: Maximum mantle length known 160 mm.

Geographical Distribution: ***Mastigoteuthis magna*** appears to have a disjunct distribution. It occurs commonly throughout the western central North Atlantic, from the Bahamas, off Cape Hatteras, North Carolina, and northward, as well as along a transect in the eastern central Atlantic at 30°W. The species also occurs over deep water in the western North Pacific Ocean off Japan.

Literature: Lu and Roper (1979), Vecchione and Roper (1992 [1991]), Roper and Vecchione (1997), Shea and Vecchione (2002), Vecchione and Young (2007e).

Mastigoteuthis microlucens Young, Lindgren and Vecchione 2008

Mastigoteuthis microlucens Young, Lindgren and Vecchione 2008a, *Proc. Biol. Soc. Wash.*, 121(2): 276–282. [Type locality: Hawaiian Archipelago to about ca. 26°N].

Size: Maximum mantle length 215 mm.

Geographical Distribution: Hawaiian Island, tropical Pacific Ocean.

Remarks: This is the most common species of ***Mastigoteuthis*** around the main Hawaiian Islands. It has numerous tiny photophores that lie beneath the outer layer of integumental chromatophores. The photophores are so small that they cannot be recognized as photophores without the aid of a microscope.

Literature: Young *et al.* (2008a,b), Young and Vecchione (2008e).

Mastigoteuthis psychrophila Nesis, 1977

Mastigoteuthis psychrophila Nesis, 1977b, *Zoologicheskij Zhurnal*, 65(6): 835–842 [835]. [Type locality: 59°26'S, 158°36'E, Antarctic Ocean waters south of eastern Australia at 500 m at night].

Size: Maximum mantle length is 150 mm.

Geographical Distribution: Circumpolar in the sub-Antarctic and Antarctic waters, with records from mesopelagic to bathypelagic depths over sub-Antarctic and Antarctic island trenches, e.g. South Sandwich, Macquarie and Hjort Trenches and off South Georgia's northwest slope.

Literature: Nesis (1982, 1987), Lu and Williams (1994a), Young and Vecchione (2007e).

Mastigoteuthis pyrodes Young, 1972

Mastigoteuthis pyrodes Young, 1972a, *Smithsonian Contributions to Zoology,* 97: 1–159 [64]. [Type locality: 33°32'N, 118°23'W, far eastern North Pacific Ocean].

Size: Maximum mantle length is known to reach 170 mm.

Geographical Distribution: Limited to the California Current waters off Southern California, eastern North Pacific Ocean.

Remarks: This is the only species of ***Mastigoteuthis*** known to occur in eastern North Pacific waters.

Literature: Roper and Young (1975), Young and Vecchione (2007f).

DOUBTFUL AND QUESTIONABLE SPECIES FOR WHICH ADDITIONAL MATERIAL, NEW DATA AND FURTHER RESEARCH ARE NECESSARY BEFORE THEY CAN BE CONSIDERED VALID

Mastigoteuthis hastula (Berry, 1920)

Chiroteuthoides hastula Berry, 1920a, *Proceedings of the United States National Museum*, 58(2335): 293–300, 1 plate [293, pl. 16 fig. 3]. [Type locality: 28°59'N, 69°22'W, Sargasso Sea, western North Atlantic Ocean].

Mastigoteuthis inermis Rancurel, 1972

Mastigoteuthis inermis Rancurel, 1972, *Bulletin de la Société Zoologique de France*, 97(1): 25–34 [25]. [Type locality: 4.5°N, 4°W, Gulf of Guinea, eastern tropical North Atlantic Ocean,].

Mastigoteuthis iselini MacDonald and Clench, 1934

Mastigoteuthis iselini MacDonald and Clench, 1934, *Occasional Papers of the Boston Society of Natural History*, 8: 145–152 [150]. [Type locality: 39°04'N, 71°29'W, western North Atlantic Ocean].

Mastigoteuthis latipinna Sasaki, 1916

Mastigoteuthis latipinna Sasaki, 1916, *Annotationes Zoologicae Japonenses*, 9(2): 89–120 [108]. [Type locality: 'outside" the Okinose Bank, Sagami Sea, Japan, western North Pacific Ocean].

Mastigoteuthis okutanii Salcedo-Vargas, 1997

Mastigoteuthis okutanii Salcedo-Vargas, 1997, *Beaufortia*, 47: 91–108 [101]. [Type locality: approximately 51°N, 09°E, off the coast of Somalia, Arabian Sea, western Indian Ocean].

Mastigoteuthis tyroi Salcedo-Vargas, 1997

Mastigoteuthis tyroi Salcedo-Vargas, 1997, *Beaufortia*, 47(3): 91–108 [99] [Type locality: approximately 08.1°N, 56.1°E, off the coast of Somalia, Arabian Sea, northwestern Indian Ocean].

Size: Maximum mantle length known is 15 mm.

Geographical Distribution: Arabian Sea, northwestern Indian Ocean.

Remarks: The holotype, a paralarva, is the only specimen known, so the status of the species requires additional material, at least of the subadult stage.

Literature: Salcedo-Vargas and Young (2007).

2.20 Family NEOTEUTHIDAE Naef, 1921

by Clyde F.E. Roper and Patrizia Jereb

Neoteuthidae Naef, 1921a, *Mitteilungen aus der Zoologischen Station zu Neapel*, 22(16): 527–542 [540].

Type Genus: *Neoteuthis* Naef, 1921: 540.

FAO Names: En – Neosquids; **Fr** – Loutènes nouveau; **Sp** – Neolurias.

Diagnostic Features: Small- to medium-sized squids (to 270 mm mantle length). Mantle medium to elongate to very narrow, conical; weakly muscled. **Fins unusual with posterior fin lobes present, anterior lobes absent**; attach laterally onto mantle muscle. **Head relatively enlarged, wider than mantle**. Tentacular clubs with dorsal keels, terminal pads and carpal/stalk locking apparatus; **clubs divided into distinct dual sections**: **1) the proximal manus with extremely numerous closely-packed, minute suckers in irregular, numerous transverse series (more than 10)**; **2) the distal manus with 4 series of suckers, somewhat larger to much larger than the distal manal suckers**; **dactylus with smaller suckers than distal manus, in 4 transverse series** (reduced near tip); club locking apparatus extends along proximal manus and in most genera along the tentacular stalk (*Neoteuthis* excepted). Arms with biserial suckers, some develop hooks in adults. Buccal connectives attach to dorsal margins of arms IV. Funnel-locking apparatus a simple, straight groove. Fins variable among genera; length 35 to 70% of mantle length; anterior fin lobes absent, posterior fin lobes present, free; fins usually attach to dorsolateral surface of mantle, especially anteriorly, not attached along midline of mantle. Aboral surfaces of arms and the head and mantle covered with thick white tissue in most genera. **Photophores absent**.

Size: Small- to medium-sized squids up to 270 mm mantle length.

Geographical Distribution: Variously distributed in the North and South Atlantic oceans, North and South Pacific oceans and Antarctic waters, in water masses that range from subtropical to Antarctic.

Habitat and Biology: Relatively few specimens are available for most species, but in general the paralarvae tend to be captured in the upper several hundred metres, while the subadults and adults tend to be captured in the mesopelagic and upper bathypelagic zones, 1 000 to 2 000 m. *Alluroteuthis antarcticus* seems to be very abundant, as its young are reported as prey to albatrosses and emperor and king penguins, while southern elephant seals, southern bottlenose whales and sperm whales prey on adults. All species appear to have a buoyancy mechanism; in *A. antarcticus* it is known to be ammoniacal in nature.

Interest to Fisheries: None. The relatively small size of most species and, especially the ammoniacal nature of the mantle tissue, preclude an interest in utilization at this time. *Alluroteuthis antarcticus* might be an exception, because of its size (270 mm mantle length) and abundance.

Local Names: USA: New squids.

Remarks: The Neoteuthidae currently is recognized to consist of 4 genera, each with a single species: *Alluroteuthis, Narrowteuthis, Neoteuthis* and *Nototeuthis*. The long-used family designation of Alluroteuthidae was corrected to Neoteuthidae based on priority (Voss, 1967a).

Literature: Roper *et al*. (1969b), Nesis (1982, 1987), Nesis and Nikitina (1986b), Vecchione and Roper (1992 [1991]), Nesis (1999b), Sweeney and Young (2003s), Vecchione and Young (2003a,b), Young and Vecchione (2005a,b), Vecchione and Young (2008c).

Table 4

Comparison of characters among genera[1/]

Genus	Club length	Proximalmanus length relative to remaining distal club length	Tentacle locking apparatus	Manal sucker laterally compressed	Two greatly enlarged suckers on distal manus	Arm sucker dentition	Fin length
Alluroteuthis	33%	<1/3 X	Manus, stalk	No	No	Single large tooth	35–40% ML
Narrowteuthis	20% ML	1.1 X	Manus, stalk	Yes	No	Smooth	35% ML
Neoteuthis	60% ML	4.8 X	Manus	No	No	Truncated teeth	70% ML
Nototeuthis	37% ML	3/4 X	Manus, stalk	No	Yes	Truncated teeth	60% ML

[1/] Vecchione and Young (2003a, Tree of Life).

Neoteuthis Naef, 1921

Neoteuthis Naef, 1921a, *Mitteilungen aus der Zoologischen Station zu Neapel,* 22(16): 527–542. [540].

Type Species: *Neoteuthis thielei* Naef, 1921.

Frequent Synonyms: None.

Neoteuthis thielei Naef, 1921

Fig. 269

Neoteuthis thielei Naef, 1921, *Mitteilungen aus der Zoologischen Station zu Neapel*, 22(16): 527–542. [540]. [Type location: 32°08'S, 08°28'W, Benguela Current, west of South Africa, South Atlantic Ocean].

Frequent Synonyms: None.

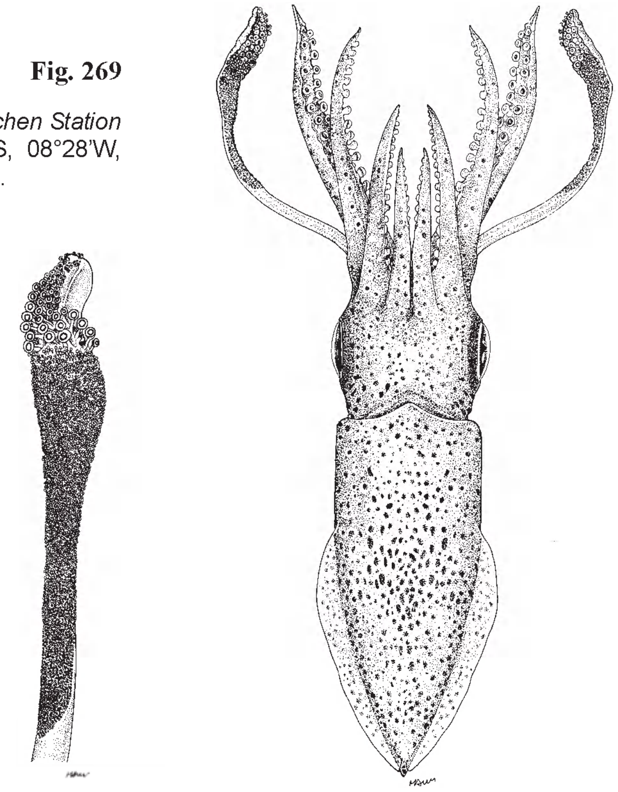
FAO Names: En – Thiele's new squid; **Fr** – Loutène nouveau de Thiele; **Sp** – Neoluria de Thiele.

Size: 100 mm mantle length.

Geographical Distribution: South Atlantic Ocean, North Atlantic Ocean and North Pacific Ocean, north of Hawaiian Islands.(Fig. 270).

Habitat and Biology: Paralarvae and juveniles epipelagic to mesopelagic; adults are mesopelagic to bathypelagic.

Literature: Vecchione and Young (2003a). See family literature list.



tentacular club

dorsal view

Fig. 269 *Neoteuthis thielei*

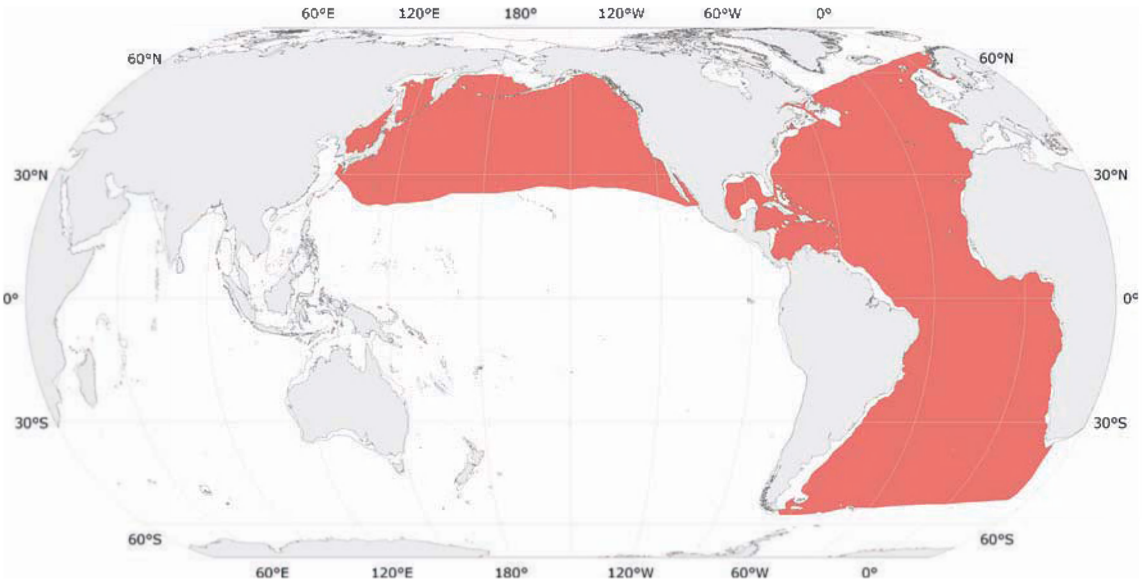


Fig. 270 *Neoteuthis thielei*

🟥 Known distribution

Alluroteuthis Odhner, 1923

Alluroteuthis Odhner, 1923, *Zoological Results of the Swedish Antarctic Expedition*, 1901–1903, 1(4): 1–7 [2].

Type Species: *Alluroteuthis antarcticus* Odhner, 1923.

Frequent Synonyms: None.

Alluroteuthis antarcticus Odhner, 1923

Fig. 271

Alluroteuthis antarcticus Odhner, 1923, *Zoological Results of the Swedish Antarctic Expedition*, 1901–1903, 1(4): 1–7. [2]. [Type locality: 63°25'S, 45°39'W, Weddell Sea, Antarctic Ocean].

Frequent Synonyms: *Parateuthis tunicata* Thiele, 1920.

FAO Names: En – Antarctic new squid; **Fr** – Loutène australe; **Sp** – Neoluria antárctica.

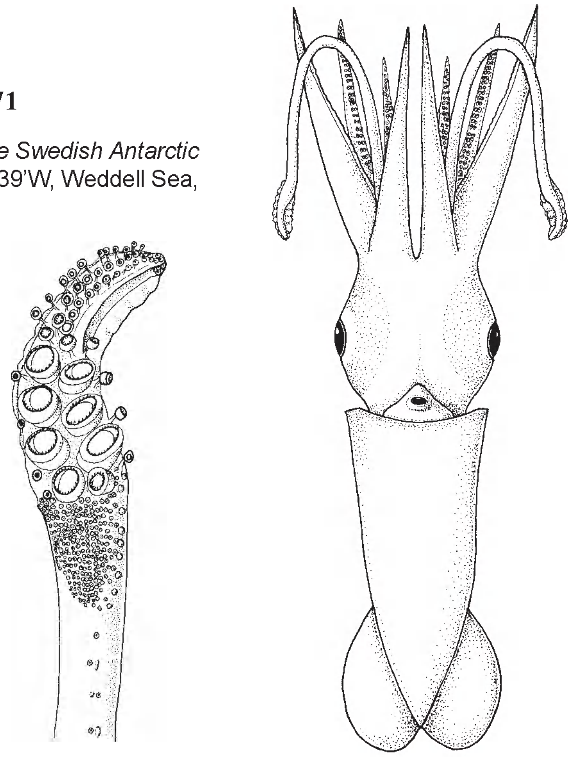
Diagnostic Features: Tentacular clubs short (33% of mantle length) with proximal manus <33% of mantle length, manal and stalk locking apparatus, circular proximal manal suckers with toothed inner rings, **greatly enlarged manus suckers in medial series**, enlarged tooth/hook on proximal arm suckers, **fins short** (35 to 40% of mantle length).

Size: The maximum mantle length extends to 270 mm.

Geographical Distribution: This species is circumglobal in Antarctic oceanic waters south of 50°S (Antarctic Convergence) (Fig. 272).

Habitat and Biology: Paralarvae and juveniles are mesopelagic; adults are mesopelagic to bathypelagic at 750 to 2 800 m. Adults concentrate at 800 to 900 m during the day, spread out vertically at night; ontogenetic descent occurs with juveniles and subadults. Prey of southern elephant seals. In turn, adult ***A. antarcticus*** prey upon myctophid fishes and krill (*Euphausia superba*).

Literature: Filippova and Yukhov (1982), Rodhouse (1988), Lu and Williams (1994a), Rodhouse and Piatkowski (1995), Young *et al.* (1999a), Filippova (2002a,b).



tentacular club

dorsal view

Fig. 271 ***Alluroteuthis antarcticus***

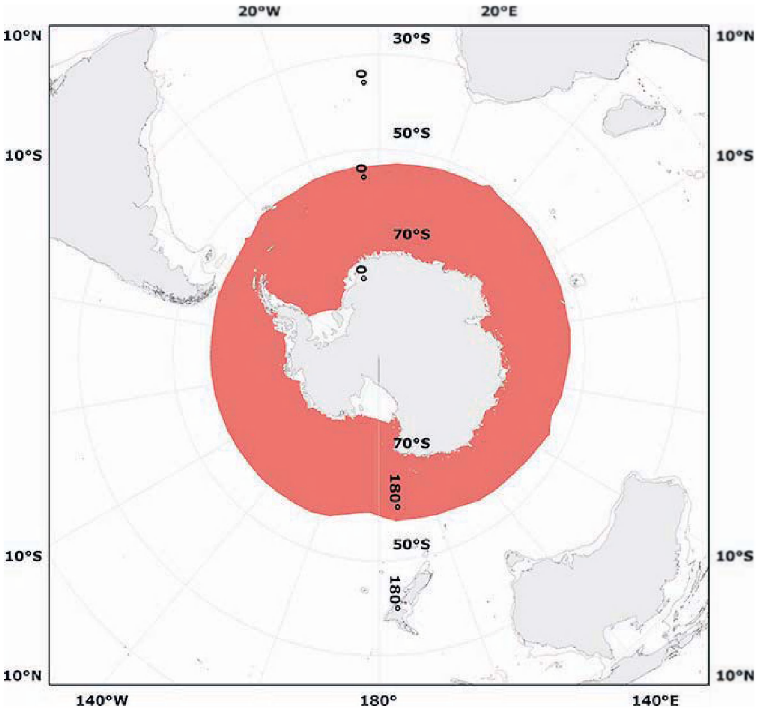


Fig. 272 ***Alluroteuthis antarcticus***

🟥 Known distribution

Narrowteuthis Young and Vecchione, 2005

Narrowteuthis Young and Vecchione, 2005a, *Proceedings of the Biological Society of Washington*, 118(3): 566–569 [566].

Type Species: *Narrowteuthis nesisi* Young and Vecchione, 2005.

Frequent Synonym: None.

Narrowteuthis nesisi Young and Vecchione, 2005

Fig. 273

Narrowteuthis nesisi Young and Vecchione, 2005a, *Proceedings of the Biological Society of Washington*, 118(3): 566–569. [566]. [Type locality: 27°18'N, 19°44'W, off Canary Islands, eastern North Atlantic Ocean].

Frequent Synonym: None.

FAO Names: En – Nesis' narrow squid; **Fr** – Loutène nouveau de Nesis; **Sp** – Neoluria de Nesis.

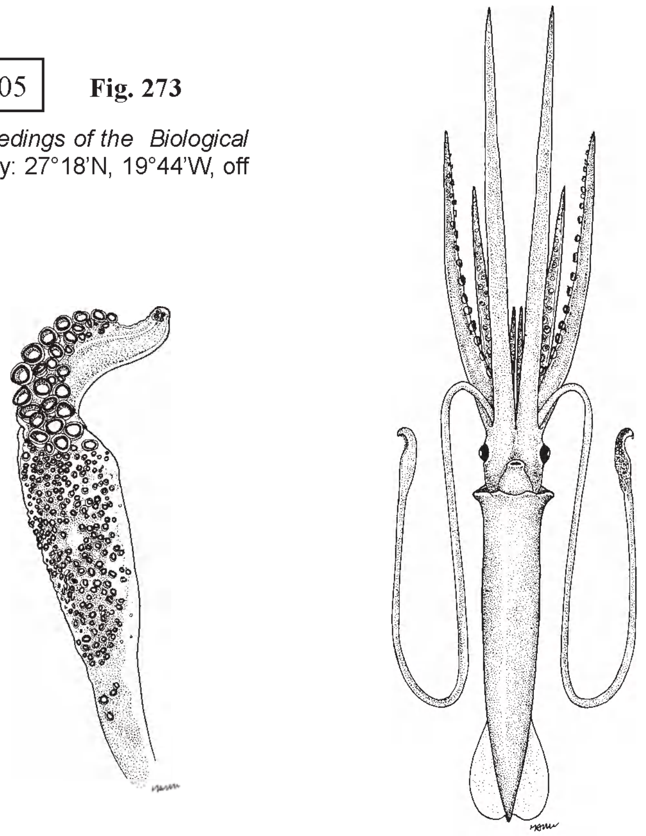
Size: Mantle length 100 mm.

Geographical Distribution: Eastern North Atlantic Ocean, off Canary Islands (Fig. 274).

Habitat and Biology: Specimens are bathypelagic at 1 750 to 2 000 m.

Remarks: Only 2 specimens of this species are known.

Literature: Young and Vecchione (2005a,b).



tentacular club ventral view

Fig. 273 *Narrowteuthis nesisi*

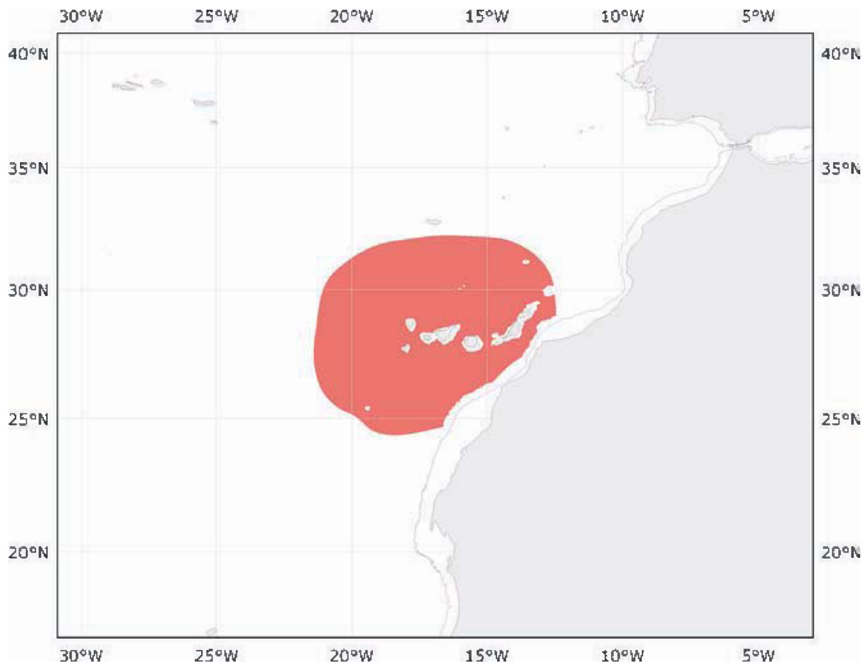


Fig. 274 *Narrowteuthis nesisi*

🟥 Known distribution

Nototeuthis Nesis and Nikitina, 1986

Nototeuthis Nesis and Nikitina, 1986b, *Zoologicheskij Zhurnal*, 65(2): 290–294. [290].

Type Species: *Nototeuthis dimegacotyle* Nesis and Nikitina, 1986.

Frequent Synonyms: None.

Nototeuthis dimegacotyle Nesis and Nikitina, 1986

Fig. 275

Nototeuthis dimegacotyle Nesis and Nikitina, 1986b, *Zoologicheskij Zhurnal*, 65(2): 290–294 [290]. [Type locality: 50°38.5'S, 081°40.5'W, off southern Chile, eastern south Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Large sucker neosquid; **Fr** – Loutène nouveau grand-ventose; **Sp** – Neoluria ventosa-grande.

Diagnostic Features: Clubs short (<40% of mantle length), **fins long** (60% of mantle length); **2 greatly enlarged suckers on distal-manus**.

Size: The mantle length grows to 83 mm.

Geographical Distribution: Eastern and southern South Pacific Ocean between the Southern Subtropical and the Antarctic Polar frontal zones (Fig. 276).

Habitat and Biology: This species is mesopelagic to bathypelagic, it occurs from the surface down to 500 m depth.

Literature: Nesis and Nikitina (1986b, 1992), Vecchione and Young (2003b), Okutani (2005).

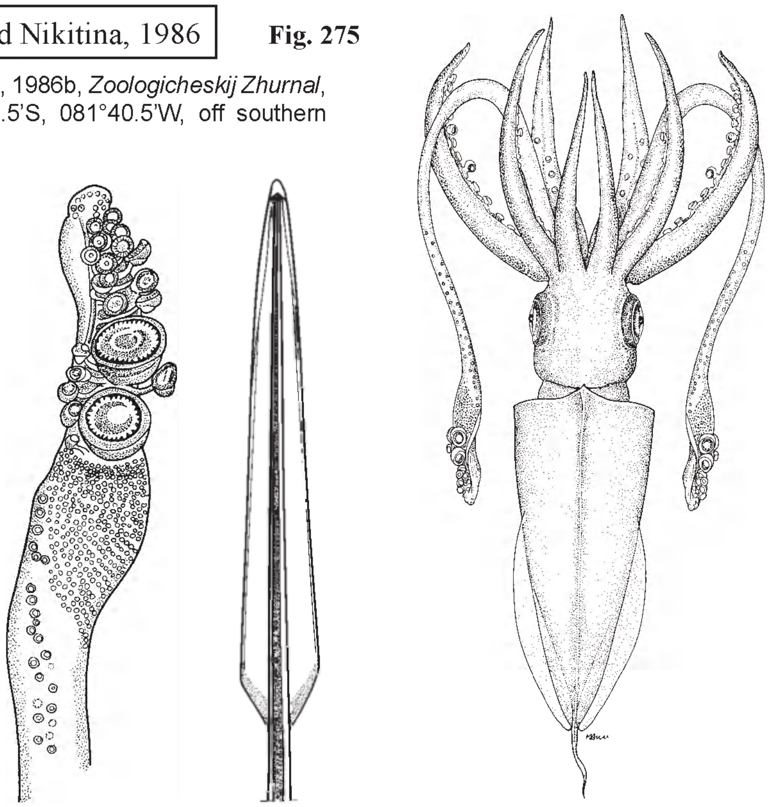

tentacular club gladius dorsal view

Fig. 275 ***Nototeuthis dimegacotyle***

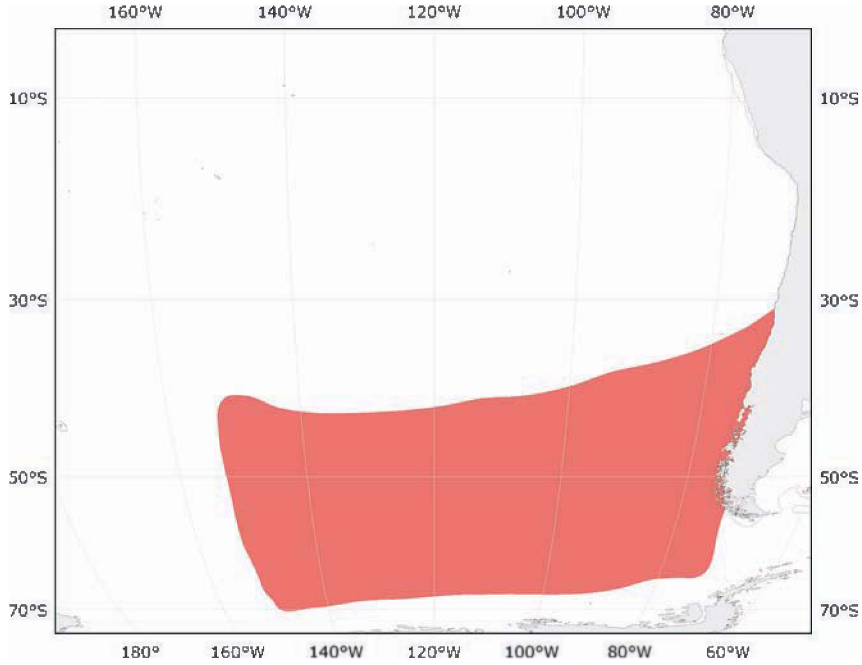


Fig. 276 ***Nototeuthis dimegacotyle***

🟥 Known distribution

2.21 Family OCTOPOTEUTHIDAE Berry, 1912

by Clyde F.E. Roper and Patrizia Jereb

Octopoteuthidae Berry, 1912, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 64(2): 380–444 [432].

Type Genus: *Octopoteuthis* Rüppell, 1844:[134].

FAO Names: En – Octopus squids; **Fr** – Encornets poulpes; **Sp** – Pulpotas.

Diagnostic Features: Body mainly soft, semi-gelatinous. Mantle broad, elongate, subconical, weakly muscled; tapers posteriorly to bluntly to moderately acuminate tip (tail). **Fins very long, broad, transversely oval, muscular**; **fused together along dorsal midline of mantle**; **fin length approaches mantle length in adults**; a small U-shaped area occurs on anterior edge of fins, and demarcates the small anterior fin lobes. Head broad, with large prominent eyes. **Arms with biserial hooks enveloped in soft integumentary sheaths**; small to minute suckers in 2 series occur only near the arm tips. **Tentacles** occur only in paralarvae and very early juveniles; **absent in adults**; clubs short, spatulate with about 8 proportionally large suckers in 2 series; a few suckers may be "greatly" enlarged. Buccal membrane with 6 supports and lappets; buccal connectives attach to ventral borders of arms IV. Funnel-locking cartilage a simple, straight, elongate groove, slightly widened posteriorly. Gladius very thin; a wide vane originates at anterior end, extends posteriorly to small terminal conus. **Photophores present on tips of some or all arms**; photophores may be embedded in the tissue of head and/or mantle and/or arms. **Hectocotylus absent**; **penis often greatly enlarged, elongate**; **may extend well beyond the mantle opening**.

Size: Medium- to large-sized squids, up to 1.5 m mantle length.

Geographic Distribution: Globally distributed in tropical and subtropical waters.

Habitat and Biology: Species of this family inhabit mesopelagic to bathypelagic and benthic-bathyal zones of tropical and temperate waters, but they also venture into boreal waters. They frequently are preyed upon by odontocete cetaceans, particularly sperm whales.

Interest to Fisheries: As a relatively soft-bodied, semi-gelatinous form, its generally mesopelagic habitat and its rarity in collections, this family would seem to have little current potential for a sustainable fishery.

Local Names: USA: Eight-arm squids.

Remarks: The family consists of 2 genera, ***Octopoteuthis*** and ***Taningia***. ***Octopoteuthis*** includes 7 species, mostly poorly known, while ***Taningia*** is currently recognized as monotypic. While the arm tips of ***Octopoteuthis*** species possess delicate elongate photophores, they frequently are missing in specimens, because the arm tips seem especially fragile and break off during capture. ***Taningia*** has a very large, bulbous photophore on the tips of arms II. Considerable confusion has existed over the correct familial name for this group and for the type genus. Rüppell's (1844) original (and intended) designation was ***Octopoteuthis***, clearly in reference to the absence of tentacles in adults (the paralarvae and juveniles were unknown at the time of the original description). Krohn (1845) introduced ***Octopodoteuthis*** as a replacement name, but that was without explanation or justification; subsequently this name has been officially designated an "unjustified emendation". Then Krohn (1847) changed the name to ***Verania*** because the tentacles were discovered on the paralarvae; this name, too, is untenable. Likewise the designations of the family as Octopodoteuthidae or Veranyidae are untenable, being based on junior synonyms of ***Octopoteuthis*** (see discussions in Berry, 1912; Adam 1952; Roper *et al*., 1969b; Roper and Vecchione, 1993).

Literature: Young (1972a), Nesis (1982, 1987), Stephen (1985a, b), Stephen and Jefferts (1992), Roper and Vecchione (1993), Young and Vecchione (1996b), Sweeney and Young (2003t).

Key to the genera of Octopoteuthidae (adults)

1a. A small, narrow, spindle-shaped photophore on the tips of all arms; photophores embedded in tissue of mantle, head and arms (varies among species); tentacles present in paralarvae; always weak, gelatinous; lost at about 12 mm mantle length; mantle lengths to 500 mm, usually not in excess of 200 mm . . . . ***Octopoteuthis***

1b. A large oval, swollen composite photophore on tip of each arm II; it consists of a creamy white crenulate, luminous-producing surface, exposed when eyelid-like skin flaps are retracted; no photophores on any other arms; no (known) photophores embedded in tissues of mantle, head or arms; tentacles conspicuous in paralarvae with robust stalks up to about 40 mm mantle length, after which they diminish and disappear; mantle length up to 1.5 m . . . . ***Taningia***

Key to the genera of Octopoteuthidae (paralarvae, juveniles)[1/]

1a. Tentacles with weak, gelatinous stalks that are lost at sizes greater than 12 mm mantle length; when still present, tentacles longer than arms with up to about 8 proportionally large suckers; tentacle bases may be present up to about 25 mm mantle length; arms usually proportionally longer; some arm suckers develop into hooks by 2.5 mm mantle length in some species; paired photophores may develop on ink sac by 15 mm mantle length . . . . ***Octopoteuthis***

1b. Tentacles with robust stalks, clubs with 8 small suckers; tentacles much shorter than arms II (except longer at 2 mm mantle length in Hawaiian species), occur up to about 38 mm mantle length before being lost; arms proportionally short, robust; no hooks develop before 5 mm mantle length; large, single, median photophore on ink sac by 5 mm mantle length . . . . ***Taningia***

Octopoteuthis Rüppell, 1844

Octopoteuthis Rüppell, 1844, *Giornale del Gabinetto Letterario di Messina*, 5(27–28): 129–135 [134].

Type Species: *Octopoteuthis sicula* Rüppell, 1844.

Frequent Synonyms: *Octopodoteuthis* Krohn, 1845; *Verania* Krohn, 1847; *Octopodoteuthopsis* Pfeffer, 1912.

Diagnostic Features: Tips of all 8 arms with a terminal, small, black-pigmented, spindle-shaped photophore without lateral folds of skin ("eyelid" structure). **Small photophores deeply embedded in tissues of mantle, head and arms** (number and size vary among species). Fin width in juveniles does not exceed (or just barely) mantle length. Tentacles entirely reduced by end of paralarval stage, at about 10 to 15 mm mantle length.

Size: The mantle length can attain a maximum of 500 mm, but normally it reaches 200 mm.

Remarks: The systematics of ***Octopoteuthis*** species composition still are quite unsettled because 1) several holotypes are no longer extant or are too damaged to yield pertinent data; 2) only 1 or a very few specimens are available for some nominal species; 3) subsequently discovered characters (e.g. embedded photophores) are undescribed/unknown for some entities. At present the genus has 7 named but poorly defined species (Young and Vecchione, 2008f): ***Octopoteuthis danae, O. deletron, O. indica, O. nielseni, O. megaptera, O. rugosa, O. sicula***. Young (1972a) and Clarke (1980) consider ***O. indica*** Naef, 1923 and ***O. nielseni*** Robson, 1948 to be insufficiently characterized for specific identification/delineation. Sweeney and Young (2003t) list them as valid species from a nomenclatural point of view. ***Octopoteuthis persica*** Naef, 1923, was transferred to ***Taningia*** by Young (1972a) and ***O. longiptera*** Akimushkin, 1963, now is accepted as a *species dubium* (Young, 1972a, Clarke, 1980, Sweeney and Young, 2003t).

Literature: Young (1972a), Sweeney and Young (2003t), Young and Vecchione (2008f).

[1/] from Steven and Jefferts (1992).

Octopoteuthis sicula Rüppell, 1844

Fig. 277

Octopoteuthis sicula Rüppell, 1844, *Giornale del Gabinetto Letterario di Messina*, 5(27–28): 129–135 [135]. [Type locality: western Mediterranean Sea].

Frequent Synonyms: None.

FAO Names: En – Rüppell's octopus squid; **Fr** – Encornet-pouple de Rüppell; **Sp** – Pulpito volador.

Diagnostic Features: Mantle conical, short; **acuminate posteriorly**; musculature flabby with gelatinous integumentary layer and rugosities. **Fins large, length around 90% of the mantle length, width 115% of mantle length**; extend to posterior tip of mantle. **A pair of photophores embedded in posterior mantle**, about 20 to 25% of mantle length from posterior tip. Head gelatinous; **3 pairs of embedded photophores on lateral sides of funnel groove and near neck**; photophores embedded at bases of arms III and IV. Tail short, indistinct in juveniles.

Size: The mantle length grows to 200 mm (possibly to 500 mm).

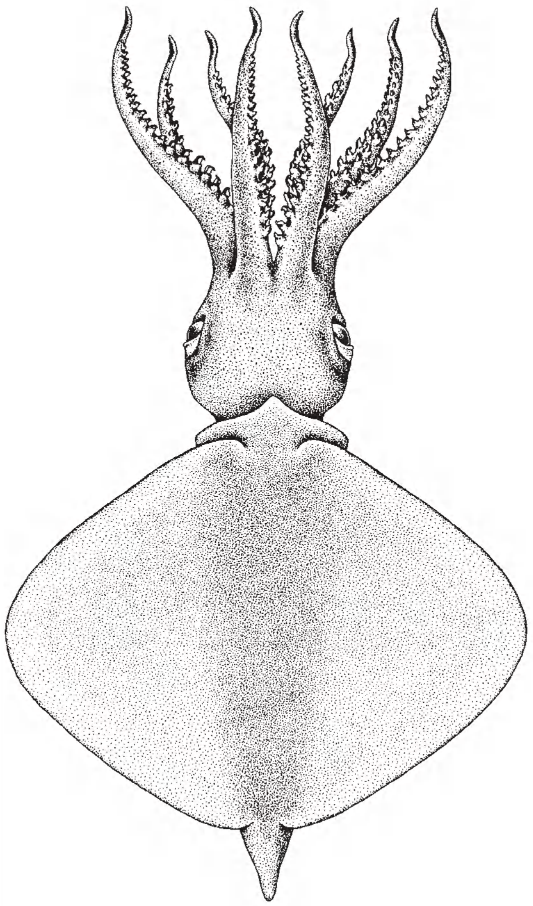
Geographical Distribution: This species occurs in tropical, subtropical, subtemperate waters in the Atlantic Ocean to South Africa and in the Indo-West Pacific Ocean; Mediterranean Sea; possibly tropical eastern Pacific Ocean from Mexico to Chile, westward to Hawaii (Fig. 278).

Habitat and Biology: Its vertical distribution is mesopelagic to bathypelagic (to 2 000 m) during daytime with nocturnal ascent into epipelagic zone. In the eastern North Atlantic Ocean juveniles are caught from May to September as planktonic vertical migrators. Predators include numerous oceanic fish species, such as tunas, swordfish, dolphin fish, lancetfish, albatrosses, dolphins, toothed whales, including sperm whales and Cuvier's beaked whales, and ***Sthenoteuthis*** squid.

Interest to Fisheries: Because of the semi-gelatinous consistency of the flesh, it seems unlikely that this species will be fished for human consumption until processing techniques develop; it does, however, grow to a suitable size.

Local Names: ITALY: Totano-polpo; RUSSIA: Vosmirukyi kalmar.

Literature: (See list under family); Nesis (1982, 1987), Stephen (1985a,b), Guerra (1992), Dunning and Lu (1998), Hoving *et al*. (2006b, 2008).



dorsal view

Fig. 277 *Octopoteuthis sicula*

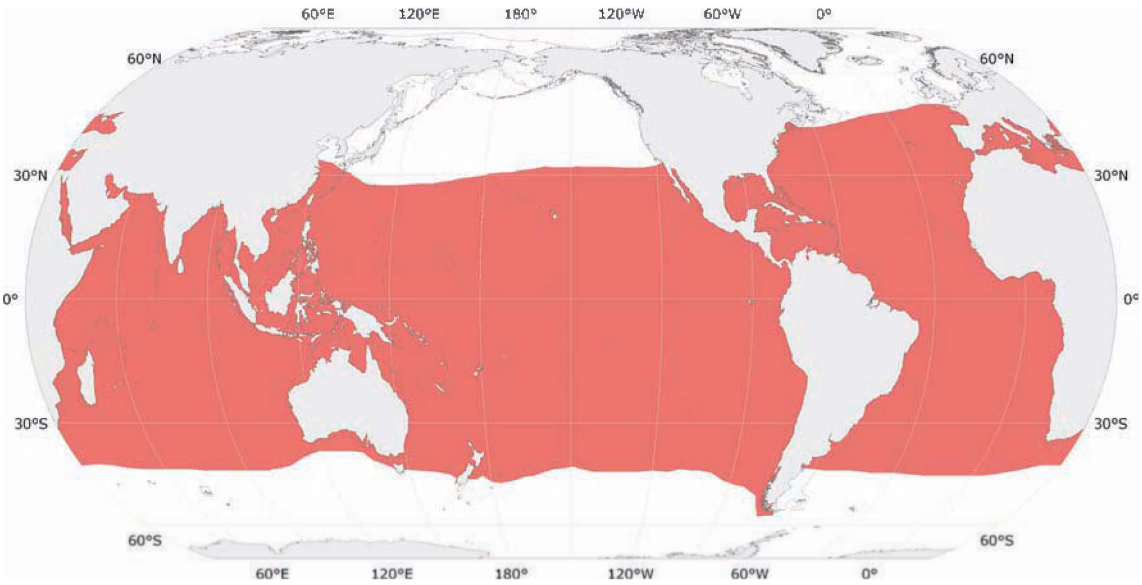


Fig. 278 *Octopoteuthis sicula*

🟥 Known distribution

Taningia Joubin, 1931

Taningia Joubin, 1931, *Annales de l'Institut Océanographique, Monaco*, 10(7): 169–211 [181].

Type Species: *Taningia danae* Joubin, 1931.

Frequent Synonyms: *Cucioteuthis* Steenstrup, 1882a.

Diagnostic Features: Mantle broad, robust, muscular, entirely pigmented an intense maroon. **Tips of arms II only with a large, oval, swollen, composite photophore with a creamy white, crenulate biolouminescent-producing surface, exposed when black eyelid-like skin folds are contracted open (no photophores on tips of any other arms)**; photophores begin to develop at about 4.5 to 5 mm mantle length; no photophores (known to) exist embedded in the tissues of the mantle, head or arms; 1 photophore is embedded on each side of the intestine ventral to the ink sac. **Fins very large, occupy nearly entire mantle length** by about 3 mm mantle length of the paralarva and throughout life; fins **very broad, far in excess of mantle length** (up to 130% of mantle length). Tentacles robust on paralarvae, with some of the 8 suckers considerably enlarged; **tentacles** cease to develop and are **lost at a mantle length of 40 to 45 mm** (although stumps may remain for some time). **Arms with large hooks in 2 series to the tips**, where minute suckers may occur as incipient hooks; hooks begin to develop at about 5 mm mantle length. ***Taningia*** currently is recognized as monotypic. Lower beak broad; jaw edge visible from side is slightly longer than wing length in small specimens or slightly shorter in larger specimens; hood broad, with a distinct medial notch; wing fold poorly developed, covered with cartilage and hardly concealing jaw angle in profile; the shoulder is mainly cartilage but near jaw angle the chitin forms a shoulder ridge; crest slightly thickened; a distinct thickened fold runs to a position about halfway between the crest and the corner of the lateral wall.

Size: These squids attain mantle lengths in excess of 1.5 m.

Remarks: ***Taningia*** currently is recognized as monotypic.

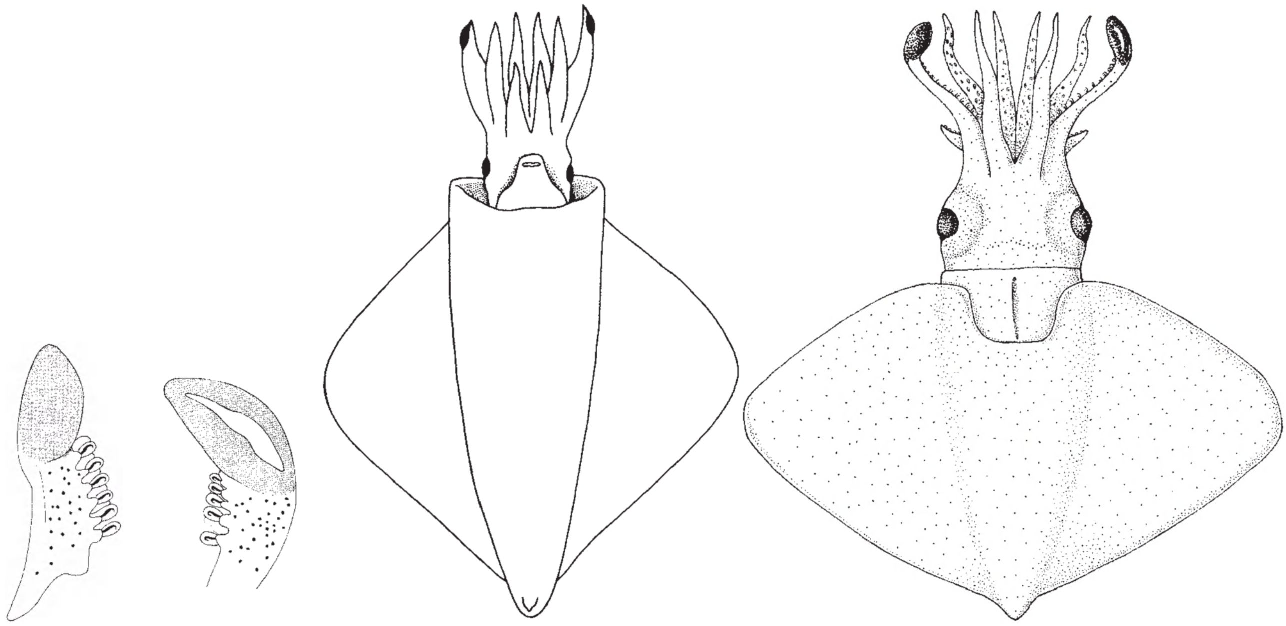
Taningia danae Joubin, 1931

Fig. 279; Plate VIII, 47–48

Taningia danae Joubin, 1931, *Annales de l'Institut Océanographique, Monaco*, 10(7): 169–211 [181]. [Type locality: 14°52'N, 28°04'W, central Atlantic Ocean].

Frequent Synonyms: *Sepia unguiculata* Molina, 1782; *Cucioteuthis unguiculatus* Joubin, 1898b, 1900; *C. unguiculatus*, Clarke, 1966; *C. unguiculata*, Rees and Maul, 1956; *C. unguiculata*, Clarke, 1962.

FAO Names: En – Taning's octopus squid; **Fr** – Encornet-poulpe de Taning; **Sp** – Pulpota de Taning.



ventral view dorsal view

arms II photophores

ventral view

dorsal view

Fig. 279 *Taningia danae*

Diagnostic Features: The characters are those of the monotypic genus.

Size: The maximum mantle length recorded is 170 cm; maximum weight 161 kg (see Remarks section for details).

Geographical Distribution: ***Taningia danae*** is circumglobal in tropical and subtropical waters; it occurs from 50°N to 55°N to 40°S to 45°S throughout the Atlantic Ocean, throughout the Pacific Ocean, including Hawaiian, Japanese and New Zealand waters, and across the Indian Ocean. It was captured for the first time 2006 in the Mediterranean Sea during a trawl survey of the Algerian coast at 385 to 395 m (Fig. 280).

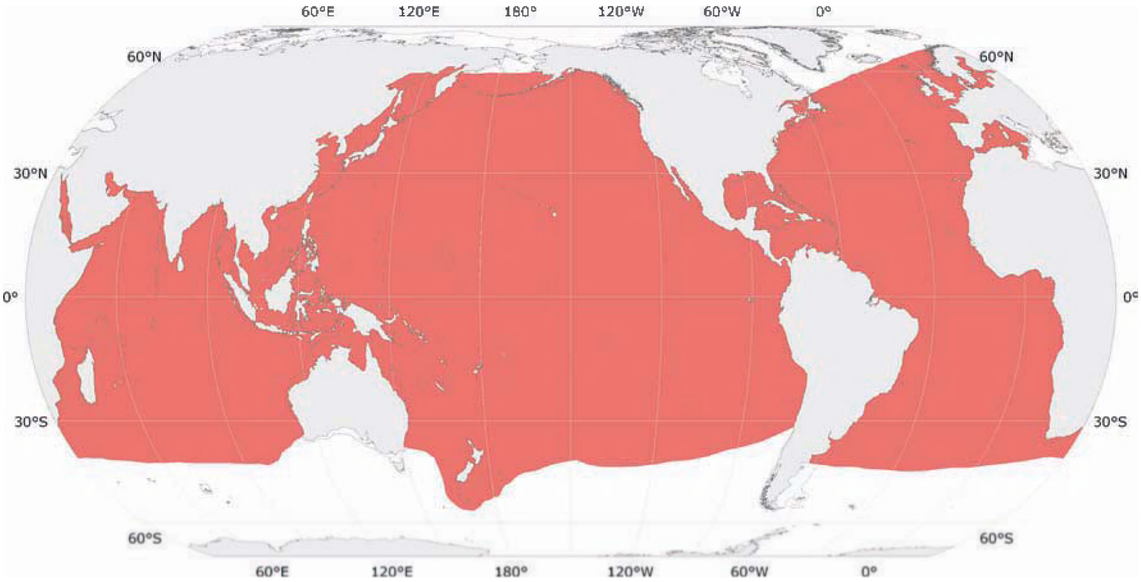


Fig. 280 *Taningia danae*

🟥 Known distribution

Habitat and Biology: ***Taningia danae*** is an oceanic species; paralarvae and juveniles are epipelagic to upper mesopelagic, then undergo ontogenetic descent into the lower mesopelagic, bathypelagic and bathyal zones. Adults undergo diel vertical migration and ascend into the epipelagic zone at night. Juveniles have been captured at night within 175 m of the surface, while the remains of a large specimen (50 kg) were taken from the stomach of the bottom-living shark, *Centroscymnus coelolepis*, caught on a bottom-set longline at 1 246 m. A mature female of 1.4 m mantle length had 250 000 ovarian eggs. Observations on bioluminescence from living animals verified a rapid flash response from the arm tip photophores, as a startling or warning function, and a steady glow from the visceral photophores as is common for protective counter illumination. *In situ* video footage reveals that ***T. danae*** is a strong swimmer; both forward and backward, propelled by its huge fins, and it changes directions quickly by bending its body. It attained speeds of 7.2 to 9 km/h when it attacked the bait rig. It emitted short, bright flashes from its 2 arm-tip photophores before it attacked. It also emits long and short glows intermittent glows when swimming around the lighted bait rig. ***Taningia danae*** is preyed upon by many species of pelagic fishes, including lancetfish (*Aleposauris ferox*), tunas, swordfish (*Xiphias gladius*), hammerhead, tiger and blue sharks, as well as odontocete cetaceans: short-finned pilot whale and most especially, sperm whales in all oceans.

Interest to Fisheries: ***Taningia danae*** grows to a very large size, up to 170 cm mantle length and 161.4 kg, with thick mantle and fin musculature. It is thought that a good potential exists for the development of a significant fishery for this species.

Remarks: The maximum reported mantle length for the species is 170 cm (Nesis, 1982, 1987). The maximum reported weight is 161.4 kg, for the specimen of 160 cm mantle length recorded in the North Atlantic Ocean (Roper and Vecchione, 1993); in that paper, however, a typographical error occurred and a weight of 64.4 kg was reported. This species was captured for the first time in the Mediterranean Sea in 2006, during a trawl survey off the Algerian coast, at 385 to 395 m (Quetglas *et al*., 2006).

Local Names: None available.

Literature: Okutani (1974a), Roper and Young (1975), Herring *et al*. (1992a), Roper and Vecchione (1993), Nesis (1999a), Gonzalez *et al*. (2003), Quetglas *et al*. (2006), Kubodera *et al*. (2007a).

SPECIES OF NO CURRENT INTEREST TO FISHERIES, OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST TO DATE

Octopoteuthis danae Joubin, 1931

Octopodoteuthis danae Joubin, 1931, *Annales de l'Institut Océanographique, Monaco*, 10(7): 169–211 [185]. [Type locality: 35°15'N, 68°20'W, northwest of Bermuda Islands, western North Atlantic Ocean].

Frequent Synonyms: *Octopodoteuthis danae* Joubin, 1931.

Size: Mantle length small, undetermined.

Geographical Distribution: Subtropical North Atlantic Ocean, Sargasso Sea, Senegal. One specimen captured in closing net at 100 to 50 m at night in eastern North Atlantic Ocean.

Literature: Lu and Clarke (1975b), Herring *et al*. (1992a), Okutani (2005).

Octopoteuthis deletron Young, 1972

Octopoteuthis deletron Young, 1972, *Smithsonian Contributions to Zoology*, 97: 1–159 [40]. [Type locality: 33°15'N, 118°37'W, off southern California, eastern North Pacific Ocean].

Size: Mantle length attains a total of 170 mm.

Geographical Distribution: Range extends approximately from off Washington to off Baha California; 1 record off northern Peru (07°45'S) represents a possible disjunct distribution.

Habitat and Biology: Vertical distribution is 200 to 700 m during day time, mostly 200 to 400 m; at night population ascends and disperses to 0 to 500 m.

Literature: Young (1972a), Nesis (1982, 1987), Young (1999c), Young and Vecchione (2006b).

Octopoteuthis indica (Naef, 1923)

Octopodoteuthis indica Naef, 1923, *Fauna e Flora de Golfo di Napoli, Monograph 35*, 1(1)(part 2): 149–863 [336]. [Type locality: Agulhas current, off South Africa, eastern South Atlantic Ocean].

Frequent Synonyms: *Octopodoteuthis indica* Naef, 1923.

Size: Undetermined.

Geographical Distribution: Eastern South Atlantic Ocean, off South Africa.

Literature: Roeleveld (1998).

Octopoteuthis megaptera (Verrill, 1885)

Ancistrocheirus megaptera Verrill, 1885, *Transactions of the Connecticut Academy of Sciences*, 6(2): 395–452 [399]. [Type locality: 39°12'N, 72°03'W, off New Jersey, western North Atlantic Ocean].

Size: The mantle attains a length to 200 mm.

Geographical Distribution: Subtropical to tropical cosmopolitan, western, central and eastern Atlantic Ocean, western tropical Pacific Ocean to 36°S off east coast Australia and to Cape Leeuwin off west coast Australia, Indian Ocean.

Habitat and Biology: Vertical distribution of this species is mesopelagic, bathypelagic and bathyal with vertical ascent into epipelagic zone at night. One specimen was captured in closing net at night at 230 m.

Literature: Roper and Young (1975), Nesis (1982, 1987), Nesis (1999b), Vecchione *et al.* (2002), Okutani (2005).

Octopoteuthis nielseni (Robson, 1948)

Octopodoteuthis nielseni Robson, 1948, *Zoologica*, 33(3): 115–132 [120]. [Type locality: off Cocos Island, Galapagos Islands, eastern tropical Pacific Ocean].

Size: The mantle length attains 200 mm.

Geographical Distribution: The species occurs from Mexico to northern Chile and westward to Hawaiian Islands region.

Habitat and Biology: This is a mesopelagic to bathypelagic species that ascends into the epipelagic zone at night.

Literature: Nesis (1982, 1987), Dunning *et al*. (1993), Norman (2000).

Octopoteuthis rugosa Clarke, 1980

Octopoteuthis rugosa Clarke, 1980, *Discovery Reports*, 37: 1–324 [156]. [Type locality: off southeastern South Africa, western South Indian Ocean].

Size: The mantle length reaches 230 mm.

Geographical Distribution: It occurs in the tropical and subtropical Atlantic Ocean and the Indo-West Pacific Ocean, e.g. Mauritania, and the equatorial Atlantic Ocean, southern Africa, southwestern Australia, Sulu and Flores Seas (south Georgia unconfirmed).

Habitat and Biology: This is a mesopelagic species.

Literature Clarke (1980), Nesis (1982, 1987), Roper *et al*. (1995), Okutani (2005).

2.22 Family OMMASTREPHIDAE Steenstrup, 1857

by Clyde F.E. Roper, Chingis Nigmatullin and Patrizia Jereb

Ommastrephidae Steenstrup, 1857c, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1857(1/2): 11–14 [12].

Type Genus: *Ommastrephes* d'Orbigny, 1834.

FAO Names: En – Flying squids; **Fr** – Encornet, Calmar; **Sp** – Jibia, Pota, Volantes.

Diagnostic Features: The **mantle** is cylindrical or conical; **densely muscular**. Fins terminal, transversely rhomboidal or heart-shaped. Head and eyes are large. **Arms strong with well-developed protective membranes and swimming keels**. Suckers biserial with denticulate rings. **Tentacles with well-defined stalk, carpus, manus and dactylus**. Manus and dactylus bear 4 series of suckers, except ***Illex*** which has 8 series of suckers on the dactylus. The suckers of the 2 median series on the manus are larger than those on the marginal series. The large sucker rings on the manus have sharp teeth, low broad plates, or are smooth (last 2 conditions mainly in ***Illex***). The special fixing apparatus with knobs and opposing smooth-ringed suckers occurs on the carpus only in Ommastrephinae. **One or both ventral arms hectocotylized**. If one arm is hectocotylized, it may be longer than the adjacent non-modified ventral arm, or both arms are equal-sized. **Three types of hectocotylization distinguish the subfamilies according to differences in the distal protective membranes**. **Buccal membrane connective formula is DDVD**. The funnel groove is deeply recessed, distinct, triangular, either smooth, without a foveola (Illicinae, ***Todaropsis***), or with a foveola, with either; 1) an arched transverse fold (pocket) of skin (other Todarodinae), or 2) a foveola with additional small, arched, cutaneous pockets situated on each side of the funnel groove (Ommastrephinae). **Funnel-locking cartilage with 2 deep grooves joined to each other in the form of an "inverted-T" shape: this form is the principal family characteristic**, and it is present and stable throughout ontogenesis from the earliest paralarval stage. Mantle-locking cartilage consists of 2 merging ridges (horizontal and vertical) that correspond to the form of the funnel cartilage grooves. The funnel- and mantle-locking cartilages are fused in 2 species, beginning at the end of the paralarval stage in ***Sthenoteuthis oualaniensis*** and ***Eucleoteuthis luminosa***. The nuchal cartilage is a relatively long, narrow ridge and groove plate with rounded ends; the mantle component conforms to fit into the nuchal component. The gladius is narrow and sword-shaped, consists mainly of rachis; vanes absent. The rachis is supported by 3 rigid ribs: the median rib and 2 marginal ribs. Lateral plates are extremely narrow, transformed into rigid ribs on each side of the rachis. The posterior part of the gladius, anterior to the cone flags, is transformed into a narrow, flexible, supportive stem. The vanes (wings) are absent. The conus is small and the rostrum on the apex of the cone is reduced to a minute cup, which usually is distinguished only with a microscope. The morphology of the beaks is typical for an oegopsid squid. The lower beak is most suitable for identification with the following characters: a tooth on its shoulder, a transparent strip below the jaw angle in young and some adults, a low wing fold (or no wing fold), a broad hood with notch, a relatively long rostral edge compared with the wing, a rather square profile, the hood in the midline about as long as the rostral edge, and a lateral wall fold that extends to a point about half-way between the crest and the free corner of the lateral wall (or no fold at all). The regression of the lower rostral length in millimetre (r) against wet weight in grams (w) for the family is: $\ln w = 2.714 + 293 \ln r$. Radula consists of 7 rows of teeth: the central (rachidian) row of trident-shaped teeth, 2 lateral rows of bicuspid teeth flanking it on each side, then 2 rows of canine-like unicuspid marginal teeth on each side. Marginal plates present, reduced. Light organs (photophores) are absent in Illicinae and Todarodinae and present in Ommastrephinae, either as small, subcutaneous granules, or as round, oval, or longitudinal, reflective, cutaneous photophores. Ocular and intestinal photophores also can be present. Spermatozoa possess 2 flagella (***Illex***) or 1 flagellum (all other Ommastrephidae).

Size: Minimum adult size is 80 to 100 mm mantle length and 10 to 13 g in weight (***Hyaloteuthis***), and maximum adult size extends to 1.2 m mantle length, and to 55 to 65 kg in weight (***Dosidicus***).

Geographical Distribution: The family has representatives in all oceans of the world.

Habitat and Biology: Ommastrephid squids are the most abundant, widely distributed and ecologically active family of cephalopods. They are strong, muscular, active, nektonic, small, medium- and large-sized squids that are distributed throughout the World Ocean from sub-Arctic seas to sub-Antarctic seas. They inhabit waters of the shelf, slope and open ocean, from the surface to depths that range to 2 000 m. Almost all species, particularly the oceanic ones, are abundant and widely distributed. As a rule the range of populations has a complex spatial structure and it is subdivided into reproductive zones and spatial feeding areas. Three main ecological groups (life forms) are distinguished among ommastrephids by characteristics of habitat, especially spawning habitat, which includes the degree of relationship with the bottom. 1) Slope-shelf group: the main habitats are the waters of the continental slope and shelf; ***Illex***, ***Todaropsis***, ***Todarodes pacificus***, ***T. angolensis***, ***T. sagittatus*** (the North African coast population), ***Nototodarus sloanii***, ***N. gouldi***. 2) Nerito-oceanic group: the main habitats are the waters of the continental slope, oceanic seamounts and islands, and adjacent oceanic waters; ***Todarodes sagittatus*** (the North Atlantic population), ***T. filippovae***, ***Nototodarus hawaiiensis***, ***Martialia***, ***Ornithoteuthis***, ***Dosidicus***. 3) Oceanic group: the entire life cycle takes place only in oceanic waters and no connections or relationships ever exist with the bottom; ***Ommastrephes***, ***Sthenoteuthis***, ***Eucleoteuthis***, ***Hyaloteuthis***. The majority of ommastrephids are among the fastest growing squids. The maximum relative daily growth rates (RDGR) of body weight were observed in paralarvae at 15 to 20% body weight. RDGR in juveniles of fast-growing species (e.g. ***Dosidicus***, ***Sthenoteuthis***) are high, up to 10 to 12% body weight, while those of slow-growing (e.g. summer-spawning ***Illex argentinus***) are 3 to 4% body weight. Immature and maturing subadults exhibit 2 to 3% body weight. The maximum absolute daily growth rate observed in large-form females of ***Dosidicus*** at 350 days old was 104 g/day (about 0.8% body weight). Somatic growth of mature shelf-slope ommastrephids (***Illex***, ***Todaropsis***, ***Todarodes***) sharply decreased to 0.3 to 0.6% body weight, then ceased during the spawning period when feeding activity ceased completely. Mature and spawning oceanic squids (***Dosidicus***, ***Ommastrephes***, ***Sthenoteuthis***) demonstrated slow growth at a level of 1.5 to 2% body weight while active feeding continued. Considerable variation of adult sizes exists in large, medium-sized and dwarf ommastrephids basically dependant on the differences of RDGR at the larval and juvenile stages. Usually males are smaller than females due to earlier maturation and consequent earlier decrease of somatic growth. Individual and group phenotypic variability of growth and maturation rates with regard to intraspecific structure and year-round spawning with high fecundity (from 0.1 to 35 million ova) enables ommastrephids to maintain stability of their populations under considerable variation in numbers. In spite of differences in growth rates, adult size (e.g. mantle lengths from 80 to 120 mm up to 600 to 900 mm), as well as ecological and zoogeographic life styles, life cycles of almost all ommastrephids are one year. However, some tendencies exist to shorten the life cycle to half a year, e.g. in some tropical populations of ***Illex coindetii*** and ***Todaropsis eblanae***, the dwarf form of ***Sthenoteuthis oualaniensis*** and ***Hyaloteuthis pelagica***. The length of spermatophores formed by ommastrephid males ranges between 5 and 53 mm (4.4 to 27% mantle length), depending on the species, mantle length and stage of spermatophorogenesis. Minimum male fecundity ranges from 100 spermatophores (***Hyaloteuthis***), through 600 to 1 800 (***Illex***) up to 1 000 to 2 500 (***Dosidicus***, ***Ommastrephes*** and ***Sthenoteuthis***). Spermatophores are transferred to the mantle cavity (***Illex***) or to the buccal membrane where 7 to 265 seminal receptacles are situated (all other Ommastrephidae). Ommastrephid squids mate in the “male-parallel” or “head to head” position. Mating is quick, not more than 1 to 2 minutes, and promiscuous, with both sexes accepting multiple partners. The oocyte stock development is asynchronous throughout the entire ontogenesis with constant predominance of the small protoplasmic oocytes. The ripe egg size varies in different species from 0.75 to 1.2 mm (***Illex***, ***Todaropsis***, some ***Todarodes***, ***Nototodarus***, ***Ornithoteuthis***, Ommastrephinae) to 1.6 mm (***Martialia***) and to 2.4 mm (North Atlantic and Mediterranean ***Todarodes sagittatus***). The range of female potential fecundity varies from 40 thousand to 35 million oocytes depending on species and adult mantle length. Maximum egg number in oviducts varies from species to species from 50 up to 1.2 million eggs. Ommastrephids are intermittent spawners with multiple filling and evacuation of the oviducts, with up to more than 10 cycles.

Two strategies of spawning exist: the coastal type and the oceanic type. The coastal type is characteristic of Illicinae and Todarodinae (potential fecundity is 0.04 to 2.5 million). After maturation and initiation of spawning activity, females cease to feed. During the spawning period of life, with continuous oocyte maturation and periodical laying of egg-masses, the main source of energy is the digestive gland and mantle tissue. This is called the descending type of spawning, during which initial egg masses laid are the largest with the greatest number of eggs, then in subsequent egg masses, the number of eggs gradually decreases due to reduction of the female energetic reserves. Consequently, the somatic growth becomes negative and by the end of the spawning period the female’s body proportions are significantly changed. The oceanic type is characteristic for the Ommastrephinae (potential fecundity is 0.1 to 35 million). During the spawning period a significant number of oocytes mature, periodical laying of egg masses of approximately the same size exists, active feeding between egg-laying events continues and appreciable somatic growth occurs. Total post-spawning mortality occurs in all ommastrephid species. Large, pelagic, gelatinous, egg masses either float near the surface or at the near-bottom habitat depending on the species. Egg masses are slightly more dense than seawater and they mostly inhabit the near-surface or midwater pycnoclines. Duration of embryonic development in species for which data are available, with egg sizes of 0.75 to 0.9 mm varies from 3 to 22 days; duration depends mostly on water temperature. post-embryonic development is achieved with a unique paralarval stage (rhynchoteuthion) that is characterized by the tentacles fused together to form a trunk-like proboscis with a few suckers on the distal tip. The proboscis is present at hatching, and by the end of the paralarval stage, between 6.5 and 10 mm mantle length, the proboscis progressively splits, starting from the proximal base, and soon the tentacles are separated.

Ommastrephids exhibit the following ecological traits of r-strategies: monocyclia (a complete life cycle within one year), small eggs, very high fecundity, prolonged intermittent multi-batch individual spawning and prolonged population spawning, presence of the planktonic rhynchoteuthion paralarvae and juveniles, very high growth rates, complex intraspecific spawning structure with presence of different seasonal spawning groups, significant long-term fluctuations of abundance (by an order of magnitude or more), and complete annual renewal of the population composition. The most important factor that determines the pattern of abundance, dynamics and distribution of exploitable ommastrephid populations is the availability of planktonic paralarvae and juveniles that inhabit subsurface depths for about 2 to 2.5 months. These stages are characterized by a high mortality rate. Therefore, spawning success and paralarval survival rates constitute the principal factor that determines recruitment level. Another important ecological-population feature of these squids is their 1-year life cycle. These 2 key factors govern the problems and specifics of ommastrephid fishery biology and the annual abundance dynamics. All ommastrephids are obligate shoaling and schooling animals from the young juvenile stages. The number of individual squid in schools ranges from 2 to 5 up to some hundreds, even thousands, generally of equal-sized individuals. Most ommastrephid species are characterized by long daily vertical migrations (hundreds of metres) and ontogenetic seasonal horizontal migrations, both parallel to the coastline, up to 1 000 to1 500 miles long, and perpendicular (bathymetric) migrations from 10 to 50 miles and even to 150 miles offshore. During these migrations squids traverse the boundaries of a diversity of climatic zones and ecosystems. Throughout the life cycle, with continuous body size increases, most ommastrephids “permeate” the trophic pyramid, consecutively transferring from consumers of II to III orders to consumers of IV to VI orders and respectively changing the taxonomic and ecological spectrum of their food organisms (prey), enemies (predators) and parasites. In some oceanic communities, large-sized adult ommastrephids actually are the top-level predators. Ommastrephids are strongly active predators. Their food composition depends on their mantle length: in young small-sized squid, prey consist predominantly of meso- and macroplanktonic crustacea and juvenile fishes; in middle-sized squid prey consists of micronektonic fishes (mainly myctophids) and marcroplanktonic euphausiids and shrimps; and in large-sized individuals prey are only fishes, squids and to a lesser degree, shrimps. Cannibalism is common. Ommastrephids have a high general and active metabolism, and a daily food consumption rate of 6 to 12% of the body weight of adult squids. Protein is the main substrate for energy metabolism. The unique combination of ecological and physiological traits confirms that ommastrephid squids are one of the most important elements in the “rigid framework” of highly mobile predators that unites local ecosystems into ecosystems of the next higher rank, and they function as “ecosystem enzymes”: they significantly accelerate all ecosystem-related processes. The total instantaneous ommastrephid biomass is around 55 million tonnes on average; the total yearly production is about 400 million tonnes (production/biomass coefficient is P/B = 5 in inshore species and P/B = 8 in oceanic species), and the total annual food consumption is around 1 000 million tonnes. Ommastrephids are food for numerous animals – sea birds, marine mammals and especially large predacious teleosts (alepisaurids, gempilids, coryphaenids, tunas, billfishes, swordfishes, etc) and sharks.

Interest to Fisheries: The Ommastrephidae are the most important commercial fishery group among cephalopods. **During the last decade (1997–2007) the annual world catch of ommastrephids varied between 1 and over 2 million tonnes, which represents 50% of the total world cephalopod catch**. The most important species in terms of catch tonnage were ***Todarodes pacificus*** in the northwestern North Pacific Ocean, ***Nototodarus sloanii*** in New Zealand waters and ***Dosidicus gigas*** in the eastern Pacific Ocean. The current level of exploitation of inshore ommastrephids, principally species of ***Illex***, ***Todarodes*** and ***Nototodarus***, is close to the maximum calculated yield and any significant increase in the catch of these ommastrephids sems unlikely in priniciple. Of the oceanic species group, only ***Ommastrephes bartramii*** in the northwestern Pacific Ocean and ***Dosidicus gigas*** in the Gulf of California and off Peru are exploited commercially. The bulk of populations of the oceanic squids ***Ommastrephes*** and ***Sthenoteuthis*** are widely scattered, consequently are not easily captured in large numbers. The combined potentially fishable aggregations of ***Dosidicus***, ***Ommastrephes*** and ***Sthenoteuthis*** are calculated to be about 4 to 7 million tonnes. The total world fishery potential for all exploitable ommastrephid species is estimated at 6 to 9 million tonnes, while the total for all cephalopods combined is considered to be 6 to 12 million tonnes. In general, oceanic ommastrephids are considered the only remaining abundant underexploited fishery resource in the World Ocean that could provide an increase in world commercial catch of high-quality food protein. Oceanic ommastrephid stocks may be exploited on a year-round basis if the following problems can be solved: 1) optimization of search methodologies for fishery aggregations; 2) methods of artificial aggregation techniques for targeted squid species; 3) development of more effective, efficient fishing methods, tactics and gear; 4) wasteless utilization of total catch. Certainly, in order to solve these problems, considerable financial support and scientific effort will be required. Jigging with light attraction and trawling currently are the main fishing methods for ommastrephids. Jigged squid command the highest prices because they are the highest quality of marketable product. The main edible parts of squid, the mantle, fins, arms and tentacles, have the best quality for culinary presentation and they are a highly nutritious food. The common types of product on the market are frozen whole squid, processed/cleaned “tubes” (mantle) and arms; more rarely are squid available in fresh condition as sashimi. In Japan, however, about 70% of ***Todarodes pacificus*** is consumed as sashimi. The remaining 30% is comprised of processed squid products, such as, dried, smoked, salted, salted-fermented, canned, paste products, breaded rings or steaks, as ingredient in seafood cocktail, and pickled digestive gland (“liver”). Moreover, the viscera (principally digestive gland, then reproductive organs, inc sac, gladius, optical lobes of brain) are a source for production of important and promising biologically active substances that include anti-tumor, anti-shock, anesthetic and anti-parasitic drugs, cytostatics, powerful toxins, chitin, chitosan, squid-liver oil with wound healing properties, bactericidal and detoxification activity among others. The development of numerous and varied squid products on the premise of wasteless catch utilization will significantly increase the cost efficiency of ommastrephid fisheries and supply a high quality, abundant stock for the pharmaceutical and biochemical industries. Finally, squids are used extensively as bait mainly for tunas, billfishes, swordfishes and in the cod longline fishery. Many species of ommastrephids are used extensively as experimental animals in studies that examine care and maintenance, feeding, rearing (eggs, embryos, juveniles), treatment of disease, tagging and tracking, collecting, handling and transport, and anesthetics and euthanasia.

Remarks: Since the mid-twentieth century the traditional classification of the Ommastrephidae consisted of 3 subfamilies: Illicinae, Todarodinae and Ommastrephinae (e.g. Roeleveld, 1988; Guerra, 1992; Wormuth, 1998; Young *et al*. 2009). Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayshi *et al*., 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodinae). The subfamilial classification has been further subdivided with the addition of 2 new subfamilies, Todaropsinae and Ornithoteuthinae (Nigmatullin, 1979, 1992 [1991], 2000). In this presentation we choose to use the more conservative system with the 3 traditional subfamilies.

A complete list of the recognized genera and species is reported below. From the phylogenetic point of view, ***Illex*** and ***Todaropsis*** are the 2 most primitive ommastrephid genera, and the Ommastrephinae is the most advanced subfamily. In general, evolution within the family from the morpho-functional aspect (i.e. the development of active nektonic swimmers) and the ecological aspect (i.e. the shift from shelf-slope to oceanic realms), there are 3 basic stages: 1) the shelf-slope Illicinae, 2) the nerito-oceanic Todarodinae, and 3) the true oceanic Ommastrephinae.

Due to the paramount relevance of this family to the world fishery, a particularly detailed treatment has been given to it in this Catalogue. However, such an extensive literature exists on most Ommastrephid species, that only those publications considered comprehensive of biological and fisheries information are quoted in the main literature sections below. Many others are reported in the Appendices.

Literature: Wormuth (1976), Nigmatullin (1979), Roper *et al*. (1984), Guerra (1992), Dunning (1998b,c,f), Wormuth (1998), Dunning and Wormuth (1998), Dunning *et al*. 1998d, Nigmatullin (2004), Sweeney and Young (2003u), Wakabayshi *et al*. (2006), Young *et al*. (2009).

Family Ommastrephidae *Steenstrup, 1857*

Classification

(Species listed in **bold type** are the type species of the indicated genus)

1. Subfamily **ILLICINAE** Posselt, 1891
    - Genus *Illex* Steenstrup, 1880: 82
        - ***I. illecebrosus*** (Lesueur, 1821: 95)
        - *I. argentinus* (Castellanos, 1960: 55)
        - *I. coindetii* (Verany, 1839: 94)
        - *I. oxygonius* Roper, Lu and Mangold, 1969a: 299

2. Subfamily **OMMASTREPHINAE** Posselt, 1891
    - Genus *Ommastrephes* d'Orbigny, 1834: 45 [in 1834–1847]
        - ***O. bartramii*** (Lesueur, 1821: 90)
    - Genus *Dosidicus* Steenstrup, 1857a: 120
        - ***D. gigas*** (d'Orbigny, 1835: 50 [in 1834–1847])
    - Genus *Eucleoteuthis* Berry, 1916: 60
        - ***E. luminosa*** (Sasaki, 1915b?: 144)
    - Genus *Hyaloteuthis* Gray, 1849: 63
        - ***H. pelagica*** (Bosc, 1802: 46)
    - Genus *Ornithoteuthis* Okada, 1927c: 15
        - ***O. volatilis*** (Sasaki, 1915b: 138)
        - *O. antillarum* Adam, 1957: 3
    - Genus *Sthenoteuthis* Verrill, 1880b: 222
        - ***S. pteropus*** (Steenstrup, 1855: 200)
        - *S. oualaniensis* (Lesson, 1830–1831: 240)

3. Subfamily **TODARODINAE** Adam, 1960b
    - Genus *Todarodes* Steenstrup, 1880: 83
        - ***T. sagittatus*** (Lamarck, 1798: 130)
        - *T. angolensis* Adam, 1962: 32
        - *T. filippovae* Adam, 1975: 3
        - *T. pacificus* (Steenstrup, 1880: 79)
        - *T. pusillus* Dunning, 1988b: 149
    - Genus *Martialia* Rochebrune and Mabille, 1889: H8
        - ***M. hyadesi*** Rochebrune and Mabille, 1889: H9
    - Genus *Nototodarus* Pfeffer, 1912: 434
        - ***N. sloanii*** (Gray, 1849: 61)
        - *N. gouldi* (McCoy, 1888: 255)
        - *N. hawaiiensis* (Berry, 1912: 434)
    - Genus *Todaropsis* Girard, 1890: 204
        - ***T. eblanae*** (Ball, 1841: 364)

Key to the subfamilies and genera of Ommastrephidae

1a. Photophores present . . . . **Subfamily Ommastrephinae → 2**
1b. Photophores absent . . . . **→ 7**

2a. Mantle narrow, elongate, posteriorly drawn out into a pointed tail; funnel groove side pockets often obscure; tentacle fixing apparatus without tubercle-like knobs; rings of large club suckers with 15 to 25 equal-sized pointed teeth; no external photophores, nor any small subcutaneous photophores; 1 photophore on each eyeball, 2 intestinal photophores; in adults a narrow pinkish photogenic band extends along viscera from rectum to near posterior end of mantle cavity with 2 gaps . . . . ***Ornithoteuthis***

2b. Mantle wide, end of mantle without pronounced tail; funnel groove side pockets clearly defined; tentacle fixing apparatus with 1 or several knobs alternating with smooth ringed suckers; rings of large club suckers with either 1 large median tooth in distal part of ring, or with 4 large teeth, 1 at each quadrant; small yellow subcutaneous photophores (like short rice grains) on head, mantle, fins and arms; some species may have arrangement of different form (large mantle photophores) with reflective subjacent layer; 1 ocular and 1 or 2 intestinal photophores present . . . . **→ 3**

3a. Tips of all arms in adults thin and very attenuate, bearing numerous, minute, densely packed suckers; arms have up to 200 pairs of suckers; large mantle photophores absent, small, scattered subcutaneous photophores present; 1 ocular and 2 intestinal photophores present in juveniles and subadults . . . . ***Dosidicus***

3b. Tips of arms not attenuate; arms have about 32 to 35 pairs of suckers; large cutaneous mantle photophores present; ocular and intestinal photophores present or absent . . . . **→ 4**

4a. No large cutaneous photophores in form of spots and stripes on ventral surface of mantle; small subcutaneous photophores present; no or 2 intestinal photophores; rings of large club suckers with 4 large teeth, 1 at each quadrant . . . . **→ 5**

4b. Large cutaneous photophores of spot or stripe-like form occur on ventral surface of mantle; 1 intestinal photophore; rings of large club suckers with 1 large medial tooth in distal part of ring . . . . **→ 6**

5a. Large, compound, subcutaneous photophore absent on anterodorsal part of mantle; no ocular or intestinal photophores; 1 wide gold or silvery longitudinal, cutaneous, bioluminescent stripe extends along ventral midline of mantle from near mantle edge to beginning of fin; end of fin slightly attenuate posteriorly; 4 to 7 suckers with denticulate rings in carpal part of club proximal to first knob . . . . ***Ommastrephes***

5b. Squid of mantle length greater than 140 mm with single, large, oval, compound, subcutaneous photophore on anterodorsal part of mantle; 1 ocular and 2 intestinal photophores present; no longitudinal, cutaneous, bioluminescent stripe on ventral side of mantle; fin rhomboidal, not attenuate posteriorly; not more than 2 suckers with denticulate rings in carpal part of club proximal to first knob . . ***Sthenoteuthis***

6a. Pair of long stripes of cutaneous, bioluminescent tissue (large elongate photophores) extends along ventral side of mantle, 1 on each side of midline, each stripe broken posteriorly by gap at level of maximum width of fin; 2 oval bioluminescent patches on head near anterior margin of mantle aligned with base of each ventral arm . . . . ***Eucleoteuthis***

6b. Nineteen round, cutaneous, bioluminescent patches arranged in a fixed pattern on ventral side of mantle that form converging or separated pairs; cutaneous, bioluminescent patches at base, in middle and near tip of each ventral arm . . . . ***Hyaloteuthis***

7a. Eight longitudinal series of small to minute suckers on dactylus of tenatacular club . . **Subfamily Illicinae →** ***Illex***

7b. Four longitudinal series of small suckers on dactylus of tentacular club . . . . **Subfamily Todarodinae → 8**

8a. Funnel groove smooth, without foveola . . . . ***Todaropsis***

8b. Funnel groove with foveola . . . . **→ 9**

9a. Biserial row of finger-like projections extends from first suckers almost to base of tentacular stalk; finger-like cirri project beyond protective membranes along both sides of arms and tentacular clubs . . . . ***Martialia***

9b. Finger-like projections and cirri absent on arms and tentacular clubs . . . . **→ 10**

10a. One ventral arm hectocotylized, usually right, rarely left; species distributed in all 3 oceans, mainly in temperate and cold waters . . . . ***Todarodes***

10b. Both ventral arms hectocotylized: 1 arm in proximal and distal parts, other arm only in proximal part; species distributed in tropical, subtropical and partly temperate waters of Indo-Pacific region and Australian-New Zealand area . . . . ***Nototodarus***

Table 5

Character states within genera of the Ommastrephidae

Character State	*Illex*	*Todaropsis*	*Martialia*	*Todarodes*	*Nototodarus*	*Ornithoteuthis*	*Dosidicus*	*Ommastrephes*	*Sthenoteuthis*	*Eucleoteuthis*	*Hyaloteuthis*
Funnel groove: a) smooth	X	X									
b) with foveola			X	X	X	X	X	X	X	X	X
c) with side pockets						X[1/]	X	X	X	X[1/]	X[1/]
Tentacular carpal-fixing apparatus: a) absent	X	X	X	X	X	X					
b) present							X	X	X	X	X
Central club sucker ring dentition: a) smooth or bluntly crenulated	X										
b) uniform-sized pointed teeth		X		X[2/]	X[4/]	X					
c) 1 pointed distal tooth larger			X	X[3/]	X[5/]					X	X
d) 4 large teeth, one at each quadrant			X				X	X	X		
Hectocotylization of ventral arms: a) both		X			X						
b) one	X		X	X		X	X	X	X	X	X
Hectocotylization, distal membrane: a) absent	X										
b) ventral enlarged						X	X	X	X	X	X
c) thickened trabeculae		X	X	X	X						
Photophores on intestine: a) absent	X	X	X	X	X			X			
b) present						X	X-juv.		X	X	X
Photophores on eyeball: a) absent	X	X	X	X	X						
b) present						X	X-juv.		X	X	X
Small subcutaneous mantle photophores: a) absent	X	X	X	X	X	X					
b) present							X	X	X	X	X
Large mantle photophores: a) absent	X	X	X	X	X	X	X	X			
b) present									X	X	X

[1/] side pockets often obscure; [2/] in *T. pacificus* including *T. pusillus*; [3/] in rest *Todarodes*; [4/] in *N. gouldi* and *N. sloani*; [5/] in *N. hawaiiensis*.

FAO English names for Ommastrephidae

Flying Squids

Dosidicus		
	D. gigas	Jumbo flying squid
Eucleoteuthis		
	E. luminosa	Luminous flying squid
Hyaloteuthis		
	H. pelagica	Glassy flying squid
Illex		
	I. argentinus	Argentine shortfin squid
	I. coindetii	Broadtail shortfin squid
	I. illecebrosus	Northern shortfin squid
	I. oxygonius	Sharptail shortfin squid
Martialia		
	M. hyadesi	Sevenstar flying squid
Nototodarus		
	N. sloanii	Wellington flying squid
	N. gouldi	Gould's flying squid
	N. hawaiiensis	Hawaiian flying squid
Ommastrephes		
	O. bartramii	Neon flying squid
Ornithoteuthis		
	O. volatilis	Shiny bird squid
	O. antillarum	Atlantic bird squid
Sthenoteuthis		
	S. pteropus	Orangeback flying squid
	S. oualaniensis	Purpleback flying squid
Todarodes		
	T. angolensis	Angolan flying squid
	T. filippovae	Antarctic flying squid
	T. pacificus	Japanese flying squid
	T. pusillus	Little flying squid
	T. sagittatus	European flying squid
Todaropsis		
	T. eblanae	Lesser flying squid

2.22.1 Subfamily ILLICINAE Posselt, 1891

Illicinae Posselt, 1891, *Videnskabelige Meddelelsor fra den Naturhistoriske Forening i København*, 1890: 301–359.

Type Genus: *Illex* Steenstrup, 1880.

Diagnostic Features: Ommastrephids with **smooth funnel groove, without foveola or side pockets**; **8 longitudinal series of small to minute suckers on dactylus of tentacular club**; rings of large manal suckers smooth or with flattened small teeth or low broad plates; **photophores absent**; tentacular stalks **without carpal-fixing apparatus**; either right or left arm IV hectocotylized (papillary type).

Remarks: The Illicinae formerly included ***Illex*** and ***Todaropsis***, but the latter genus has been shifted to the Todarodinae as a better phylogenetic fit. While the relationships among the ommastrephid subfamilies remain unresolved, there seems little doubt that ***Illex*** is distinctive with several apomorphic characters, e.g. club sucker dentition and arrangement, absence of protective membranes on the hectocotylized tip, and secondary modifications on the medial portion of the hectocotylus. Some species of ***Illex*** have been or currently are the target of extremely important fisheries. Formerly ***I. illecebrosus*** supported a significant fishery that produced catches in excess of 100 000 tonnes (up to 160 000 tonnes) for several years. But probable overfishing and changing environmental factors drove the unmanaged fishery into a total collapse from which it has not recovered in more than 20 years. ***Illex argentinus*** on the other hand, after a marked negative fluctuation in the years 2004–2005, continues to support an extremely productive fishery that consistently produces catches of around 700 000 tonnes. This fishery is the object of a very comprehensive management system based on pre-assessed and constantly monitored biological factors and real-time catch statistics. ***Illex coindetii*** represents a reasonably significant bycatch in the Mediterranean fin-fish trawl fishery.

Illex Steenstrup, 1880

Plate IX, 52

Illex Steenstrup, 1880, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1880: 73–110 [82].

Type Species: *Illex illecebrosus* (Lesueur, 1821).

Diagnostic Features: The **funnel groove is smooth, without foveola or sidepockets**. No photophores present; no carpal-locking apparatus occurs on the tentacular stalk. Tentacular club moderately to broadly expanded. The dactylus of the tentacular club has 8 rows of small to minute suckers. Manus tetraserial; rings of largest medial suckers on manus have smooth, bluntly crenulate or flattened small teeth or low broad plates; lateral suckers of manus small. Carpal suckers are small, biserial. **Either right or left arm IV hectocotylized by the papillary type with equal frequency**; dorsal and ventral protective membranes of hectocotylus terminate near base of distal modified tip; secondary modification present on medial part of hectocotylized arm. The gladius has wide, long, cone flags that do not bear radial creases. The greatest width of the cone flags is roughly equal to that of the rachis. The marginal rigidity ribs of the rachis are doubled, and the axial rigidity rib of the rachis is T-shaped in cross-section. The lateral plates of the gladius adhere entirely to the dorsal surface of the rachis. The stem is short and pince-nez-shaped in cross-section. The cone is narrow, slightly compressed laterally; the rostrum is absent. The alveola is thick, and its surface bears tiny thorns. Each spermatozoum has 2 flagellae.

Remarks: Four species of ***Illex*** are recognized, initially based on morphological characters. While ***Illex argentinus*** is geographically isolated, thus easily identified, the remaining 3 species, ***I. coindetii***, ***I. illecebrosus*** and ***I. oxygonius*** can be difficult to identify in areas where their distributions overlap. The systematics and distribution sections confirm the valid specific status of all 4 nominal species, provides distinguishing morphological characters, enumerates detailed geographic distribution, presents tables of meristic characters, a table of comparative morphological features and a key to species. Adults of the 4 species of ***Illex*** can be distinguished principally on the basis of the **hectocotylus, dentition of largest medial manal suckers, and morphological and meristic characters of the head, mantle, fins, arms, beaks and spermatophores**. ***Illex argentinus*** is the southermost species but is rather broadly distributed from off Rio de Janiero southward to the tip of the continent off Argentina and well offshore around the Falkland Islands. ***Illex coindetii*** is a single, variable, widely distributed species, morphotypes of which occur throughout the Mediterranean Sea, the eastern Atlantic from the North Sea to Namibia and the western Atlantic from the southeastern Caribbean, the Gulf of Mexico and the southern Straits of Florida. ***Illex illecebrosus*** is highly seasonally distributed, from off northern Florida, along the entire east coast of the United States of America and Canada to Newfoundland, the Labrador Sea, perhaps occasionally to Iceland. ***Illex oxygonius*** is the most restricted of the 4 species in its distribution, as it occurs from off New Jersey and the middle Atlantic states southward into the eastern Gulf of Mexico. Discriminate analysis of large suites of morphometric data on body and beaks can yield positive species identifications up to 90% correct for the 3 dominant species of ***Illex***. Genetic analysis of the 4 nominal species of ***Illex*** using allozyme polymorphisms (Martinez *et al.* 2005a, b), confirms their valid specific status and reveals that ***I. illecebrosus*** and ***I. oxygonius*** are sister species, with a close relationship to ***I. argentinus***, while ***I. coindetii*** forms a more remote, different lineage.

Definitions of Hectocotylus Features

HAb	(length of) suckerless area at base of hectocotylized arm measured from V-notch between arms IV to first sucker.
HALs	length of hectocotylized arm measured from most proximal sucker to distal tip (equivalent to HcA in Roper and Voss, 1983).
HALt	total length of hectocotylized arm measured from V-notch between arms IV to distal tip.
HA1	(length of) proximal sucker-bearing section on hectocotylized arm with normal-sized, graded suckers.
HA2	(length of) medial section of hectocotylized arm (distal sucker-bearing section) with suckers of reduced diameter, fringed trabeculae, or other modifications.
HA3	(length of) modified distal tip of hectocotylus characterized by absence of protective membranes and replacement of suckers with lamellae and papillae.

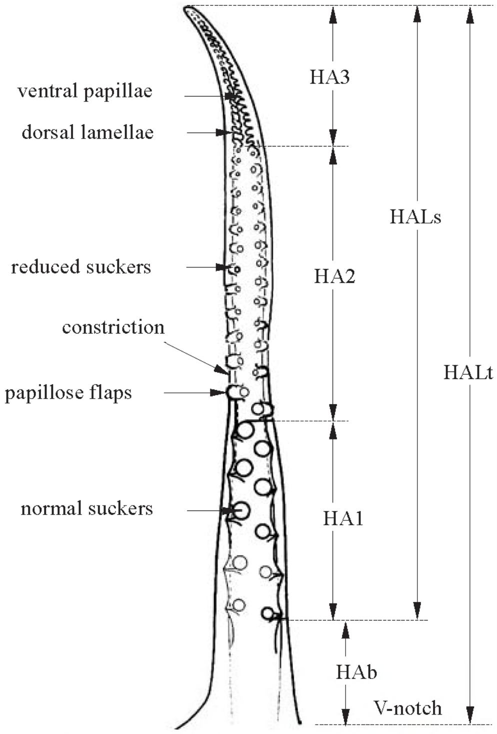


Fig. 281 Diagram of *Illex* hectocotylus showing morphological features, proportions and measuremets

Table 6

Hectocotylized arm length[1/] indices (HALsI) and hectocotylized tip length[2/] indices (HAsSI) for mature specimens of the four *Illex* species (from Roper and Mangold, 1998).

	Mean	Range	Standard deviation	No.
HALI:				
I. illecebrosus	53.0	(39.7–66.0)	7.9	27
I. coindetii	63.7	(42.3–87.1)	9.9	65
I. argentinus	67.6	(49.5–82.0)	7.4	68
I. oxygonius	51.5	(40.6–59.9)	5.7	10
HA3LI:				
I. illecebrosus	22.1	(13.0–30.3)	4.6	27
I. coindetii	25.1	(17.1–30.0)	2.7	65
I. argentinus[3/]	50.3	(19.8–70.3)	11.0	68
I. oxygonius	28.8	(23.8–32.0)	2.7	10

[1/] Length of hectocotylized arm measured from most proximal sucker to arm tip.

[2/] Length of hectocotylized tip measured from most distal sucker to arm tip.

[3/] Includes HA2, which loses suckers at full maturity, making it difficult to determine the junction point of HA2 and HA3.

Table 7

Head length indices (HLI) and head width indices (HWI) for males and females of the four species of *Illex*[1/]

	Male		Female	
	Mean	**Range**	**Mean**	**Range**
HLI:				
I. illecebrosus	16.4	(10.6–24.7)	15.7	(11.4–22.6)
I. coindetii	21.8	(13.7–29.6)	19.0	(10.0–23.6)
I. argentinus	19.5	(16.0–23.9)	16.8	(14.3–19.7)
I. oxygonius	18.2	(15.0–21.3)	16.3	(12.9–18.6)
HWI:				
I. illecebrosus	17.0	(10.0–21.8)	16.3	(12.9–18.6)
I. coindetii	21.1	(13.2–29.1)	18.4	(12.9–25.1)
I. argentinus	17.8	(11.8–21.1)	16.0	(11.7–18.8)
I. oxygonius	20.0	(18.2–22.9)	17.5	(14.7–19.7)

[1/] Based on Roper *et al*. (1969a) and Lu (1973).

Table 8

Fin length indices (FLI), fin width indices (FWI) and fin base length indices (FbLI) for males and females of the four species of *Illex*[1/]

	Male		Female	
	Mean	**Range**	**Mean**	**Range**
FLI:				
I. illecebrosus	43.8	(31.3–49.3)	44.1	(38.1–53.5)
I. coindetii	39.2	(31.3–46.4)	39.4	(29.4–46.2)
I. argentinus	41.9	(36.3–47.2)	42.3	(37.3–45.2)
I. oxygonius	45.0	(42.0–47.9)	45.0	(42.5–48.1)
FWI:				
I. illecebrosus	55.4	(43.0–64.2)	54.6	(40.9–65.8)
I. coindetii	56.4	(45.7–66.5)	53.7	(37.0–65.9)
I. argentinus	58.0	(51.9–66.3)	56.4	(52.2–64.2)
I. oxygonius	51.5	(43.8–62.4)	50.5	(43.1–56.9)
FbLI:				
I. illecebrosus	39.5	(28.4–44.3)	39.5	(33.8–50.3)
I. coindetii	33.9	(19.3–40.7)	34.5	(25.0–41.6)
I. argentinus	37.5	(35.2–43.0)	37.8	(34.4–40.3)
I. oxygonius	40.2	(35.8–42.4)	40.0	(37.9–43.2)

[1/] Based on Roper *et al*. (1969a) and Lu (1973).

Table 9

Arm length indices (ALI) (hectocotylus not included) for males and females for the four species of *Illex*[1/]

Arm	*I. illecebrosus*		*I. coindetii*		*I. argentinus*		*I. oxygonius*	
	Mean	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**
Males:								
I	39.1	(25.5–56.0)	47.4	(27.1–77.4)	55.6	(45.8–65.0)	43.9	(35.2–53.3)
II	48.2	(32.4–70.0)	62.5	(37.4–96.6)	70.2	(57.9–84.2)	54.8	(45.0–64.2)
II	48.2	(32.4–70.3)	61.0	(37.6–95.9)	71.2	(52.5–86.4)	54.7	(43.8–63.0)
IV	43.0	(27.5–62.9)	54.1	(29.3–87.8)	61.6	(42.6–74.4)	47.9	(39.4–60.6)
Females:								
I	36.5	(29.2–49.3)	37.6	(25.0–56.1)	46.2	(39.3–53.7)	34.3	(27.9–39.3)
II	44.5	(35.3–56.8)	48.7	(36.4–67.1)	57.4	(48.5–66.5)	42.9	(34.7–50.9)
III	44.5	(34.7–57.6)	48.3	(36.4–67.1)	58.5	(47.1–70.0)	43.4	(36.5–54.0)
IV	40.4	(29.4–52.6)	42.4	(25.0–63.5)	52.0	(43.4–59.7)	38.1	(31.9–46.0)

[1/] Based on Roper *et al*. (1969a) and Lu (1973).

Table 10

Comparison of the beaks of the four *Illex* species[1/]

Feature	*I. illecebrosus*	*I. coindetii*	*I. argentinus*	*I. oxygonius*
Upper Beak:				
Hood	long, strong	long, strong	long, strong	short, weak very thin
Shoulder	serrated	smooth	serrated	smooth, straight or slightly curved
Jaw angle	large notch, with tooth	small notch	large, notch with tooth	small notch
Rostrum	long	long	long	short
Lateral wall	short, shallow; crest curved	short, shallow; crest curved	short, shallow; crest curved	long, deep; crest straight
Wing	short	short	short	short
Lower Beak:				
Jaw edge	straight, short	straight, long	curved, long	curved, long
Wing	long, wide, no lobe; regular outline	long, wide, no lobe; slightly irregular outline	long, wide, no lobe; regular outline	short, narrow lobate; irregular outline
Lateral wall	short, blunt	short, blunt	short, blunt	long, pointed
Rostral width	narrow	narrow	narrow	wide

[1/] Based on Roper *et al*. (1969a) and Lu (1973).

Literature: O'Dor (1983), Rodhouse et al. (1998a), Roper *et al*. (1998), Roper and Mangold (1998), Martinez *et al*. (2005a,b) Carlini *et al*. (2006).

Key to the species of *Illex* (from Roper *et al.* 1998)

1a. Proportional length (ALI) of all arms long (e.g. 8 to10% larger than in other species); tentacular club not broadly expanded, medial manal suckers exceptionally enlarged, lateral manal suckers extremely small; distal modified portion of hectocotylized arm >50% of total arm length (=HA2 + HA3); distribution restricted to western South Atlantic Ocean, 23°S–55°S . . . . ***Illex argentinus***

1b. Proportional length (ALI) of all arms moderate to short (e.g. 8 to 23% smaller than in *I. argentinus*); tentacular club expanded, medial manal suckers enlarged, lateral manal suckers small (not so markedly disproportionate as above); distal modified portion of hectocotylized arm (HAS) <33% of total arm length; distribution North Atlantic, Caribbean, Gulf of Mexico, or Mediterranean . . . . ***→ 2***

2a. Distal enlarged manal-sucker rings notched, 7 or 8 low, broad, flat, plate-like teeth; relative lengths of fins and fin bases short; relative length of head (HLI) long; relative length of arms (ALI) long; base of hectocotylized arm (HAb) devoid of suckers for 13% of total arm length; trabeculae on hectocotylus midsection (HA2) modified to papillose, fringed flaps; distribution pan-Atlantic, only *Illex* species in eastern Atlantic and Mediterranean . . . . ***Illex coindetii***

2b. Distal enlarged manal-sucker rings smooth, toothless, rarely with 1 or 2 notches; relative lengths of fins and fin bases long; relative length of head (HLI) short; relative length of arms (ALI) short; base of hectocotylized arm (HAb) devoid of suckers for 4 to 6% of total arm length; trabeculae on hectocotylus midsection (HA2) not modified; distribution restricted to western North Atlantic . . . . ***→ 3***

3a. Relative width of fins broad, 55% of mantle length; head length and width indices relatively low, 16 to 17% of mantle length; arm lengths relatively short in males, 39 to 48% of mantle length; arm sucker diameter indices relatively small, 1.02 to 1.75; hectocotylized arm equal to or slightly shorter than opposite arm IV and of equal thickness; lower beak jaw edge straight, short; wing long, wide; lateral wall short, blunt; rostral width narrow . . . . ***Illex illecebrosus***

3b. Relative width of fins narrow, 51% of mantle length; head length and width indices relatively high, 16 to 20% of mantle length; arm lengths relatively long in males, 44 to 55% of mantle length; arm sucker diameter indices relatively large, 1.12 to 2.47, especially in males; hectocotylized arm relatively long, more robust than opposite arm IV; lower beak jaw edge curved, long; wing short, narrow; lateral wall long, pointed; rostral width wide . . . . ***Illex oxygonius***

Illex illecebrosus (Lesueur, 1821)

Fig. 282; Plate IX, 53

Loligo illecebrosus Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101, pl. 11. [95]. [Type locality: Isles of Shoals, New Hampshire, USA, western North Atlantic Ocean].

Frequent Synonymy: *Illex illecebrosus illecebrosus* (Lesueur, 1821); *Loligo illecebrosus* Lesueur, 1821; *Loligo piscatorum* La Pylaie, 1825; *Illex coindetii* (Veranyi, 1839); *Ommastrephes illecebrosus* Verrill, 1880a,b; non *Illex illecebrosus*, Adam, 1952 (= *Illex coindetii* Verany, 1839).

FAO Names: En – Northern shortfin squid; **Fr** – Encornet rouge nordique; **Sp** – Pota norteña.

Diagnostic Features: The **mantle is robust, widest at midpoint** between anterior end and beginning of fins; **tail not sharply pointed**. **Fin angle mostly 45° (40° to 50°) never greater than 50°**; fin width greater than fin length. Head small, short, narrow; head width index low: 16.3 to 17.0. **Arms relatively short**, about equal length in both sexes. **Right or left arm IV hectocotylized with distal hectocotylized portion limited to about 22% (13 to 30%) of total arm length**; papillae and lamellae weakly developed; basal (proximal) suckerless part of hectocotylized arm short, about 4 to 6% of total arm length; proximal sucker-bearing part with 7 or 8 pairs of normal suckers that increase in diameter distally; distal sucker-bearing part with slight secondary modification of one-quarter reduction in sucker diameter compared to normal proximal suckers; oral surface of arm IV not expanded, sucker rows not abnormally separated; very slight muscular constriction in transition zone between proximal and distal sucker-bearing parts; trabeculae not

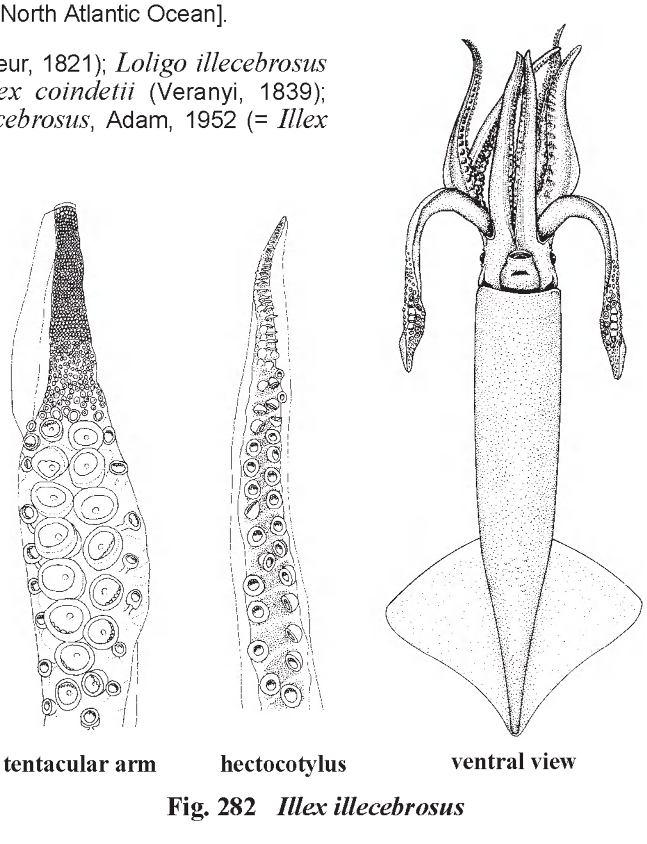

tentacular arm hectocotylus ventral view

Fig. 282 ***Illex illecebrosus***

modified as papillose fringed lobes; hectocotylized arm shorter than or equal to its opposite arm in length and always equal in thickness. One or 2 knobs present on dorsal row of lamellae on modified arm tip. Tentacular club expanded; largest distal medial manal sucker rings smooth, only rarely with crenulations or notches. Lower beak with jaw edge straight, short; wing long, wide, no lobe; rostral width narrow; lateral wall short, blunt. Upper beak with long, strong hood; shoulder serrated; rostrum long; wing short; jaw angle with large notch, with tooth; lateral wall short, shallow; crest curved. Spermatophore cone at oral end of cement body a low, right-isosceles triangle with rounded corners in outline; oral tube long, narrow; aboral neck long, narrow. **Colour**: reddish brown to deep purple, more intense on head, arms and dorsal surfaces of mantle and fins; a dark purple stripe extends along dorsal midline of mantle; paler on ventral surfaces; a brilliant yellowish green tint.

Size: Maximum mantle length 340 mm in females and 270 mm in males in the northern part of its distributional range, but 200 mm in females and 180 mm in males in the southern part. Weight to 1 kg.

Geographical Distribution: Northwestern North Atlantic Ocean off the east coast of North America from about 26°N to 29°N off the east coast of Florida to 66°N (Iceland, southern Greenland, Baffin Island) (Fig. 283).

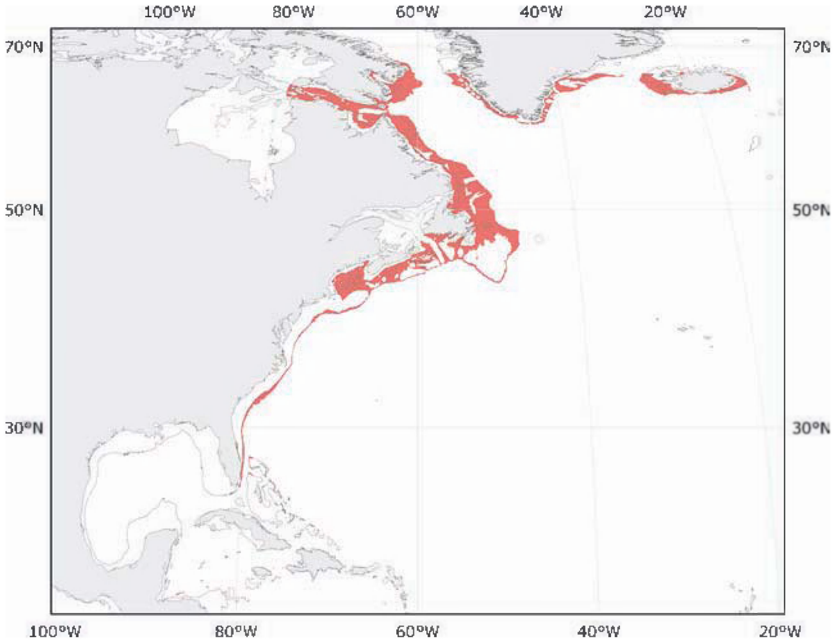


Fig. 283 ***Illex illecebrosus***

🟥 Known distribution

Habitat and Biology: The northern shortfin squid principally is a neritic species that inhabits continental shelf and upper slope waters, associated with the high-velocity Western Boundary Current (Florida Current, Gulf Stream) and nutrient-rich upwellings. The Blake Plateau is a major spawning area for the species in Slope Water shoreward of the Gulf Stream Frontal Zone. The Gulf Stream system entrains, transports and disperses paralarvae and juveniles during their current-assisted northern migration toward the feeding grounds in late spring and early summer. ***Illex*** rhynchoteuthion paralarvae are concentrated where water temperatures converge at 13° to 18°C at 150 to 200 m depth between the water mass known as the slope-water thremostad and the Gulf Stream water. In the area of distributional overlap of ***I. illecebrosus*** and ***I. oxygonius***, from Cape Hatteras to south of Cape Canaveral, ***Illex*** rhynchoteuthion paralarvae are taken only in the slope water/Gulf Stream interface; and further southeastward, off Fort Pierce, Florida, only in the narrow band of "transitional water" just shoreward of the Florida Current (Gulf Stream). The interactions between the slope water and the Gulf Stream seem to be of critical importance to ***Illex*** spawning, paralarval distribution and recruitment. Because the physical characteristics of the slope-water thermostad-Gulf Stream water mass remain relatively constant year-round, prolonged or "non-seasonal" spawning by ***I. illecebrosus*** seems quite possible. The vertical distribution of ***I. illecebrosus*** extends over a broad range of depth depending on season, size/age, and time of day. For example, subadults/adults generally concentrate on or near the bottom during the day then disperse into the water column at night, based on benthic and midwater trawling and *in situ* observations from submersibles. During spring, the 15°C isotherm lay between 80 and 150 m where only juvenile and paralarval ***I. illecebrosus*** specimens were caught; in the autumn, the isotherm was at less than 200 m (temperatures of 12° to 13°C) and only maturing and large mature specimens were caught. During winter the isotherm was at 25 to 0 m, where only paralarval and juveniles (6 to 18 mm mantle length) specimens were captured. No specimens were caught in the summer because they migrate to northern inshore waters in time for intensive feeding. Seven survey cruises (1986–1989) conducted with pelagic trawls over bottom depths from 169 to 4 800 m in slope waters off Nova Scotia revealed that ***I. illecebrosus*** was by far the most abundant species overall (nearly twice as numerous as the secondmost abundant species), and it also constituted the most specimens taken in a single trawl. The minimum bottom depth above which the species was captured was 497 m. Six exploratory pelagic and benthic trawling surveys to the Bear Seamount off New England, western North Atlantic Ocean, found ***I. illecebrosus*** to be the most abundant species in all habitats sampled. During the years of high to peak landings by East Asian squid jigging vessels off Newfoundland and Nova Scotia, the largest catches were taken in the region of the confluence of the warm, northward-flowing Gulf Stream (the western boundary current of the northwestern North Atlantic Ocean) and the cold, southward-flowing Labrador Current. Numerous *in situ* observations have been made from submersibles on ***I. illecebrosus*** in continental slope waters of the western North Atlantic Ocean. ***Illex illecebrosus*** was observed both in midwater and on the bottom, where it rests on its arm tips with its head, mantle opening and funnel raised off the substrate. Resting sites apparently are selected because of their paucity of epibenthic fauna as potential predators. Feeding behaviour was observed in midwaters. *In situ* observations from submersibles have documented high concentrations in association with strong daytime Deep Scattering Layer (DSL) recordings at 12 kHz in midwater at 220 to 250 m and 490 to 510 m off Cape Hatteras. Numerous observations show ***I. illecebrosus*** "resting" on the bottom, as well as in midwater, actively swimming, capturing prey, in large aggregations and small groups, or just "hanging" diagonally head-down and motionless in the water in the "J" posture, with arms and tentacles held together and arched dorsally over the head and anterior mantle.

Illex illecebrosus serves as a biological pump that transfers energy/biological production gained on the feeding grounds back to the spawning grounds over 1 000 km to the south. These fast-acting biological pumps between ecosystems, spawning grounds to feeding grounds and back to spawning grounds, is possible because of semelparity, low levels of predation on paralarval and juvenile stages during northward transport in the Gulf Stream, relatively low mortality on the feeding grounds because rapid growth enables individuals to outgrow most predators, high food conversion rates that convert most of the biological production on the shelf into body mass, and one-way transfer of production from feeding grounds to spawning grounds in a short period of time. Interannual variations in abundance and size of ***I. illecebrosus*** seem to be associated with the variations in the latitudinal position of the Shelf-Slope Front. These variations affect the efficiency of downstream dispersal by the Gulf Stream and consequently the survival of paralarvae and young forms.

Feeding strategies of ***I. illecebrosus*** differ according to the size of the targeted fish prey. Squid attack their prey head first, initially with their arms and tentacles (brachial crown) held closely together in a hydrodynamic cone. Just prior to impact with the prey, the arms and tentacles splay widely, effectively creating a disproportionately huge mouth that captures the prey and manipulates it to the beaks, where it is subdued and consumed. The functional result of the arm crown serving as the mouth enables squid to capture prey much larger than their piscine competitors of equivalent size. During experiments, attacks on trout (large prey) are characterized by rotation from tail-first to head-first swimming, rapid acceleration toward the prey, slow tracking of the prey, accelerated attack. No tracking phase occurs in attacks on mummichogs (small prey). Fishes are captured by a quick headfirst atack with rapidly out-thrust tentacles, which then withdraw the fish into the open arm crown; the entire process is accomplished in less than 2 seconds. When swarms of pelagic crustaceans euphausids, for example, are encountered, the squid rapidly flares and expands its arms to create an in-flowing trbulence in which to trap, then encircle the prey. The rate of digestion of ***I. illecebrosus*** is very rapid at first, then slows progressively, but it is not phased. Although this species lives in relatively cold water, its digestion is quite rapid and very efficient (0.6% of body weight digested per hour). Starvation of female ***I. illecebrosus*** in the laboratory induces significant increases in weight and volume of the ovary and the nidamental gland. Causal factors are thought to be the size of the females and their stage of maturity, the season and duration of starvation exposure. During jetting locomotion, ***I. illecebrosus*** demonstrates very high-power consumption rates, exceeded only by some terrestrial animals at much higher temperatures.

Fishes are the most nutritious prey for promoting growth, whereas crustaceans are the least suitable. High weight at length in July in years of high squid abundance is related to a high level of predation on fish. After July in years of high squid abundance the incidence of cannibalism increases dramatically as predation on fish declines sharply. In years of low squid abundance, no seasonal dietary shifts occur, diet remains mixed all season and cannibalism remains at relatively low levels.

Several models using 75-year and 25-year time series of environmental parameters and ***I. illecebrosus*** annual abundance data indicate that squid abundance is positively related to a favourable oceanographic regime associated with a negative North Atlantic Oscillation Index (i.e. weak winter northwesterly winds), high water temperatures and a southward shift in the position of fronts within the Gulf Stream System.

Recruitment of juvenile ***I. illecebrosus*** to the adult feeding ground on the continental shelf off eastern Canada constitutes an important transition from warm, food-limited Gulf Stream waters to cold, productive slope and coastal waters. Young ***Illex*** are energetically expensive and food-limited in Gulf Stream waters, their hatching environment. Growth conditions improve inshore, where metabolic costs are reduced and more food is available. Juvenile onshore migration is driven by elevated food requirements, but it involves physiological adaptations to compensate for decreased temperatures. Ultimate success in terms of growth and survival depends on access to patches of concentrated food, which is determined by timing and transport dynamics of the main water masses.

Total population size or year class strength is affected predominantly by the winter spawning group, the paralarvae of which are transported into the northern grounds by the Gulf Stream in synchrony with the spring/summer productivity peak. This strategy is highly adaptive because environmental conditions that promote strong year classes also favour population expansion via expedient advection of young stages and a favourable oceanographic regime in the northernmost area. This high-productivity area assures rapid growth and maturation to support the subsequent long southern migration to the spawning grounds. This migration is supported in part by the high concentration of lipids stored in the digestive gland during the intensive feeding phase inshore.

Mean mantle length increases from the offshore transport water masses toward the inshore cooler feeding grounds. Intensive feeding and rapid growth occur in the northern waters in summer, then maturing squid migrate back to southern waters to spawn.

During late autumn squid from all subareas in Newfoundland waters move off the shelf and begin their southward migration.

Back-calculated hatching dates from statoliths for Newfoundland squid indicate hatching from December to June, predominantly March to May. Females grow faster than males and for the March to May hatchlings, length at age and growth rate increased with hatching month. Positive effects of late hatching dates also occur in growth in mass, gonad development and sexual maturation. Recruitment to all fishing areas for ***I. illecebrosus*** is adversely affected by cold-water events associated with the Labrador Current. Off Newfoundland, the northernmost area, warm intrusions related to a strong Gulf Stream influence are associated with high recruitment levels, but particularly cold-water events, induced by cold-water intrusions of the Labrador Current, have a dominant adverse effect that is independent of Gulf Stream variability. The life history strategy of ***I. illecebrosus*** ensures survival of the species by stabilizing recruitment in at least one of its several population areas through protracted spawning, complex population structure and interaction of spawning components.

The population structure of ***I. illecebrosus*** in the waters off Newfoundland is extremely complex. Three maturing groups occur there that result in 3 spawning groups far to the south in winter, spring and summer. Significant inter-annual variation occurs in maturation and size composition of each group, but this variation is compounded by intermixing among groups in the southern population. Mean size at maturity also varies, both geographically and annually. ***Illex illecebrosus*** is primarily an annual species, so the population can achieve diversity and stabilization only by spawning multiple micro-cohorts throughout most of the year to ensure broad dispersal throughout its range into equally variable micro-habitats. This behaviour links recruitment more rigidly to environmental variability. The population dynamics of ***I. illecebrosus*** and the strategies employed to maintain them are quite complex and may include kinship, school cohesion and cannibalism. Spawning occurs throughout the year over the Blake Plateau, south of Cape Hatteras, North Carolina (34°N). Eggs enclosed in neutrally buoyant gel masses are carried north by the Gulf Stream, where embryonic development and hatching takes place. The early life is spent along the meandering northern boundary of the Gulf Stream and the slope waters, and it ends when the offspring reach the adult habitat on the continental shelf. During this transition, offspring are subject to important temperature and food availability gradients, as determined by their encountering distinct water masses.

Gametogenesis in ***I. illecebrosus*** reveals that the development of the gonads is monocyclic. Increased day length accelerates maturation of the gonads while the squid are on the feeding grounds in preparation for their migration to the spawning grounds. During ontogeny the spermatophores grow to 18.0 to 26.0 mm (mean 23.5 mm); the total fecundity in Needham's sac during successive matings is about 1 800 spermatophores (mean 300 to 700). During copulation spermatophores are transferred via the male's hectocotylus into the female's mantle cavity, where they are implanted near the oviducal gland, attached to the interior mantle, base of the gills or the oviducal gland itself. Spermatophore implantation provides the stimulus for spawning to commence within a few days. Spawning occurs on the bottom (based on 2 *in situ* observations), where the female is in the traditional "resting position" on the bottom and the chromatophores are totally retracted so the female appears nearly pure white, with a sharply contrasting dark band near the mantle opening and very dark zones near the fin tip and arm tips. The egg mass is extruded by very strong, rapid contractions of the mantle which presumably squeeze the ova out of the oviducts, extrude the gelatinous matrix out of the nidamental glands and break off the implanted spermatophores, all components to be mixed with water and incorporated into the egg mass. Females produce nearly spherical egg masses that absorb water and swell to about 1 m in diameter; each mass contains about 100 000 eggs in the homogenous, tenuous gelatinous mass.

Spawning occurs in midwaters where temperatures exceed about 12° to 13°C. At 13°C full development to hatching requires 16 days; development is more rapid at increased temperatures. A trend exists in which spawning occurs earlier in years of high stock abundance and later in years of low abundance. This species is a batch spawner, releasing egg masses sequentially over a short period of time. The death of males and females occurs immediately following copulation and sequential egg mass laying, respectively. Laboratory culture of ***Illex illecebrosus*** rhynchoteuthions was accomplished by obtaining egg masses from captive females and incubating them under controlled conditions. Factors critical for rearing success include tank size, captive population density, turbulence, light levels and periodicity, food type and concentration. Rhynchoteuthions survived for 9 days after hatching. In nature paralarvae hatch at about 1.1 mm mantle length as the rhynchoteuthion-stage, defined by the tentacles being fused into a single "proboscis". The proboscis divides into discrete tentacles at about 8 to 10 mm mantle length to form the juvenile stage. The juveniles grow to about 100 mm mantle length, at which time habitat and food preferences (availability) change and rapid growth towards mature adulthood ensues.

Statoliths and gladii are used to determine many phases of the life history of ***I. illecebrosus*** through analyses of accretive growth lines, e.g. ecological transitions, age, growth rates, sexual maturation, mating and spawning, as well as more comprehensive applications to sex groups, seasonal and geographic populations and generations. Unfortunately biases exist between preparation techniques and the agers interpretation and enumeration of increments. These biases greatly affect estimates of growth and age. Therefore a higher level of standardization at the international level is required in order to derive accurate, comparable age and growth data.

Growth increments on the gladius of ***I. illecebrosus*** approximate those on statoliths, confirming the daily nature of the depositions during adulthood (early growth increments are masked by growth of the gladius). These increments are highly correlated with mantle growth and reflect early life cycle growth events. Studies on gladii of juvenile and young squid collected in the Slope Water/Gulf Stream front and the Scotian Shelf indicate that offshore growth is exponential and at least 6 size-specific growth stages are distinguished. Paralarval growth is completed by 10 mm gladius length (GL). At 30 to 40 mm GL a significant growth change is associated with the shift from macroplanktonic to micronektonic habitats and the transition from Gulf Stream to Slope waters. The approximation to the Shelf/Slope Water front is reflected by a growth transition at 68 mm GL. The change to linear growth occurs at 90 mm GL after the nektonic lifestyle is attained over shelf waters.

Illex illecebrosus **preys** on a broad spectrum of bony fishes based on studies of fish otoliths collected from squid stomachs. In Newfoundland waters most abundant prey are young-of-the-year Atlantic cod after July. Adult capelin are common early in the season, while juvenile sand lance are common later in the season. Other fishes include Arctic cod, Atlantic herring, redfish and hake. Otolith data do not reflect the entire species diversity of ***Illex*** prey because squid tend not to consume the heads (and otoliths) when they prey on larger fishes and because the residence time for otoliths to remain in stomachs varies considerably depending on their size and shape. Total prey of adults extends over a broad range of species, for example, other fishes: myctophids, rattails; crustaceans: amphipods, copepods, decapods, euphausids, isopods, myodocopids; cephalopods: ***I. illecebrosus***, ***Gonatus fabricii***, histioteuthids; gastropods: limacinid snails. It also preys on ***Doryteuthis pealeii*** in submarine canyons on the continental shelf edge in wintertime. Larger juveniles of about 45 to 94 mm mantle length prey on amphipods, mysids, copepods and are cannibalistic on other juveniles. Euphausids (***Thysanoessa*** and ***Meganyctiphanes***) are common prey of juveniles.

The predators of ***I. illecebrosus*** are numerous. Certain size ranges of ***I. illecebrosus*** are most vulnerable to predation, and predation on the squid varies ontogentically among predators such as finfishes, elasmobranchs and marine mammals. ***Illex illecebrosus*** is a significant prey of the cod fish (*Gadus morhua*), swordfish (*Xiphias gladius*), other billfishes and tunas, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), summer flounder (*Paralichthys dentatus*), shortfin mako shark (*Isurus oxyrinchus*) and bigeye thresher shark (*Alopias superciliosus*); seabird predators include: northern gannet, *Murus bassanus*, greater shearwaters (*Puffinus gravis*), sooty shearwaters (*P. griseus*), fulmars (*Tulmarus glacialis*), and the larger gulls, e.g. black-backs.

Illex illecebrosus was the nearly exclusive prey of the long-finned pilot whale (*Globicephala malaena*) in Newfoundland inshore waters into the mid-1970s (up to 10 million tonnes annually); their distributions and seasonal movements coincide in time and space. Peaks in landings were coincident and the availability of pilot whales in shore was dependant on ***I. illecebrosus*** abundance. Annual squid production (biomass), based on consumption of ***I. illecebrosus*** by pilot whales, was in the order of several hundred thousand tonnes.

Other mammals predators include the white-sided dolphins (*Lagenorhychus acutus*), the “squid hound” (*L. albirostris*) and the harbor seals (*Phoca vitulina*). As a consequence, the international fishery for ***I. illecebrosus*** captures marine mammals as incidental catch; pilot whale species (*Gloubicephala* spp.) and common dolphin (*Delphinus delphis*), together comprising 93% of incidental catch in Canadian and the United States waters, southward into the mid-Atlantic Bight. These species are known to be major predators on ***I. illecebrosus***, so quite naturally are foraging in the squid concentrations during trawling operations.

Natural mortality through predation by marine homeotherms can be substantial and should be taken into account in management schemes. Parasites include pleroceroid cestodes and nematodes.

Interest to Fisheries: The short-finned squid ***I. illecebrosus*** has sustained a valuable but highly unpredictable fishery in the Northwest Atlantic, that collapsed after intense, widely distributed exploitation (1976–1981). Domestic fisheries for ***I. illecebrosus*** have occurred at least since the mid-1800s, probably much earlier, primarily to supply bait for the tub trawl/long line fisheries, principally, though not exclusively, on the Grand Banks off Newfoundland. Catches were about 1 000 tonnes per year until the early 1970s when a major Japanese vessel-based fishery developed for the human consumption market. Catches expanded greatly through the 1970s. In United States waters catches peaked at 24 700 tonnes in 1976, while the primarily distant water fleets off Nova Scotia and Newfoundland landed sharply increasing catches through the 1970s to a peak of 180 000 tonnes in 1979. During peak years of the fishery well in excess of 100 000 tonnes were landed annually, over 1 million tonnes in a decade (1971–1981, mostly 1976–1981). The fishery totally collapsed thereafter. The decadal average for 1992–2002 was 13 197 tonnes, declined sharply in 2002, to increase again in the last years (i.e. over 10 000 tonnes in 2007). Population levels and catch productivity since 1970 have shown high variability in Newfoundland waters and the periods of highest productivity occurred between 2 periods of low productivity.

The jigger used in the traditional squid fishery in Newfoundland has taken several forms over the years, but once the Japanese exploitation began in the 1970s the jigs used in that fishery have become standard, even in the inshore artisinal fishery. Significant catches also are made with benthic otter trawls, particularly on the Grand Banks and along the eastern seaboard southward to the mid-Atlantic around Cape Hatteras, North Carolina. In trawl surveys with large pelagic trawls set at depths of 169 to 4 800 m off Nova Scotia, ***Illex illecebrosus*** was the most abundantly caught species by nearly 2:1 over the next most abundant species, ***Abraliopsis hoylei***.

The “boom and bust” type of fishery exemplified by the ***I. illecebrosus*** fishery in eastern Canada, principally Newfoundland waters, could be mitigated by creation of reserve areas that would minimize recovery time and maximize long-term production.

The principal product of ***I. illecebrosus*** for human consumption remains the muscle tissue of the mantle, fins, head and arm crown, that are marketed fresh, frozen and canned, as well as in various value-added preparations. The muscle tissue contains an extremely active family of proteaces that are responsible for rapid degradation of quality in postmortem tissue and also are important during frozen storage. In an effort to utilize more fully the remaining tissue, a number of products have been developed. For example, formerly underutilized parts of the squid are made into squid patties with the addition of starch and egg white albumin heat-set binders. Application of aminopeptidase from ***I. illecebrosus*** digestive glands accelerates the ripening process of cheddar cheese. Squid protein extracted from arms and tentacles of ***I. illecebrosus*** are used as an additive to gels of Atlantic pollack surimi to improve texture and impart a darker red pigmentation. Extracts from the digestive gland of ***I. illecebrosus*** are used as a supplement to develop the most desirable taste characteristics in fermented squid and herring products. Proximate composition and fatty acids of total lipids from processed viscera yield residual protein with high levels of essential amino acids that are a good source of protein supplement for animal feed.

Local Names: JAPAN: Kanadairekkusu, Taiseiyoirekkususurume, Taiseiyosurume; USA: Northern shortfin, Short-finned squid.

Remarks: Adam (1952) reported ***I. illecebrosus*** from the Bristol Channel off southwestern England, but a re-examination of Adam’s specimens confirmed that they clearly were ***I. coindetii*** based on the hectocotylus, and body meristics, especially fin angle (Roper *et al.* 1998). Genetic analysis of the 4 nominal species of ***Illex*** using allozyme polymorphisms confirms their valid specific status and reveals that ***I. illecebrosus*** and ***I. oxygonius*** are sister species, with a close relationship to ***I. argentinus***, while ***I. coindetii*** forms a more remote, different lineage (Martinez *et al.* 2005a,b; Carlini *et al.* 2006).

Literature: O’Dor (1983), Roper *et al.* (1984), Aldrich (1991), Dawe *et al.* (1992), Dawe and Hendrickson (1998),Vecchione *et al.* (1998a), Roper and Mangold (1998), Roper *et al.* (1998), Martinez *et al.* (2005a,b), Carlini *et al.* (2006), Coehlo and O’Dor (1993), Dawe *et al.* (2007).

Illex argentinus (Castellanos, 1960)

Fig. 284

Ommastrephes argentinus Castellanos, 1960, *Neotropica*, 6(20): 55–58, figs 1–5. [55]. [Type locality: Patagonia, western South Atlantic Ocean].

Frequent Synonyms: *Ommastrephes argentinus*, Castellanos, 1960.

Misidentification: *Ommastrephes bartramii* (Angelescu *et al*., 1958).

FAO Names: En – Argentine shortfin squid; **Fr** – Encornet rouge argentin; **Sp** – Pota argentina.

Diagnostic Features: Mantle long, muscular, widest at midpoint. Fins muscular, relatively short (length 42% of mantle length) and broad (width 57% of mantle length); fin angle broad, 45° to 55° (90° to 110° both fins). **Arms very long for the genus, up to 72% of mantle length for arms III in males**; **all arms of males significantly longer than in females**. Hectocotylus with distal hectocotylized portion of right (or left) arm IV (HA3) and modified HA2 greater than 50% (up to 70%) of total arm length (HALt); distal tip with 18 to 22 large, truncate or rounded lamellae on dorsal row and numerous small, indistinct, narrow lamellae on ventral row to tip; medial modified part of hectocotylized arm (HA2) with 10 to 16 enlarged, rounded, suckerless knobs on dorsal row and 7 to 10 low, suckerless knobs followed by 7 to 12 nipple-like papillae on ventral row; proximal sucker-bearing part (HA1) with 8 to 13 normal suckers; basal, suckerless part (HAb) of hectocotylized arm about 10% of total arm length; hectocotylized arm longer and more robust than opposite arm. Club only slightly expanded; **distal medial manal suckers very enlarged, lateral manal suckers extremely small**; **largest medial manal-sucker rungs smooth or notched with few, low, broad crenulate plates**. Head-width index low, 16.0 to 17.8. Lower beak with jaw edge curved, long; wing long, wide, no lobe; rostral width narrow, lateral wall short, blunt. Upper beak with hood long, strong shoulder serrated; rostrum long; wing short; jaw angle with large notch, with tooth; lateral wall short, shallow; crest curved. Spermatophore cone at oral end of cement body, flat, low, lens-shaped in outline; oral tube broad; aboral neck broad, distinct.

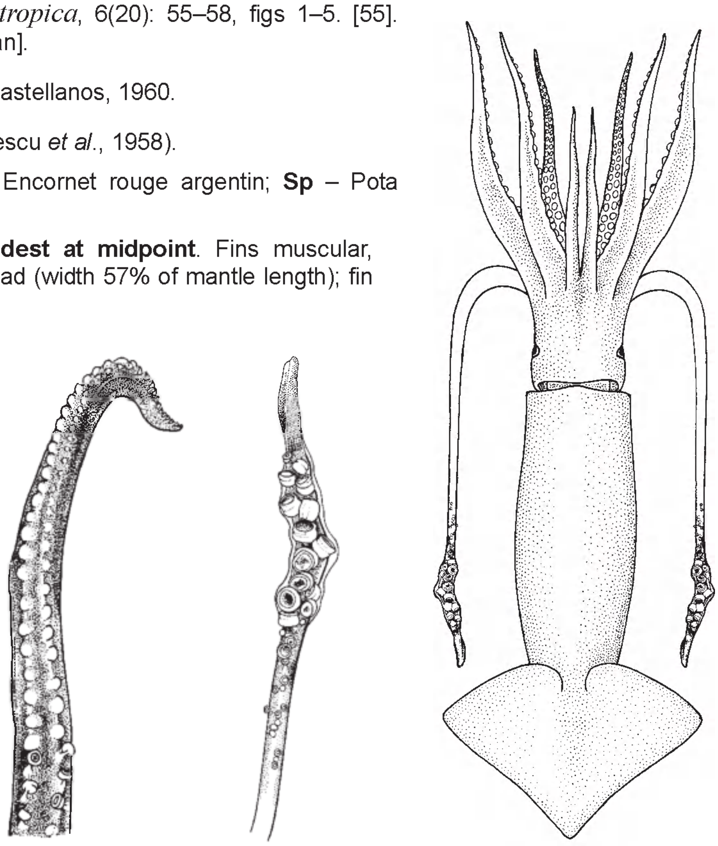

hectocotylus tentacular arm dorsal view

Fig. 284 *Illex argentinus*

Size: Maximum mantle lengths are around 380 to 400 mm.

Geographical Distribution: Western South Atlantic Ocean from about 22°S, around Rio de Janeiro and Cabo Frio, Brazil, southward to about 55°S, including the Falkland Islands, the tip of Tierra del Fuego, Staten Island (Isla de los Estados) and Burwood Bank. Greatest abundance occurs south of about 40°S (Fig. 285).

Habitat and Biology: *Illex argentinus* is the most abundant species of Ommastrephidae that occurs in the southwestern South Atlantic Ocean. It is a nerito-oceanic species that is broadly distributed from southern Brazil off Uruguay, and to southern Argentina, but it is most abundant between 35°S and 52°S at depths from 80 to 400 m. The adults are concentrated in shelf waters of subantarctic origin (8° to 12°C), mostly the cold waters of the Falkland (Malvinas) Current, while the embryos and paralarvae develop in the warmer waters to the north in the meanderings of the Brazil Current.

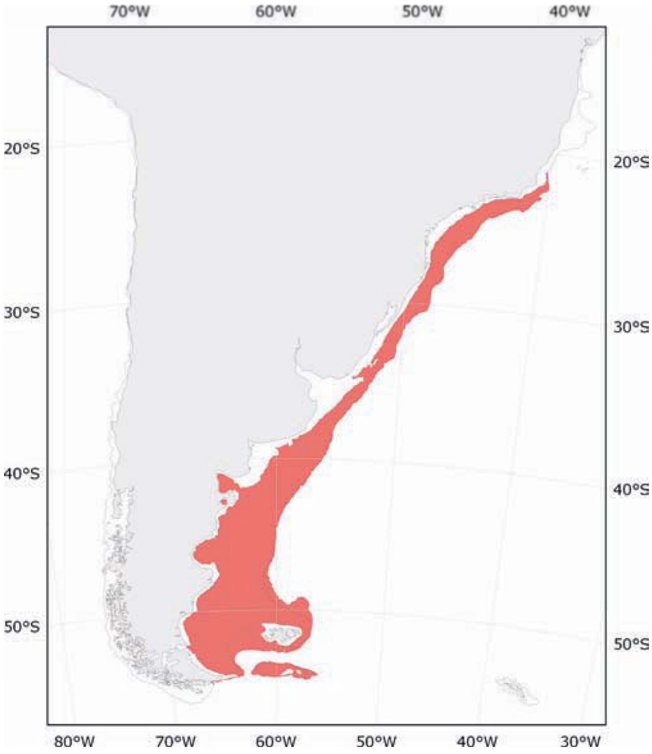


Fig. 285 *Illex argentinus*

🟥 Known distribution

This species supports one of the most productive cephalopod fisheries in the world, ranking among the top 3 species for several decades. This abundance derives from its habitat in association with the most extensive open continental shelf area in the world. The Patagonian Shelf is 1 700 km long; it extends from 39ºS to 55ºS, and it averages over 400 km wide off mainland Uruguay and Argentina, then bulges to nearly 900 km wide around the Falkland (Malvinas) Islands. Oceanographic conditions drive the high productivity of marine life in these waters, just as they do in the western North Atlantic habitat of ***I. illecebrosus***. The southwestern South Atlantic waters are under the influence of the strong western ocean boundary currents, similar to the Gulf Stream off North America. The southward flowing Brazil Current dominates the northern portion of the range, while the southern region is dominated by the northward flowing Falkland (Malvinas) Current. The 2 currents merge off Rio de la Plata, where the Falklands Current remnant component continues northward nearer the coast and the Brazil component sets offshore. These current components result in a highly developed shelf-break upwelling accompanied with strong tidal mixing that combine to create a region of very high primary and secondary productivity.

While the species range is widely distributed in the southwestern Atlantic, 4 more or less geographically distinct subpopulations, occur. Each one is characterized by its specific spawning area, spawning season, size at maturity and ontogenetic distribution.

These following subpopulations occur from north to south:

1) **The Summer Spawning Stock (SSS)** spawns principally on the intermediate and outer shelf at 80 to 150 m (range 50 to 200 m) during December to February (summer) at about 42ºS to 45º30'S; they are mature and spawn at a small size, 140 to 250 mm mantle length, in the stratified shelf waters. Spawning is completed during one short period of 30 to 60 days. Late embryonic stages and rhynchoteuthion paralarvae occur in the upper warm layer in water temperatures above 13°C. Paralarvae occur near the surface from December to March over the intermediate patagonian shelf along the tidal frontal system that develops between the shelf stratified waters and the well-mixed coastal waters. They are concentrated in the upper waters along the stratified side of the system, where abundance increases from the surface to a maximum at 40 m near the thermocline.

2) **The South Patagonic Stock (SPS)** spawns in autumn (April–May to July) in the southern shelf ecosystem along the Falkland (Malvinas) Current (45ºS to 48ºS), over the outer shelf and upper continental slope, when adults are 180 to 350 mm mantle length. Eggs and paralarvae are swept northwards by the current into warmer waters where development is enhanced.

3) **The Bonaerensis-North Patagonic Stock (BNPS)** that occurs between 35ºS and 38ºS, spawns in near-oceanic waters in winter (July–August) along the western boundary of the Brazil-Falkland (Malvinas) Current Confluence, at a size of 180 to 350 mm mantle length. Eggs and paralarvae are carried northward by the current into warmer waters where their development is enhanced.

4) **The Spring Spawning Stock (SpSS)** with adults of 230 to 350 mm mantle length, spawns in stratified shelf waters of the inner to intermediate shelf (50 to 100 m) at around 38ºS to 40ºS in the spring, September to November. Late embryonic stages and rhynchoteuthion paralarvae occur in the upper warm waters at greater than 13°C.

Juveniles 10 to 100 mm mantle length from the **SPS** and **BNPS** populations are pelagic and occur on the Bonaerensis-North Patagonic shelf during August through September. The SPS forms then migrate southward to the region of 45ºS to 49ºS, while the BNPS juveniles remain in the Bonaerensis-North Patagonic shelf area. Both stocks, then in their breeding grounds, recruit to the bottom by late spring. Other juveniles, 10 to 50 mm mantle length and 2 to 3 months old, occur in the oceanic region off coastal Argentina, mostly in the meanders and eddies formed in the Brazil–Falkland Confluence, while smaller numbers occur in the sub-Antarctic waters of the Falkland (Malvinas) Current during August through September. These juveniles probably had been transported as paralarvae from their spawning grounds into the oceanic region by the eastward shift of the Brazil current.

The vertical distribution pattern of ***I. argentinus*** is essentially one of ontogenetic descent. Smallest juveniles inhabit the epipelagic layer. Then, along with other forms of sub-Antarctic macrozooplankton, they move into the 25 to 40 m zone where they feed intensively and grow rapidly. Following this period they begin their recruitment into the final phase of their ontogenetic descent through the water column and recruit to the bottom when they are larger than 180 mm mantle length. From this point on they undergo daily migrations and disperse at night into the water column where they feed. They return to the vicinity of the bottom, or onto the bottom, during the daylight hours, descending to depths of 125 to 850 m.

Maturation of subadults to reproductive condition occurs relatively quickly, generally as the squids undergo their migrations to their respective spawning grounds. The biochemical composition and energy content of the gonads differs between males and females. Whereas they remain relatively constant during sexual maturation of the testis in males, the composition of the ovary changes significantly in mature females, with the concomitant development of the nidamental glands and oviducal glands. The nidamental glands of female ***Illex argentinus*** can account for more than 7% of body weight.

Individuals of the winter–spawning stock grow and mature on feeding grounds on the southern Patagonian Shelf, then migrate northward to the spawning grounds. They prey on rich zooplankton stocks and grow rapidly as they mature. The majority of tissue growth goes into somatic tissue; in females, 23% goes into the mantle, 17% to arms, tentacles and head, and 46% to the digestive gland, while only 16% goes into reproductive tissue; males grow significantly slower, mature at a smaller size and only 6% of accumulated energy goes into reproductive tissue. This strategy, while differing from many other squids, directs a large proportion of the energy budget into somatic tissues required to conduct the long migration to the spawning grounds. Once the spawning grounds are reached it is not yet known whether somatic reserves are then converted for gonadal production, as occurs in other squid species, e.g. ***Moroteuthis ingens***.

The total fecundity of oviduct eggs of females from the Summer Spawning Stock averages 18 854 ova, while that of females from the Bonaerensis-North Patagonic Stock averages 59 644. The individual fecundity of fully mature females (240 to 270 mm mantle length) from the South Patagonic Stock is 113 835 to 246 098 mature oocytes from the ovary and oviducts. An estimate of total fecundity based on oviduct eggs and previtellogenic oocytes in the ovary, that would eventually mature and be spawned, ranges from 75 000 (150 to 170 mm mantle length) to 1 200 000 (360 to 380 mm mantle length).

The reproductive strategy in males involves the slowing of growth at maturity of the accessory reproductive organs (that function to manufacture and store spermatophores). The size of spermatophores that accumulate in Needham's sac increases slowly and modal sizes of spermatophores produced at different times usually are the same. Males produce relatively smaller spermatophores than other ommastrephids, but they are more numerous. Male fecundity depends on the volume of Needham's sac and on the number of periods of active formation of spermatophores between copulations, which are more numerous in the larger males. The goal of the reproductive strategy is to maximize effective sperm production (the number of sperm packaged in proper spermatophores during ontogeny). In Illicinae the mechanisms to attain this goal are an increase in the relative volume of Needham's sac and an increase in the number of periods of formation and accumulation of spermatophores between matings. In males of 164 to 290 mm mantle length, spermatophores vary from 16.4 to 36.0 mm (mean 26.0 mm) and average about 11.5% of mantle length; the fecundity can be up to 1 600 spermatophores.

The nutritional value of ***I. argentinus*** for predators is high, because it is very muscular, thus rich in protein, and its large digestive gland is rich in lipids. Fresh Argentine shortfin squid are composed of 78 to 80% water (typical for marine invertebrate soft tissue), 10 to 17% protein, 12% lipid and minor carbohydrate content. The total proximate biochemical composition of the squid tissue does not alter during the life cycle, but a proportional shift in composition and mass of various organs and tissues occurs with sexual maturation, especially of the gonads and digestive gland.

Illex argentinus is preyed upon by a broad spectrum of predators, based on stomach content analyses. These include marine mammals, fishes, birds and conspecifics. Among major predators there are the Argentine hake (*Merluccius hubbsi*), the Patagonian hake (*Merluccius australis*) the Patagonian whiphake (*Macrouronus magellanicus*) and the southern blue whiting (*Micromesistius australis*). All these fishes probably are both prey and competitor of ***I. argentinus***. Other predators on this squid, and probable competitors for fish prey, are the southern cod (*Notothenia ramsayi*), elasmobranchs (skates and dogfish sharks), including the picked dogfish (*Squalus acanthias*), lings (*Genypterus blacodes*) and, probably, *Loligo* squid. Also, ***I. argentinus*** is ranked as very frequent in the diets of the bigeye tuna (*Thunnus obesus*), swordfish (*Xiphius gladius*), wreckfish (*Polyprion americanus*), hammerhead shark (*Sphyrna lewini*), yellowfin tuna (*Thunnus albacares*), and the albacore tuna (*Thunnus alalunga*). Other fishes that feed less frequently on ***I. argentinus*** include bluefish (*Pomotomus saltatrix*), red porgy (*Pagrus pagrus*), cutlassfish (*Trichiurus lepturus*), billfishes, (Istiophoridae) and shortfin mako shark (*Isurus oxyrinchus*).

Additional predators from off southern Brazil include the São Paulo squid (***Loligo sanpaulensis***), the Argentine angel shark (*Squatina argentina*), the skate (*Squatina ocula*), channel seabarrfish (*Evoxymetopon taeniatus*), the school shark (*Galeorhinus galeus*), the blackbelly rosefish (*Helicolenus d. lahillei*), the polkadot catshark (*Scyliorhinus besnardi*), the common dolphinfish (*Coryphena hyppurus*), the Atlantic sailfish (*Istiophorus albicans*), skipjack tunas (*Katsuwonus pelmas*), pilotfishes (*Naucrates ductor*), blue sharks (*Prionace glauca*) and white marlins (*Tetrapturus albidis*). Several marine birds prey on ***I. argentinus***, including the magellanic penguin (*Sphesniscus magellanicus*), the wandering albatrosses (*Diomedea exulans*) and white-chinned petrels (*Procellaria aequinoctialis*). Marine mammal predators include pygmy sperm whales (*Kogia breviceps*), sperm whales (*Physeter macrocephalus*), common dolphins (*Delphinis* sp.), longfinned pilot whales (*Globicephala melas*), southern elephant seals (*Mirounga leonina*) and sub-Antarctic fur seals (*Arctocephalus tropicalis*).

A complex trophic system exists among ***I. argentinus***, the Argentine hake (*M hubbsi)* and the Argentine anchovy (*Engraulis anchoita*), in the demersal-pelagic community: squid and hake prey on anchovy, squid prey on young pelagic hake, and older hake prey on all sizes of squid. Consequently, hake are prey, predator and competitor of ***I. argentinus***; they feed more intensely on squid in the southern part of its range from January to July and in the northern part from April to June. Clearly the total contribution of ***I. argentinus*** to the overall trophic system is highly significant throughout its range in waters of the Patagonian shelf, slope and adjacent oceanic region. Rough estimates indicate that it comprises between 40 and 75% by weight of the diet of predatory fishes.

Illex argentinus is an opportunistic predator that preys mainly on zooplankton when young, but fishes and squids can represent a significant proportion of the diet in some areas and with increasing age. The principal prey for squids less than 200 mm mantle length are crustaceans. Cannibalism occurs throughout the range, but it is more prevalent north of 42ºS.

Generally, adults feed on large prey, such as fishes and squids, but occasionally, large squids in the Patagonian shelf area prey mainly on crustaceans, which are available in great abundance. Feeding behaviour is reflected in the diel vertical migration habits of ***I. argentinus***. Two patterns exist: 1) immature and maturing squid feed on the bottom during the day then vertically migrate to near the surface to feed at night; 2) prespawning and spawning squid feed near the bottom at night and in the water column during the day, up to 200 to 300 m, preying on myctophid fishes in the acoustic scattering layer. The prey of ***I. argentinus*** generally are those that have a high lipid content, such as crustaceans (euphausiids, amphipods) and mesopelagic fishes (myctophids), and they accumulate high levels of lipid in their digestive gland, which grows at a considerably higher rate than the rest of the somatic tissues. This suggests a role as energy storage, or possibly increased buoyancy, in preparation for the long spawning migration. However, if spawning migrations are long, as in the case of the winter spawning population that feeds around the Falkland Islands, the squid must migrate to spawning grounds 1 000 km to the north. In this case the somatic energy reserves are insufficient to fuel the entire migration. Consequently, cannibalism occurs on smaller individuals during the journey, and on juveniles of earlier-spawned individuals on the spawning grounds.

Major prey items include copepods (*Oncaea media*), peneids, mysids, young Argentine hakes (*Merluccius hubbsi*), Argentine anchovies (*Engraulis anchoita*), macrourids, myctophids (*Diaphus dumerilii*), scianids, sternoptychids (*Maurolicus muelleri*) and cephalopod such as ***Argonauta*** sp., enoploteuthids, *Spirula spirula*, loliginid squid and conspecifics (***I. argentinus***). ***Illex argentinus*** is host to a broad range of parasites, including cestodes (*Phyllobothrium* spp., *Pelichnibothrium speciosum I*, and *Hepatoxylon trichiuri*), trematodes (*Derogenes varicus*, *Hirudinella ventricosa*) and nematodes (*Porrocaecum* sp. *I*, *Contracaecum* sp. *I*, *Anisakis simplex I*, *Anisakis* sp. *I (II)*, *Hysterothylacium* sp. *I*, *Spinitectus* sp. *I*). Trophic relations can be inferred from the existence and intensity of parasites. For example, throughout the squids' geographical range, the cartilaginous fishes, the final hosts for cestodes, and marine mammals, the final hosts of nematodes, are the main predators of ***I. argentinus***. While further north in its distribution, tunas and xiphoid fishes, the final hosts of didymozoids, are the most significant predators. The different spawning groups of ***I. argentinus*** are not distinguishable by their parasite fauna, because, while they spawn at different times, they all are caught in the same regions and their parasitic composition is similar, not cohort-specific. However, in the northern part of the range, off southern Brazil, immature and maturing squid caught in all seasons frequently are infected by didymozoids, which are absent in the colder waters south of the subtropical convergence. Of all the mature specimens, only those caught in autumn are infected with didymozoids, while large mature and spawning specimens caught in winter and spring, had no didymozoid parasites. This suggests that most of the winter and spring spawners off Brazil are migrants that feed and grow in colder southern waters, then migrate north to the Brazil Current to spawn.

Interest to Fisheries: The development of the fishery for ***I. argentinus*** in the southwestern South Atlantic Ocean occurred relatively recently in comparison to its congeners in the North Atlantic (***I. illecebrosus***, ***I. coindetii***) and Mediterranean (***I. coindetii***). Before the species was named and described, its ecological importance in the Argentine shelf waters was already recognized, as ***Ommastrephes bartramii***, during a studies of the biology and trophic relations of the common hake (*Merluccius hubbsi*). The Argentine shortfin squid was landed in small numbers only as bycatch from the then developing bottom trawl fishery for hake. In 1966, an extensive bottom trawl survey on the shelf by the FRV Walther Herwig indicated that an estimated catchable stock size of several hundred thousand tonnes existed in those waters. A small directed bottom trawl fishery developed in 1973, and combined bycatch and directed catch remained less than 6 000 tonnes through 1977.

The collapse of the ***I. illecebrosus*** fishery led to the rapid shift of the international jigging fleet in the late 1970s and early 1980s to the southwestern South Atlantic to pursue the ***I. argentinus*** fishery. This has been the most important squid fishery in the world, overall, since the early 1980s. By 1990 the catch had grown to 410 000 tonnes and continue to increase to peak in the late 1990s (over 1 million tonnes in the 1999); an important decrease (actually a collapse) was registered in the years 2004–2005, then catch values arose again to over 950 000 in 2007.

Squid fisheries have represented an extremely important resource in the southwest Atlantic Ocean, and ***I. argentinus*** represents its dominant species. However, since the inception of the directed fishery began in the late 1970s, both total abundance and total catches have been very variable. The most severe decline was the system-wide collapse of the ***I. argentinus*** stock in 2004. Both the shelf summer and autumn spawning stocks, as well as the winter spawning slope-oceanic stock experienced sharp declines. Two main factors are attributed to the collapse: 1) environmental changes, due mainly to the water dynamics of the Falkland–Brazil Current system with consequent high mortality of the paralarval stage; 2) overfishing. Retrospective analyses of catch data show correlations with various spatio–temporal patterns and explain interannual variations in catches with effects of year, month, latitude, position on continental shelf and body size.

Stock abundance has a non-linear relationship with SST so that the highest CPUE occurs at SST temperatures of 13° to 14°C. The years of collapse in the fishery, particularly 2004, were defined by low SSTs, around 10°C.

An analysis of the spatio–temporal distribution of ***I. argentinus*** based on over 11 000 trawl and jig haul records placed the areas of maximum abundance in deeper waters of the high seas between 44.5°S and 47°S outside the Argentine Exclusive Economic Zone (EEZ) and northwest of the Falkland (Malvinas) Islands. The jigging and trawling fishery is conducted by long range fleets from Argentina to southern Brazil, but a major portion of the catch is taken by the international fleet under a well-regulated management system. The principal fishing nations with the longest participation in the fishery are: Japan, Korea, Portugal, Spain and Taiwan Province of China. Other jigging fleets have been from Chile, Falklands, France, Italy, Poland and the United Kingdom. The greatest tonnage has been taken, in descending order by: Korea, Japan, Taiwan Province of China, Poland, Spain, China, Brazil, Falklands, Cambodia and Honduras. In general, the jigging fishery is conducted by the Asian-country fleets, while the trawling fishery is executed by the European and South American participating countries. While the trawl fishery off southern Brazil in the Exclusive Economic Zone (EEZ) concentrates on 3 species of fish (Gulf hake, Argentine hake and monkfish) a significant bycatch of ***I. argentinus*** is taken, principally in the winter over the upper slope at 250 to 500 m. Trawling peaked in 2002, and has steadily declined since: the "gold rush" development of the slope fishery with such high fishing capacity is incompatible with a sustainable fishery. The fishery operates in coastal and shelf waters, mostly along the edge of the shelf break north of 52°S where a well-defined frontal boundary zone persists along nearly the entire length of the shelf.

The fishery developed so rapidly during its early years that considerable concern existed over the condition and sustainability of the full stock of ***I. argentinus***, as well as the potential of overexploitation of the 3 or 4 component populations that had been distinguished. However, under the supervision of the South Atlantic Fisheries Commission, Argentina and the United Kingdom collaborated since 1990 in joint or coordinated research and management efforts that led to rational assessment, monitoring and management of the fishery, both by local and the international fleets. Under this management regimen, the Argentine shortfin squid is considered to be fully exploited in spite of the very high year-to-year variability in recruitment, abundance and harvests. Through this collaborative management, virtually real-time monitoring of the stock and the ability to coordinate management action exists. In spite of close management the fishery continues to undergo annual declines. The short life span and semelparous life style of ***I. argentinus*** makes it difficult to manage the fishery, because, once the spawners of one generation have reproduced and died, it is extremely difficult to assess the potential recruitment strength and resultant stock size of the next generation. A biologically rational quota for the harvest can not be established until the new generation is recruited into the fishery. Consequently, the fishery is managed by effort limitation and assessed in real time. Effort is established prior to the new jigging season based on historical information on putative stock size. Then, once the fishery opens for that year, the stock is continuously assessed using the Leslie-Delury depletion analysis; the fishery is closed once the CPUE estimates indicate that the remaining biomass corresponds to the precalculated target spawning escapement. This management approach was introduced in 1987 when the target escapement was established as 40% of the numbers of squid recruited into the fishery. Subsequently, the escapement target has been determined as an absolute year-to-year value in order to stabilize the size of the spawning population, regardless of the annually variable recruitment. The 40% proportional escapement policy was later refined to require an absolute minimum escapement of 40 000 tonnes, which insures a precautionary limit in a year of poor recruitment. A further refinement involves pre-recruitment surveys that improve the initial assessment of catch effort prior to the opening of the fishing season. Empirical modelling to predict the level of recruitment for the next season employs predictive variables of the environmental conditions on the spawning grounds off the Plate River during the previous year. Recognition and incorporation of the strong association of oceanographic paramenters to recruitment is necessary. The sustainability of the multi-cohort stocks depends on the ability of the management approach to respond to changing environmental conditions, both between years (response to variable recruitment by in-season management of single-age cohorts) and to long-term periods of oceanographic regime shifts.

Regional sea surface temperature data taken by remote sensing over the southwestern South Atlantic indicate that about 55% of the recruitment variability in ***I. argentinus*** in the Falkland (Malvinas) Islands fishery is created by area changes in the optimum temperature for larval development on the spawning grounds during the spawning season prior to recruitment of that year class.

The sea surface temperature conditions that predict strong recruitment also are associated with a reduction in horizontal temperature gradients (3°C over a 15 km span) in the spawning grounds. Such effects in the South Atlantic are associated with sea surface temperature anomalies that occur in the El Niño Southern Oscillation (ENSO) system in the southeastern South Pacific Ocean; these variations stimulated by the ENSO cycle eventually affect the recruitment, population size and fishery catches of ***I. argentinus*** in the Patagonian Shelf/Falkland Islands fishery 2 to 5 years later. Knowledge about the variability and behaviour of the ENSO each year ultimately can help to predict environmental variability on the spawning grounds in subsequent years, thus to forecast recruitment and population levels and enable a management system to more precisely establish sustainable catch levels in the fishery. The Southern Oscillation Index (SOI) and sea surface temperatures (SSTs) on southern and northern parts of the Patagonian Shelf have different effects on ***I. argentinus*** abundance. SSTs in both areas show a link with the SOI at lag times of 2 and 3 years, respectively. No significant correlation exists between the SOI and squid abundance, or between SSTs of the southern portion of the shelf and squid abundance within a 10 year lag time. However, SSTs in the northern portion of the shelf correlate negatively with squid abundance with a 1-year lag time. Consequently, cold events in this region in the previous year could cause high squid abundance in the current year. In any case, the distribution patterns of ***I. argentinus*** on the Patagonian Shelf are influenced locally by the thermal fronts, which in turn depend on the intensity and distribution of the cold currents. Catch rates vary monthly with peak catches in February and March. SSTs of 7° to 14°C are suitable for catching ***I. argentinus***: 11° to 12°C in February, 10° to 12°C in March, 8° to 9°C in April and 7° to 8°C in May. Catches are best where SSTs are slightly higher than the historical average level.

In addition to known effects of environmental factors on survival, growth, recruitment, abundance and availability of ***I. argentinus***, commercial exploitation also should be expected to have discernible effects. The short life span of squids makes them highly susceptible to the selective effects of commercial exploitation. Life history characteristics can be altered and there exists a strong selection for an even earlier age of maturation than has already been demonstrated, as well as the potential loss of a migratory component of the population (migrations from feeding grounds to spawning grounds and return are critical components of the life history cycle).

As with any well-managed squid fishery, sound management of the ***I. argentinus*** resource ultimately requires a full understanding of the life cycle of the species.

Remarks: In studies off the central South Brazilian Bight on cadmium concentrations in marine fishes and cephalopods, the mean cadmium concentration in ***I. argentinus*** digestive gland was 1002.9 mu g/g wet weight (Dorneles *et al*., 2007). This represents the highest cadmium level ever recorded in a cephalopod. Causative factors for such remarkable cadmium levels include anthropogenic action from coastal industrial and urban development, upwelling systems and cannibalism.

Local Names: ARGENTINA: Calmar; JAPAN: Argentina matsu ika; URUGUAY: Calmar.

Literature: Roper *et al.* (1984), Nigmatullin (1989b), Brunetti *et al.* (1998a,b), Barton *et al.* (2004), Boyle and Rodhouse (2005), Chen et al. (2005b), Martinez *et al.* (2005a,b), Chen *et al.* (2007a,b).

Illex coindetii (Verany, 1839)

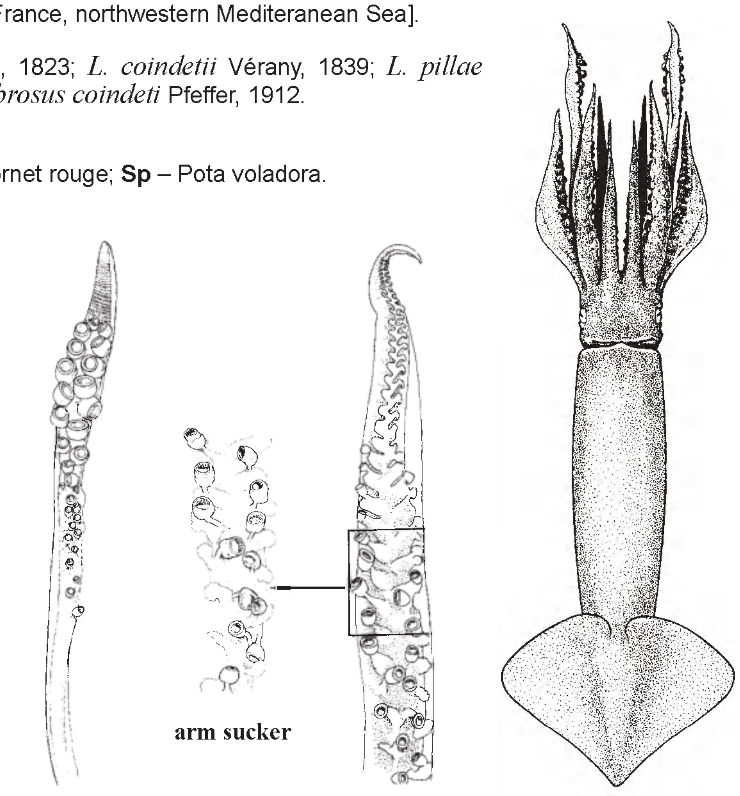
Fig. 286; Plate VIII, 50–51

Loligo coindetii Verany, 1839, *Memorie della Reale Accademia delle Scienze di Torino*, Series 2, 1: 91–98. [94, pl. 4]. [Submitted in 1837]. [Type locality: off Port Vendres, France, northwestern Mediteranean Sea].

Frequent Synonyms: *Loligo brogniartii* Blainville, 1823; *L. coindetii* Vérany, 1839; *L. pillae* Vérany, 1851; *L. sagittata* Vérany, 1851; *Illex illecebrosus coindeti* Pfeffer, 1912.

Misidentifications: *Illex illecebrosus*, Adam, 1952.

FAO Names: En – Broadtail shortfin squid; **Fr** – Encornet rouge; **Sp** – Pota voladora.



tentacular arm arm sucker hectocotylus dorsal view

Fig. 286 *Illex coindetii*

Diagnostic Features: Mantle moderately long and narrow, widest at anterior end (except in fully ripe females); **tail pointed**. Fins rhomboidal, fin angle >50%. **Head wide and robust, especially in mature males**; head-width index high, 23 (19 to 26) in mature males, 19 (15 to 22) in mature females. **Funnel groove smooth, without foveola or side pockets**. **Dactylus of tentacular club with 8 longitudinal rows of small suckers**. Club expanded; **largest distal manal sucker rings notched in distal half or all around with low crenulations, not smooth**. Arms relatively long and robust, especially in males. **Either left or right ventral arm hectocotylized**, with distal hectocotylized portion of the arm (HA3) relatively short, about 25% (17 to 30% on fully mature males) of total arm length (HALt); basal, suckerless part (HAb) of hectocotylized arm about 13% (10 to 14%) of total arm length; proximal sucker-bearing part (HA1) with 5 to 7 (mostly 5 or 6) pairs of normal suckers, increasing in diameter distally; distal sucker-bearing part (HA2) starts with a pair of suckers immediately decreased in diameter by one-half or more in comparison with the proximal adjacent **pair on** HA1; rows widely separated, suckers in both rows remain small; oral surface of arm constricted in transition zone between HA1 and HA2; at proximal origin of HA2, trabeculae distal to largest normal suckers (HA1) transformed into distinctive fringed flaps; modified distal portion (HA3) bears fully developed truncate lamellae on dorsal rows and digitate papillae (no lamellae) on ventral row.

Size: Maximum mantle length recorded is 379 and 279 mm respectively, for a female and a male from Spanish Atlantic waters. Common at 200 to 250 m throughout its distributional range.

Geographical Distribution: ***Illex coindetii*** has an unusual widespread, disjunct, distribution for a neritic cephalopod. It occurs in the eastern Atlantic, from as far north as the Oslo Fjord, off the Norwegian coast (i.e. 60°N), throughout the North Sea and southward, along the Atlantic European and African coasts, southward to the Namibian waters at 19ºS to 20ºS. It is distributed throughout the Mediterranean Sea, from the western to the eastern ends; Aegean and lower Adriatic Seas; absent from the upper Adriatic Sea and the Black Sea, but it has been reported from the Sea of Marmara. In the western Atlantic its northernmost records are from off the Virginia coast (i.e. 37°N); it is distributed southward, in association with the Gulf Stream and the Florida Current, in the Gulf of Mexico and the Caribbean Sea, and it has been reported from the French Guiana waters, so it probably extends to 3°N, but the exact extent of its southern distribution remains undetermined (Fig. 287).

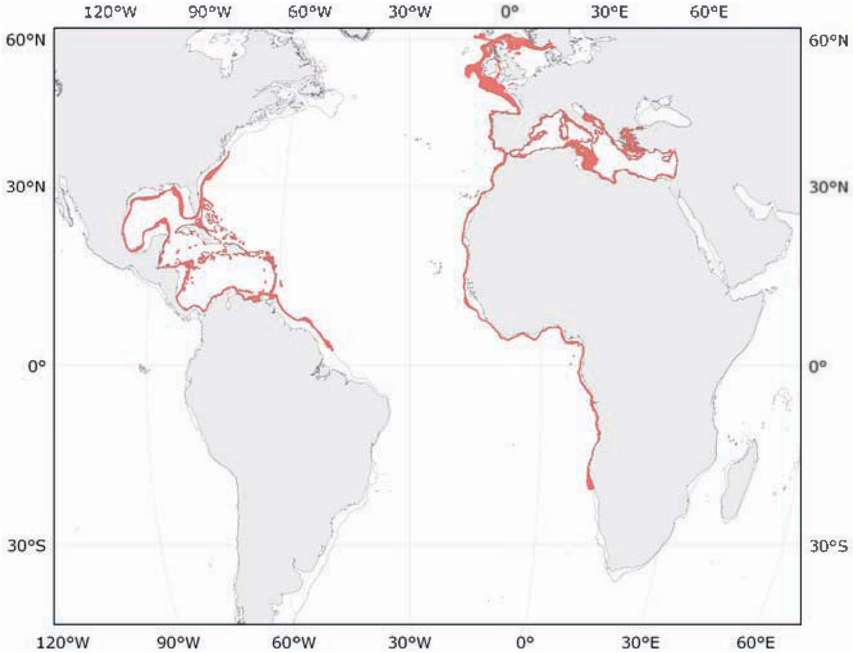


Fig. 287 *Illex coindetii*

🟥 Known distribution

Habitat and Biology: A demersal, neritic species of the continental shelf and upper slope, ***Illex coindetii*** occurs from the surface down to over 1 000 m, with maximum concentrations between 50 and 100 m and 400 to 600 m, depending on geographical location. For example, in the Mediterranean Sea, peak concentrations are at 60 to 400 m, the eastern Atlantic 150 to 300 m, the western Atlantic 200 to 600 m and the Caribbean Sea 180 to 450 m. It is found commonly on sandy and muddy bottoms typically covered by seapens (*Funiculina* spp.) asteroids and ophiuroids, often associated with fishes and crustaceans targeted by commercial fisheries, such as the giant gamba prawn (*Aristaeomorpha foliacea*), the deep-water rose shrimp (*Parapeneus longirostris*), the Norway lobster (*Nephrops norvegicus*), the European hake (*Merluccius merluccius*) and the blue whiting (*Micromesistious poutassou*) and with the lesser flying squid (*Todaropsis eblanae*). Mature squids are distributed over the whole depth range and adults undergo vertical migrations, living close to the bottom during the day, then they ascend towards the surface at night. Seasonal migrations also have been observed, at least in some areas of the distribution, e.g. the western and central Mediterranean Sea. Sex ratio usually is 1:1; significant deviations from this value were recorded in the Spanish (Galician) waters, eastern North Atlantic and Ionian populations of central Mediterranean, but such differences are attributed to ecological and/or morphological constraints rather than to actual genetic differences.

Changes in general morphology do occur with sexual maturity and can be quite dramatic in the last stages of maturation, when the relative dimensions of head and arms lead to a distinct sexual dimorphism, with males conspicuously more robust and heavier than females. Size at maturity varies significantly, but generally males mature at a smaller size than females. Also, a west–east gradient of decreasing values in mantle lenght at 50% maturity occurs in ***I. coindetii*** populations from the Atlantic to the eastern Mediterranean.

Reproduction and spawning extend throughout the year, with peaks in different seasons/months, depending on geographic location. Fecundity varies with the size of females and spermatophore number with size of males. A potential fecundity of more than 700 000 oocytes was estimated for females from the northwest African waters. Recorded spermatophore length varies between 11 and 38 mm and the maximum number reported is slightly more than 1 500. Spermatophores are deposited in bunches into the female mantle cavity and usually more than one bunch occurs in mated females, suggestive of multiple mating events; the probability that females mate with different males seems high; this behaviour would promote increased genetic exchange. Eggs are small (0.8 to 1.3 mm), embedded in a transparent egg jelly that forms floating egg masses. This gelatinous mass functions as a buoyancy mechanism which prevents eggs from sinking; the equilibration of density between egg masses and sea water, in fact, requires many days under most conditions. Therefore, if spawning occurs in the pelagic domain, the egg masses can remain suspended in the mesopelagic zone for a relatively long time. Such a mechanism would allow pelagically-spawned eggs to take advantage of temperature and other oceanographic conditions most beneficial for embryonic development. ***Illex*** egg masses have not been recorded in the natural environment, but observations in the laboratory of ***I. illecebrosus***, showed that this species produces gelatinous egg masses while swimming in open water. Embryonic development in the laboratory requires between 10 and 14 days at 15°C; this value probably reflects the period under natural conditions. Rhynchoteuthion hatchlings are about (1.4 mm), and the rhynchoteuthion-phase probably constitutes the most delicate time of the entire life cycle; since these paralarvae seem unable to attack prey, they probably feed on suspended particulate material. Favourable environmental conditions during this phase of embryonic development may cause recruitment peaks and, ultimately, may influence recruitment success. An unusually high abundance of ***I. coindetii*** paralarvae and juveniles in the Evoikos Gulf off central Greece seems related to the convergence of currents in an area of upwelling that resulted in a high concentration of nutrients, thus high productivity that was conducive to aggregations of cephalopod paralarvae and larval fishes.

Growth is rapid; females have higher growth rates than males and several groups with different growth rates usually are detectable within a population; animals hatched in spring–summer have a higher growth rate than those hatched in autumn–winter. Growth differs between sexes, being positively allometric in males and isometric or negatively allometric in females, because of the morphometric dimorphism already mentioned. The only exception to this rule is the positive allometric growth recorded for females from northwestern Spanish waters; also in this case, however, “b” value was lower than that computed for males. Recent observations indicate that parasites can negatively affect growth, as well as the general condition of the animals. Length frequency distributions in ommastrephids usually are polymodal and difficult to use to investigate growth; also, different results generally are obtained when estimating life cycle duration by direct age investigation (i.e. statolith analysis). Duration of the life cycle of ***I. coindetii*** based on length frequency analysis was estimated to range between 12 and 18 months and 24 months for populations from the eastern Atlantic and the Mediterranean Sea. However, studies on age determination based on statolith investigations, have revealed a shorter life span, such as 12 to 15 months in the eastern Atlantic, 16 months in the western Mediterranean and an even shorter life span (6 to 7 months) for individuals from the waters of Sicily (central Mediterranean). Spawning represents the terminal phase of the life cycle, but it lasts longer than previously thought; many observations indicate that ***I. coindetii*** females are “intermittent spawners” that spawn several times during a period of time ranging between a few days and a few weeks.

As is the case for cephalopods in general, and for ommastrephids in particular, ***I. coindetii*** is a voracious and opportunistic predator. It feeds on a wide spectrum of prey, including fishes, crustaceans and other cephalopods, depending essentially on those prey most available and on the size of the predators. Changes in the diet composition with growth have been noted, with smaller squids preying more intensively on crustaceans, while larger, adult animals seem to prefer fishes and other cephalopods, but these changes have been related to important changes in mouth structure of the squid and consequent foraging behaviour, and they were not considered proof of prey selection. Stomach content analysis supports a more pelagic habitus in young squids (a higher proportion of euphasiids in the diet) while adults feed both on the bottom (i.e. amphipods, cephalopods and benthic fishes) and in the water column (a wide variety of pelagic species, such as myctophids, clupeids, gadids). Cannibalism does occur, but probably it is an occasional phenomenon, related to situations of unusually high squid abundance and/or scarcity of other prey. A significantly higher number of mature females with prey remains in their stomach has been recorded, indicating an increased level of feeding in females, probably due to the higher energy required for maturation and egg production; this surplus of energy would be obtained mainly by direct feeding, since evidence seems to indicate that storage reserves are not transferred from internal tissue to gonadal tissue.

Illex coindetii is preyed upon by a wide variety of predators, including cetaceans such as common dolphins (*Delphinus delphis*), pilot whales (*Globiocephala melas*), Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*), bony and cartilaginous fishes such as sharpnose sevengill sharks (*Heptranchias perlo*), swordfishes (*Xiphias gladius*), yellowfin tunas (*Thunnus albacares*), blue whitings (*Micromesistius poutassou*), greater forkbeards (*Phycis blennoides*) and conger eels (*Conger conger*) and other cephalopods, such as larger squids like the European flying squid (***Todarodes sagittatus***) and the European squid (***Loligo vulgaris***).

Interest to Fisheries: Taken mainly as a bycatch by bottom trawl fisheries throughout its distributional range, ***I. coindetii*** also is fished by trammel and gillnets; it is caught at night by encircling seiners in the Catalan Sea and was caught by experimental jigging. Specific statistics do not exist, since the species generally is marketed along with the sympatric ommastrephid ***Todaropsis eblanae*** and occasionally with ***Todarodes sagittatus***. However, it is likely to constitute a conspicuous fraction of the annual ommastrephid squid catches both in the Mediterranean Sea and in the Atlantic waters. In the last decades landings in European waters ranged from 3 000 tonnes to more than 7 000 tonnes, the most conspicuous fraction of which was caught in Italian waters of the central Mediterranean. Catches of ***I. coindetii*** in this area may represent a valuable resource based on tonnages recorded. A marked seasonality in the landings occurs in various areas of the species distribution in the central Mediterranean and North East Atlantic. For example, ***I. coindetii*** is periodically very abundant in coastal waters of the eastern North Atlantic off Scotland, Ireland and Spain, where it supports opportunistic fisheries. The oceanographic and biological factors that drive this phenomenon, however, currently are not known. Along the Spanish Catalan coast the species is taken mainly as bycatch, and landings have increased steadily since 1987. The spawning season is protracted with maximum peaks in autumn and spring, represented as well by the period of maximum abundance. Large individuals occur year-round, but are most abundant and concentrated during the spawning seasons, spring and autumn, while juveniles are most commonly caught in winter and summer.

Local Names: GREECE: Kokkino, Thrapsalo; ITALY: Totano, Todaro; PORTUGAL: Pota voladora.

Remarks: The remarkable morphological variation observed throughout the distributional range of the species (characterized by a number of more or less distinct morphotypes), along with its disjunct occurrence on both sides of the Atlantic, has led to the suggestion of the existence of a multiple species complex. Recent studies, both on systematics, morphometry and genetics of ***I. coindetii*** from across the distributional areas, seem to reject this hypothesis (Martinez *et al*., 2005a,b, Carlini *et al*., 2006). However, the high variability observed, along with the confirmed existence of at least 2 basic distinct morphological forms, 1 inhabiting the Mediterranean Sea the other inhabiting the Atlantic Ocean, support the need for further morphological and genetic studies.

With regard to the broad variation in results of various age analyses we offer a strong cautionary note: in spite of the recognized validity of age estimation by statolith analysis, several studies suggest that values should be regarded as estimates, not absolutes.

Literature: Mangold-Wirz (1963), Roper *et al.* (1984), Guerra (1992), Jereb and Ragonese (1995b), Rasero *et al.* (1996), Lordan *et al.* (1998a), Roper and Mangold (1998), Roper *et al.* (1998), Sanchez *et al.* (1998b), Belcari (1999c), Arvanitidis *et al.* 2002, Martinez *et al.* (2005a,b), Ceriola *et al.* (2007), Hastie *et al.* (2009).

Illex oxygonius Roper, Lu and Mangold, 1969

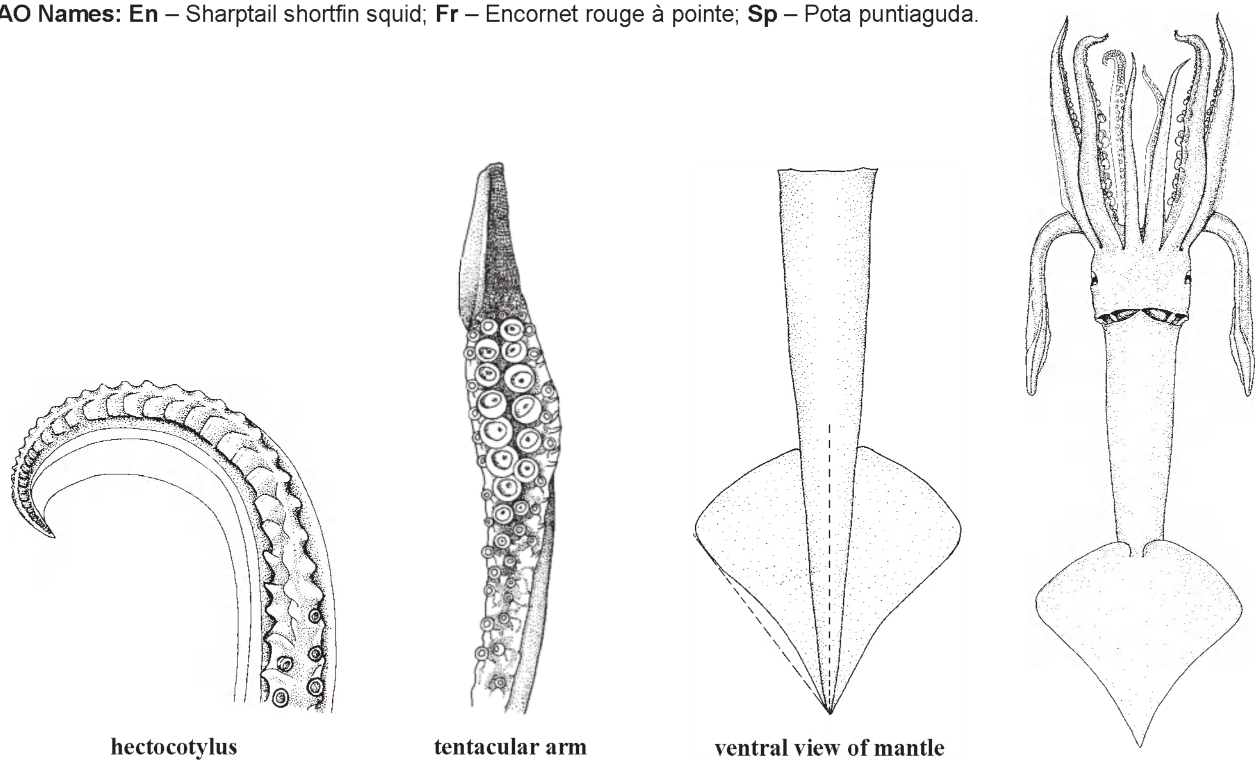
Fig. 288

Illex oxygonius, Roper, Lu and Mangold, 1969a, *Proceedings of the Biological Society of Washington*, 82: 295–322. [299]. [Type locality: 24°13'N, 81°58'W, western Central Atlantic Ocean].

Frequent Synonyms: None.

Misidentifications: Non *Illex illecebrosus* (Lesueur, 1821), in part; *I. coindetii* (Verany, 1839), in part.

FAO Names: En – Sharptail shortfin squid; **Fr** – Encornet rouge à pointe; **Sp** – Pota puntiaguda.



hectocotylus

tentacular arm

ventral view of mantle

dorsal view

Fig. 288 *Illex oxygonius*

Diagnostic Features: Mantle widest at anterior end, long and narrow; **tapers gradually to elongate point posteriorly**; males with **sharp triangular dorsal lobe at mantle opening**. The hectocotylus with distal hectocotylized portion of arm IV (HA3) moderately long, about 29% (24 to 32%) of total arm length (HALt); 3 knobs and 2 slightly flattened papillae proximal to well-developed lamellae in dorsal row; basal, suckerless part (HAb) of hectocotylized arm 4% of total arm length; proximal sucker-bearing part (HA1) with 7 pairs of normal suckers; distal sucker-bearing part (HA2) with sucker diameters reduced in size by about one-quarter on both rows. Rows normally separated; oral surface of arm constricted slightly in transition zone between HA1 and HA2, but with no distinct reduction of arm musculature between normal and reduced sucker areas; trabeculae not modified as fringed lobes; **hectocotylized arm longer and more robust than opposite arm in fully mature animals**. **Club-sucker rings of largest distal medial manal suckers smooth, without crenulations or notches**. Head-width index high, 20.7 (19 to 23) in mature males, 17.8 (16 to 20) in mature females. Arms long, robust, especially Arms II and III in males. Lower beak with jaw edge curved, long; wing short, narrow, lobate; rostral width wide; lateral wall long, pointed. Upper beak with hood short, very thin, weak; shoulder smooth, straight or slightly curved; rostrum short; wing short; jaw angle with small notch; lateral wall long, deep; crest straight. **Fin angle in mature males acute, 25° to 35°, occasionally 40°; fin width equal to fin length**. Spermatophore cone at oral end of cement body, funnel-shaped, with sides equal, broadly triangular in outline; oral tube relatively broad; aboral neck moderately short, narrow. The colour of the live animal is reddish to reddish brown, more vivid on dorsal head and mantle; more pale, yellowish ventrally.

Size: Maximum mantle length 230 mm in males, 210 mm in females.

Geographical Distribution: Western North Atlantic, off mid-Atlantic United States from off New Jersey, the Chesapeake Bight, southward through the Florida Current and into southeastern Gulf of Mexico; Gulf of Guinea, eastern Atlantic, single record. Limits of geographical distribution of species not well defined because of lack of comprehensive collections (Fig. 289).

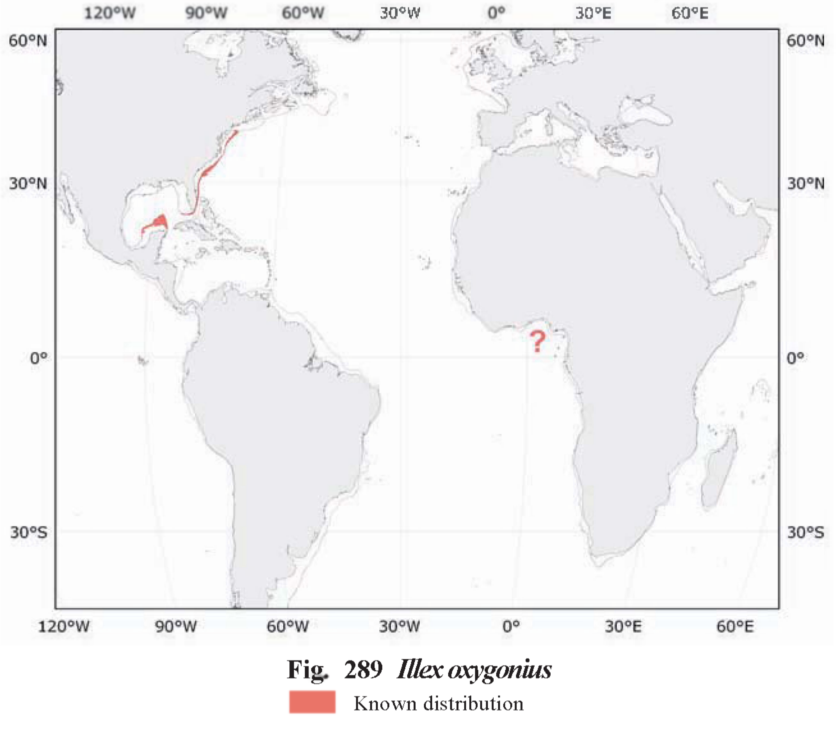


Fig. 289 *Illex oxygonius*

🟥 Known distribution

Habitat and Biology: ***Illex oxygonius*** is primarily a neritic species that occurs at depths between 50 and 550 m within a temperature range from 6° to 13°C. It is associated with the bottom during daylight hours but disperses into the water column at night. Its biology, abundance and total distribution, are largely unknown. It is believed to feed on crustaceans and fishes, similar to its congeners. It is sympatric with both ***I. illecebrosus*** in the northern parts of its range and ***I. coindetii*** in the southern parts. All 3 species appear to co-occur in the Straits of Florida, but this needs to be confirmed with more precisely located collections.

Interest to Fisheries: At present, the species is taken only as bycatch in bottom trawl fisheries. When concentrations are discovered, the species would be a valuable fishery resource because its size and consistency are excellent for human consumption, just as with its congeners.

Remarks: Nigmatullin (1989) suggested that ***I. oxygonius*** was an example of advanced spawning and spent squid traits typical of final life stages of small-sized mature squids of the 2 other species of ***Illex***. Subsequently, however, 2 significant genetic studies (Martinez *et al.* 2005a,b, Carlini *et al.* 2006) have confirmed the existence of 4 species of ***Illex***, including verification of the distinct species status of ***I. oxygonius***. The 2 different techniques used, allozyme polymorphisms (from purpose–caught, freshly prepared specimens) and cytochrome C oxydase subunit I (from formalin-fixed museum specimens), differed somewhat in results and cohesion. Consequently, especially in areas where distributions overlap, specific identification of some specimens remains tenuous until further research clarifies the situation.

Local Names: USA: Sharptail shortfin squid.

Literature: Roper *et al.* (1969a), Roper *et al.* (1998), Vecchione (2002), Martinez *et al.* (2005a,b), Carlini *et al.* (2006).

2.22.2 Subfamily **OMMASTREPHINAE** Posselt, 1891

Ommastrephinae Posselt, 1891, *Videnskabelige Meddelelser fra den Naturhistoriske Forening: Kjøbenhavn*, 1890: 301–359.

Type Genus: *Ommastrephes* d'Orbigny, 1834 *in* 1834–1847.

Diagnostic Features: Small yellow subcutaneous photophores (similar to short grains of rice) **on mantle, fins, head and arms**; some species may have different arrangement and form of photophores, e.g. large mantle photophores with reflective subjacent layer; **1 ocular and 1 or 2 intestinal photophores present**. Mantle wide, posterior end without pronounced pointed tail; **funnel groove with clearly defined side pockets**; tentacle fixing apparatus with one or several knobs that alternate with smooth-ringed suckers; rings of large suckers on manus with either one large median tooth in distal part of ring, or with 4 large teeth, 1 at each quadrant.

Table 11

Comparison of genera of Ommastrephinae[1/]

	Largest manus sucker	Visceral photophores	Enlarged, easily visible, subcutaneous photophores	Hectocotylus with lateral pores	Arm tips
Dosidicus	Toothed, enlarged tooth in each quadrant	2 round organs, no streaks	None	Yes	Attenuate at >350 mm ML, with 200–500 small suckers
Eucleoteuthis	Smooth except 1 tooth	1 round organ, no streaks	Circular pads and streaks	No	Normal
Hyaloteuthis	Smooth, sometimes 1 tooth	1 round organ, no streaks	circular pads	No	Normal
Ommastrephes	Toothed, enlarged tooth in each quadrant	None	None	No	Normal
Ornithoteuthis	Toothed, no enlarged teeth	1 or 2 round organs, streak	None	Yes	Normal
Sthenoteuthis	Toothed, enlarged tooth in each quadrant	2 round organs, no streaks	None	Yes; No in early maturing form	Normal

[1/] from Young and Vecchione (2008g)

Ommastrephes d'Orbigny, 1834 *in* 1834–1847

Ommastrephes d'Orbigny, 1834 *in* 1834–1847. Mollusques. *Voyages dans l'Amerique Meridional*, 5(3): 1–758, 85 pls. [45].

Type Species: *Ommastrephes bartramii* (Lesueur, 1821).

Diagnostic Features: The funnel groove has a **foveola with 5 to 8, occasionally 9, longitudinal folds and 2 to 5 (mainly 3 or 4) distinct side pockets**. **External light organs present**, including small, scattered, subcutaneous photophores embedded in the tissue of the mantle, head and ventral arms, **but no large dorsal mantle photophore is present**. No ocular nor intestinal photophores present. **A long, wide, silvery or golden opalescent strip extends along the ventral midline from just posterior to the mantle opening to the level of the anterior edge of the fins**. Similar silvery or golden tissue occurs on the ventral surface of the head and ventral arms. A relatively dense aggregation of small subcutaneous photophores is concentrated under this opalescent tissue. The **dactylus** of the tentacular club **has 4 rows of small suckers**. The carpal-locking apparatus on the tentacular stalk has 2 to 5 knobs and 2 to 4 smooth-ringed suckers; 4 to 7 suckers with denticulate rings occur on the carpus proximal to the first knob. **The largest medial suckers on the manus of the tentacular club have 4 large pointed teeth, 1 at each quadrant**. The tips of all arms are not attenuate. The arms have 24 to 35 pairs of suckers. The tips of the trabeculae of the protective membranes do not project beyond the edge of the membrane. **The ventral protective membranes of arms III are very wide, and in adult females they expand into a large, triangular, membranous lobe**. Right or left ventral arm is hectocotylized with the smooth type of modification, without suckers. Fins rhomboidal, slightly attenuate posteriorly; fin length 40 to 50% and width 60 to 85% of mantle length; fin angle 46° to 65°. The cone flags of the gladius are short, rhomboidal, with distinct radial creases. The greatest width of the cone flags is about 56% of the width of the rachis. The marginal rigidity ribs of the rachis are doubled; the axial rigidity rib of the rachis is wide, rounded-rectangular in cross-section. The lateral plates of the gladius do not adhere to the dorsal surface of the rachis but form wide free folds over the rachis. The stem of the rachis is short, reminiscent of a mammalian vertebra in cross-section. The width of the stem is slightly greater than its thickness. The cone is short, flattened laterally. A rostrum is absent. The alveola is thick, covered with tiny ribs and thorns. Spermatozoa have 1 flagellum.

Geographical Distribution: Widely distributed in subtropical and partly temperate waters of both hemispheres in the Atlantic, Indian and Pacific Oceans.

Remarks: Monotypic: a single oceanic species is recognized. Restriction profiles of 2 endonucleases, Alu I and Tsp509 I are diagnostic for species identification.

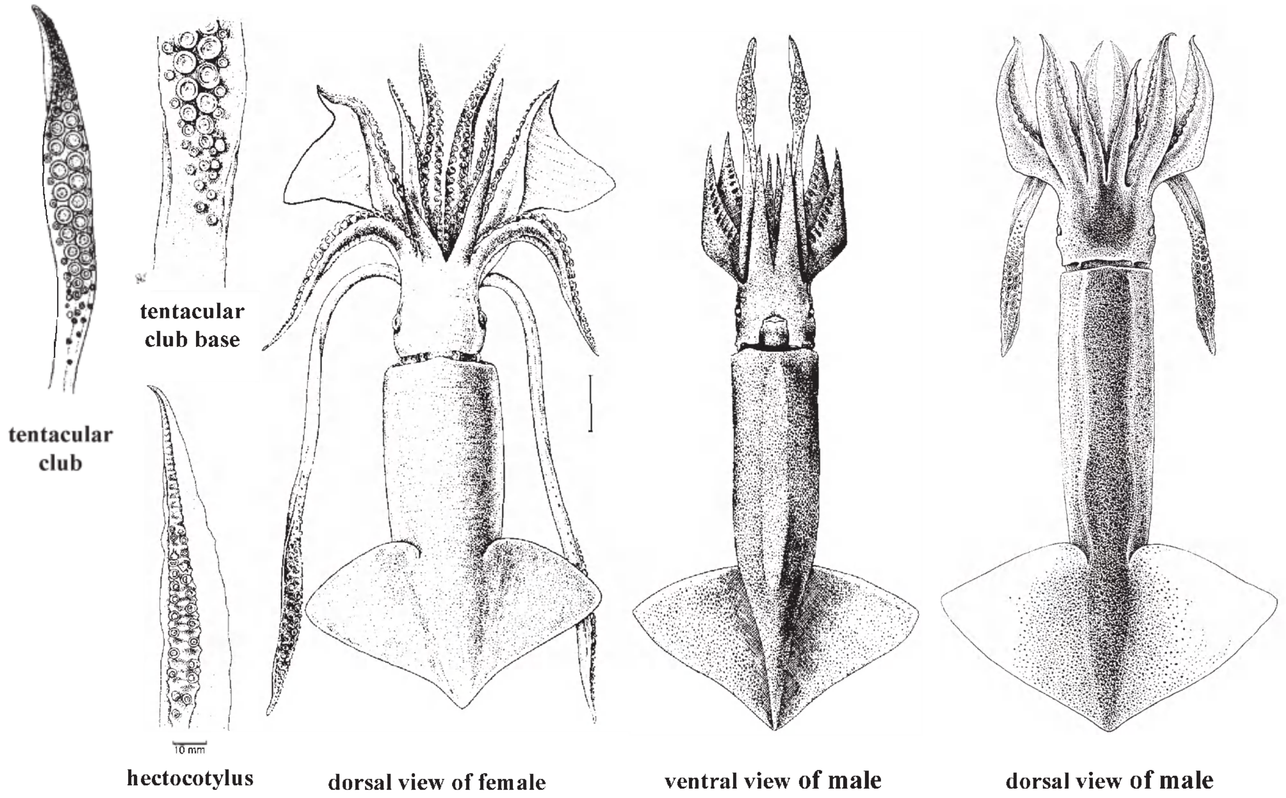
Ommastrephes bartramii (Lesueur, 1821)

Fig. 290

Loligo bartramii Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2 (1): 86–101. [90, pl. 7]. [Type locality: Not designated].

Frequent Synonyms: *Loligo bartramii* Lesueur, 1821; *Stenoteuthis bartramii* (Lesueur, 1821); *Loligo vitreus* Rang, 1835 *in* Ferussac and d'Orbigny, 1834–1847; *Ommastrephes cylindraceus* d'Orbigny, 1835 *in* Ferrusac and d'Orbigny, 1834–1847; *Loligo pironneauii* Souleyet, 1852; *L. pironneauii* Souleyet, 1852; *Onychoteuthis brevimanus* Gould, 1852; *Loligo touchardii* Souleyat, 1852; *Ommatostrephes bartrami* Steenstrup, 1880; *Sthenoteuthis bartramii* Verrill, 1880; *Ommastrephes ensifer* Owen, 1881; *O. caroli* Furtado, 1887; *Sthenoteuthis bartramii caroli* Pfeffer, 1900; *Ommastrephes caroli stenodactyla* Rancurel, 1976b.

FAO Names: En – Neon flying squid; **Fr** – Encornet volant; **Sp** – Pota saltadora.



tentacular club

tentacular club base

hectocotylus

dorsal view of female

ventral view of male

dorsal view of male

Fig. 290 *Ommastrephes bartramii*

Diagnostic Features: The same as those given for the monotypic genus.

Size: In the North Atlantic Ocean and the Southern Hemisphere the maximum mantle length of females is 800 to 900 mm (body weight 20 to 25 kg) and of males it is 400 to 420 mm (body weight 2 to 2.2 kg), and in the North Pacific the maximum mantle length of females is 500 to 600 mm (body weight about 6 kg) and of males it is 400 to 450 mm (body weight 2 kg to about 2.9 kg).

Geographical Distribution: *Ommastrephes bartramii* is an extremely widely distributed ommastrephid species with an oceanic bi-subtropical (anti-tropical) worldwide distribution. It inhabits the great subtropical ocean gyres in subtropical and partly temperate oceanic waters, but it is excluded from the equatorial waters of all 3 oceans (Fig. 291).

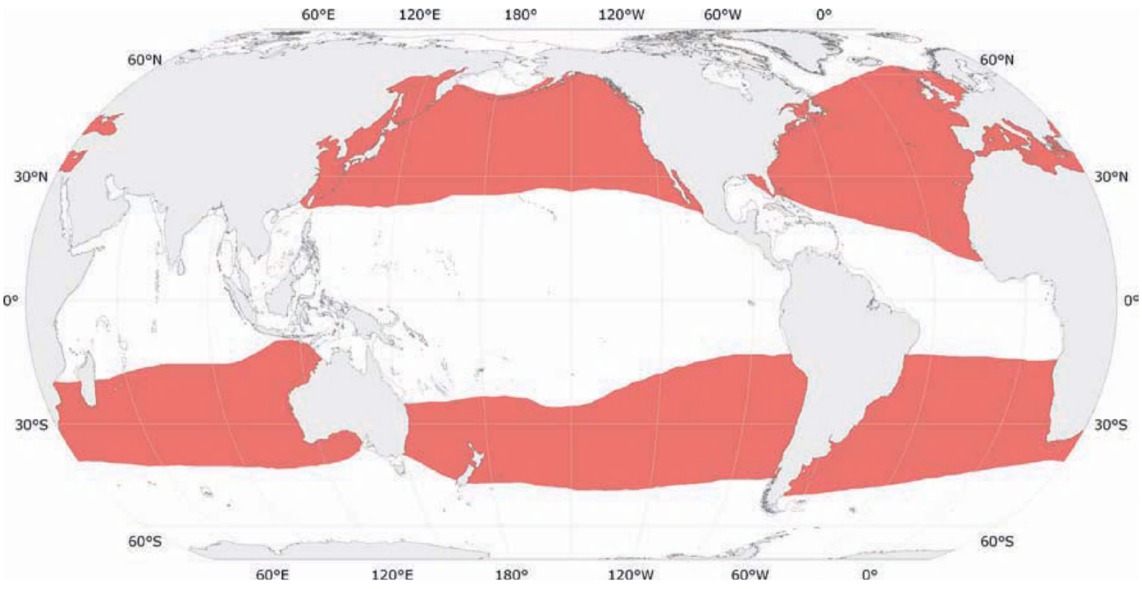


Fig. 291 *Ommastrephes bartramii*

🟥 Known distribution

Habitat and Biology: ***Ommastrephes bartramii*** principal (nuclear) part of distributional range is in subtropical water masses. In the temperate and partly tropical zones ***O. bartramii*** penetrates into warm and cold boundary currents, respectively. It occurs at sea surface temperatures from 10° to 25°C, generally over bottom depths greater than 200 m. Three major populations, or subspecies, not yet formerly described, inhabit 3 massive, but isolated, regions of the species range.

1) The North Atlantic subspecies is distributed in the Northern Hemisphere from the North Sea and the Shetland Islands (60°N) to the Grand Banks of Newfoundland (48°N), and southward from Mauritania (commonly to 18°N but sometimes to 9°N) to the southern part of the Sargasso Sea and south Florida (23°N to 25°N). Occasionally it penetrates into the most eastern part of the Gulf of Mexico.

2) The Southern Hemisphere conspecific group is distributed in a broad circumglobal band in subtropical waters of all 3 oceans. In the South Atlantic its range extends from 13°S to 46°S, rarely to 50°S in the western part, and from 14°S to 40°S in the eastern part. In the southern part of the Indian Ocean this subspecies is distributed between 20°S and 40°S to the Australian coast in the north and to the Great Australian Bight (135°E) in the south. Its range in the South Pacific extends from the Australian and Tasmanian coasts between 20°S and 46°S in the eastern part, between 25°S and 48°S in the central part, and between 12°S (commonly from 16°S to 18°S) and 46°S eastward to 78°W in the western part, where the natural boundary of its habitat probably is the core waters of the Peruvian Current.

3) The North Pacific subspecies of ***Ommastrephes bartramii*** is distributed in the same broad band that extends from east of the southern Kurile Islands (47°N) (in some years it penetrates further north to the Commander Islands (55°N)), and the western Aleutian Islands (53°N) to Taiwan Province of China and the Bonin Islands (23°N) in the western part, and from southern British Columbia (50°N) to the middle coast of Mexico (20°N) in the eastern part of the North Pacific Ocean. Occasionally it penetrates into the Sea of Japan. The North Pacific population is represented by 2 seasonal cohorts (autumn and winter-spring) and 4 stocks, each defined geographically and seasonally. Paralarvae from northern Hawaiian waters have been identified by diagnostic restriction profiles of 2 endonucleases.

This abundant oceanic/nektonic species inhabits open waters over depths greater than 200 to 400 m, and it is not associated in any way with the bottom, to the extent that it appears to actively avoid areas over seamounts. It inhabits the entire water column through epipelagic, mesopelagic and upper bathypelagic zones from 0 to 1 500 m and it has a true oceanic distribution and life style strategy, different from the "offshore" squids more associated with the continental shelf break with its upwellings, convergent flow patterns, frontal formations, etc. (e.g. ***Illex illecebrosus***, ***I. argentinus***, ***Todarodes pacificus***, ***Nototodarus*** spp.). For example, ***O. bartramii*** inhabits the unique frontal areas between the Southern Ocean and the areas to the north, where they effectively occupy the ecological niche normally associated with fishes in the epipelagic zone.

The planktonic paralarvae, post-paralarvae and juveniles up to 100 to 150 mm mantle length inhabit 0 to 100 m in surface waters during day and night. Squids of 60 to 150 mm mantle length may burst through the surface and glide through the air when they are threatened and pursued by predators. At night most juveniles of 60 to 150 mm mantle length descend from the surface layers to depths of about 40 to 100 m. Subadults and adult squids up to 600 to 650 mm mantle length undergo daily vertical migrations through a significant depth range. At night they concentrate for active feeding mostly in surface and subsurface layers between 0 and 100 m to 150 m (mainly 0 to 40 m or 30 to 70 m), but some portion of the population may remain in the deep layers of the daytime habitat. About an hour before the morning sunrise period they begin to migrate from surface waters to depths of 150 to 600 m in the higher latitudes of their geographical range and to depths from 400 to 1 500 m (mainly 600 to 800 m) in the lower latitudes; both populations remain at their depths during the daytime, principally in a state of low activity. Squids of 100 to 650 mm mantle length (modal size 150 to 350 mm) are fished in the surface layers during the night. Large females of more than 650 mm mantle length do not migrate to the surface at all, but permanently inhabit depths of 300 to 800 m throughout the 24-hour day.

The structure of ***O. bartramii*** populations (2 cohorts, 4 stocks) is complex in the most intensively studied part of the species' North Pacific range. The area for reproduction is located in the subtropical waters to the south of 35°N to 40°N, while active feeding and somatic growth occur in high latitude temperate areas occupied by migrating squid.

Spawning occurs almost year round in the **North Pacific**. **Two principal intraspecific groups**, cohorts, are distinguished by the time reproduction occurs: **1) a fall or autumn cohort** that spawns in autumn with the hatching period from September to February, and **2) and the winter-spring cohort** that spawns in winter with the hatching period principally from January to May and sometimes to August. Both groups have a 1-year life cycle. These 2 cohorts each are subdivided into 2 subgroups (stocks) by size composition, paralarval distribution and parasitic helminth infection rates (Fig. 292).

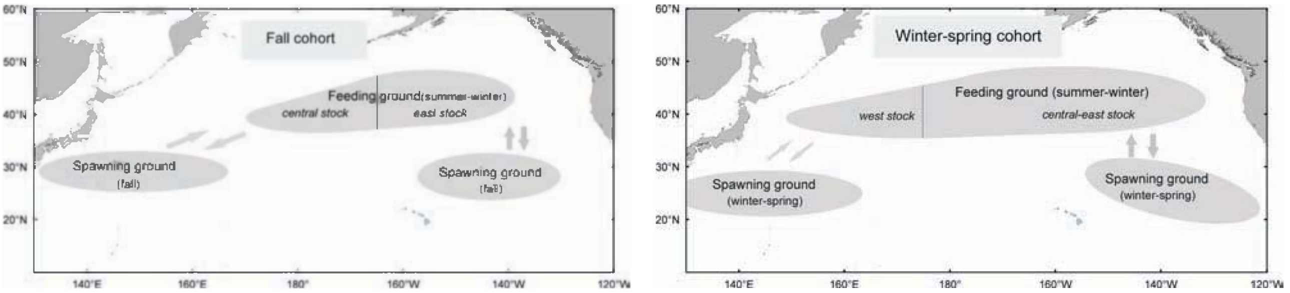


Fig. 292 Migration patterns of the autumn and winter–spring cohorts of red flying squid (*Ommastrephes bartramii*) in the North Pacific
(from Bower and Ichii, 2005)

The size of mature females of the autumn spawning group is greater than 460 mm mantle length, while the size at maturity of the winter-spring spawning group of mature females is smaller than 490 mm mantle length. The size of squid of the autumn group during the summer period is much larger than that of the winter–spring group (380 to 460 mm mantle length and 160 to 280 mm mantle length, respectively), and they also differ by maximum size (600 and 490 mm mantle length, respectively). Males are non-migratory; they remain in subtropical waters and do not migrate to the northern grounds. Migrating squid are capable of covering 5 to 10 km per day. It has been observed that the parasite load of ***O. bartramii*** is sufficiently different geographically as to differentiate between populations associated with eastern and western Pacific feeding grounds.

The North Atlantic reproductive/spawning area is located in the subtropical waters to the south of 45°N to 50°N. The more high-latitude temperate areas of these ranges are used by migrating squid, mainly females, as foraging zones in summer and early autumn. In the northeast Atlantic, after the summer feeding migration of large immature females into high latitudes, including the North Sea, some specimens (600 to 800 mm mantle length) remain in this feeding part of the range. Some of these non-migrating, large squid are stranded during strong winter storms onto the shores of the British Isles, Faeroe Islands, Denmark, Germany and Holland, and these “sea monsters” stirred the imagination of the coastal inhabitants in early times.

In the Southern Hemisphere the latitudinal, feeding and spawning structure of the population probably is similar to that in the Northern Hemisphere: the reproductive/spawning area is in subtropical waters (mainly between 20°S and 30°S to 35°S) and the foraging area occurs in temperate waters (35°S to 50°S) that are used in the southern summer period.

The North Atlantic and Southern Hemisphere males start to mature at 270 to 300 mm mantle length and all males larger than 320 mm mantle length are mature. Two groups are distinguished among females by their size at maturation: 1) females of the middle-sized group mature at 360 to 600 mm mantle length, and 2) females of the large-sized group mature at greater than 650 to 700 mm mantle length.

The life span of males and middle-sized females is 1 year; the life span of the large female group is not known.

Spawning in the North Atlantic and the Southern Hemisphere occurs throughout the year, with some seasonal activity from spring to the beginning of autumn in the corresponding hemisphere. Potential fecundity varies from 3 to 8 million oocytes in females of the middle-sized form and from 12 to 18 million in the large-sized group. Relative fecundity is 900 to 1 500 oocytes per gramme.

The size of ripe eggs is 0.9 to 1.2 mm. The maximum number of eggs in the oviducts of mature females varies between 0.5 and 2 million eggs, depending on the size of the mature females. ***Ommastrephes bartramii*** females are intermittent, multibatch spawners. After the first spawning, they continue to feed and grow in order to mature the next portions of oocytes for subsequent spawnings. Spermatophore morphometry, length and numbers are different in same-sized males from the North Atlantic and from those in the other parts of the species range. The length of spermatophores in the North Atlantic males varies between 32 and 53 mm (10.3 to 14.7% mantle length, and in other regions it is 22 to 41 mm (7.6 to 10.7% mantle length). The number of spermatophores in the Needham’s sac of mature males is 500 to 800 in North Atlantic males and 900 to 1 700 in males from the Southern Hemisphere and the North Pacific. Mass mating occurs in surface layers at night in the “head to head” position, and probably promiscuity occurs. Duration of copulation is 1 to 2 minutes. Spermatangia are attached to the buccal cone and membrane. Between 115 and 160 seminal receptacles occur on the buccal membrane.

As with its subfamilial relatives, ***O. bartramii*** is a high speed, manoeuvrable and powerful squid that reacts very quickly to any change in its surroundings. Juveniles up to 120 to 160 mm mantle length are able to “fly”: they burst from the surface and glide in the air some tens of metres when they are endangered by attacking predators. This species is a powerful, epipelagic, jet-propelled swimmer equipped with a strongly muscular mantle for maximum thrust and short, muscular, triangular fins for stabilization and manoeuvering. The measured horizontal sustained speed of adult squid (370 to 530 mm mantle length) in the sea varies between 6 and 17.6 km per hour, while the burst speed is greater. During evening and morning vertical migrations the swimming speed is less and varies on average from 3 to 5 km per hour. The species is an obligate shoaling squid throughout ontogenesis. Distinct shoals (schools) are comprised of uniform-sized squid. Shoal size varies from 2 to about 150 individuals, sometimes more. At the low-latitude periphery of the geographic range, this species may form joint schools with same-sized *Dosidicus gigas*, *Sthenoteuthis oulaniensis* and *S. pteropus*.

Ommastrephes bartramii is an active predator throughout all ontogenetic stages; this requires periodic changes in prey selection. Paralarvae feed on micro- and mainly mesozooplankton (copepods, juveniles of euphausiids and amphipods). Post-paralarvae and juveniles of 10 to 120 mm mantle length feed on meso- and macroplanktonic invertebrates, mainly euphausiids, amphipods, chaetognaths, heteropods, thecosome pteropods and the larvae and small juveniles of fishes and squids. Squid of 120 to 180 mm mantle length sharply increase their predation on planktivorous teleosts (mainly myctophids and sauries) and small squids. Feeding of subadult and adult squid of 500 to 600 mm mantle length takes place during night time in surface layers from 0 to 70 m, and feeding activity is significantly reduced during daytime at the greater depths of the mesopelagic zone. The broad spectrum of prey for this adult size group of squid is relatively similar in the different parts of the vast geographical range of the species. These squid feed principally on myctophids (*Electrona*, *Myctophum*, *Hygophum*, *Diaphus*, *Symbolophorus*, *Lasmpanyctus*, *Protomyctophum*, *Ceratoscopelus*, etc.), sternoptychids (*Maurolicus*, *Argyropelecus*), sauries (*Gololabis saira*, *Scomberesox saurus*), and to a lesser degree on juveniles of predatory fishes (chauliodontids, paralepidids, gempylids, etc), flying fishes, squids (mainly ***Onychoteuthis borealijaponica*** and spp., ***Berryteuthis anonychus***, ***Gonatus berryi*** and spp., ***Abraliopsis*** spp., histioteuthids, enoploteuthids, conspecific juveniles) and on pelagic shrimps, amphipods and euphausiids. Large females larger than 650 to 700 mm mantle length feed at mesopelagic depths on middle-sized, mesopelagic non-migratory predatory fishes, (e.g. myctophids: *Bathylagus ochotensis*, *Lampanyctus regalis*, *Protomyctophum thompsoni* and *Stenobrachius nannochir*), squids and to a lesser degree on large shrimps.

In geographical areas where the distribution of ***O. bartramii*** overlaps with other oceanic ommastrephid squid in the same ecosystem, a niche separation occurs; for example, when it overlaps with ***Todarodes pacificus***, it feeds principally on crustaceans, while ***T. pacificus*** preys on fishes.

The main predators of ***O. bartarmii*** also change during ontogenesis. Paralarvae and post-paralarvae are eaten by small squids, as well as plankton-eating and small carnivorous teleosts, including juveniles and subadults of tunas. Juveniles (3 to 14 mm mantle length) are the prey for large squids (mainly conspecific adults), cod (*Gadus morhua*), lancet fishes (*Alepisaurus ferox*), and tunas (*Thunnus alalunga, T. obesus, T. albacares, T. thynnus*, etc). The Pacific pomfret (*Brama japonica*) is an important predator of ***O. bartramii*** juveniles in the central part of North Pacific. In addition, they are eaten by sea birds: black-browed albatross (*Diomedea melanophris*), shy albatross (*Diomedea cauta*), cape gannet (*Morus capensis*) near South Africa, red-footed boobies (*Sula sula)* near the Hawaiian Islands, Parkinson's petrel (*Procellaria parkinsoni*), Herald petrel (*Pterodroma heraldica*), Kermadec petrel (*Pterodroma neglecta*), Murphy's petrel (*Pterodroma ultima*) in the South Pacific near the Pitcairn Islands, and seabirds breeding in the Hawaiian Islands. The major predators of subadult and adult ***O. bartramii*** are swordfish (*Xiphias gladius*), blue marlin (*Makaira mazara*), some active species of sharks (*Prionace glauca, Sphyrna zygaena, S. lewini, Carcharhinus longimanus*, etc.) and sperm whales (*Physeter macrocephalus*). ***Ommastrephes bartramii*** is a dominant squid species in the diets of yellowfin tuna (*Thunnus albacares*) and especially of swordfish (*Xiphias gladius*) off eastern Australia. Swordfish and sperm whales are common important predators on adult mature squid in all parts of the species range, mainly on females of 300 to 600 mm mantle length and possibly to the maximum size. Other representatives of marine mammals also are known as significant predators: northern fur seal (*Callorhinus ursinus*), cape fur seal (*Arctocephalus pusillus*), sub-Antarctic fur seal (*Arctocephalus tropicalis*), northern elephant seal (*Mirounga angustirostris*), short-beaked common dolphin (*Delphius delphis*), Cuvier's beaked whale (*Ziphius cavirostris*), killer whale (*Orcinus orca)*, false killer whale (*Pseudorca crassidens*), short-finned pilot whale (*Kurioshio Current*) and Baird's beaked whale (*Berardius bairdii*). Remains of subadult ***O. bartramii*** of 360 mm mantle length were found in stomach contents of giant squid, *Architeuthis*, in southern African waters.

An helminth fauna parasitic on ***O. bartramii*** of 14 species of larval trematodes, cestodes, nematodes and acanthocephalans has been described. Two species of nematodes affect commercial utilization and value. Larvae of *Anisakis* sp. are mortally dangerous to humans; however, they are localized in the ovaries and encysted in coelomic membranes, neither of which is used for human food, so the danger largely is eliminated. Thousands of larvae of *Porrocaecum* sp. may be encysted on the internal mantle wall, and they may reduce the quality of the marketable product with high levels of infestation.

Interest to Fisheries: In spite of its worldwide distribution, ***Ommastrephes bartramii*** is fished commercially only in the North Pacific Ocean where its populational structure and abundance seem to be maximized for exploitation. Fisheries have not developed in other parts of its distributional range, although several studies suggest that a fishery might be sustainable in the Atlantic. Experimental fisheries were carried out in the Tasman Sea and the slope waters off the coast of Uruguay without successful commercial results. However, continued demand for squid products, steady to elevated price structures, and increased knowledge about the biology and populational structure of the species may lead to geographically expanded fishery exploitation.

The total, instantaneous biomass of ***O. bartramii*** is about 10 to 13.5 million tonnes, including 8 to 10 million tonnes outside the national Exclusive Economic Zones (EEZs). The total tonnage is distributed in the different parts of the species geographic range as follows: North Pacific – 3 to 3.5 million tonnes, South Pacific – 2 to 2.5 million tonnes, North Atlantic – 2 to 2.5 million tonnes, South Atlantic – 2 to 3.5 million tonnes, Indian Ocean – 1 to 1.5 million tonnes.

The fishery in the North Pacific is seasonal; it begins in June and lasts through December. In recent years the fishery has continued through February off northeastern Honsu. The most productive period is July to August when about 50% of the total annual catch is harvested. The fishery is based on the location of squid feeding concentrations. The fishing grounds are situated in a wide belt between 30°N and 45°N from Japan to the American west coast, i.e. throughout the full extent of the feeding grounds. Regions of high biological productivity are conducive for concentrations of feeding ***O. bartramii*** and, consequently for fishing effort. Such areas where warm-core rings form and ***O. bartramii*** fisheries exist are in the Kurushio Current system off Japan and the East Australia Current off southeastern Australia. Sea surface temperatures for optimal catches range between 12^o and 22^{o}C depending on season (month) and locality on the broad fishing grounds.

Ommastrephes bartramii was first commercially fished in the North Pacific by Japanese jig vessels off the Pacific coast of Japan in 1974, and the fishery rapidly developed. The driftnet fishery was introduced for this species in September 1978 and due to overexploitation by both fisheries on the stock, serious competition developed between the driftnet and jig fisheries. To calm this conflict, the Japanese Government separated the fishing grounds for these fisheries in 1979: the jig fishery was limited to waters west of 170°E longitude and the driftnet fishery was restricted to the waters east of 170°E. longitude. Subsequently, South Korean driftnet vessels, Taiwan Province of China jig and driftnet vessels and Chinese jigging fle*et a*lso joined the fishery. Since 1993 the fishery has been limited to a jigging fishery only, due to the moratorium on the commercial use of large-scale driftnets introduced into practice by the 45th United Nations General Assembly in 1991.

Rough estimations by Japanese investigators suggest limits of 300 000 to 700 000 tonnes for the possible sustainable annual catch rate of ***O. bartramii***. However, a decreasing trend in the catches for the last years is shown by the FAO statistics (i.e. to about 18 500 tonnes in 2007).

The huge number of squid throughout the remaining part of species range is scattered over vast areas. However, potential fishery areas exist where squid concentrations are sufficiently high to warrant an experimental fishery to be carried out. These areas include: the southwestern Pacific Ocean near Australia and New Zealand and the southeastern part of the Indian Ocean near Australia; the slope and adjacent open waters around South Africa, far southeastern South Atlantic Ocean, the Brazil-Falkland Confluence area between 34°S and 44°S, as well as on the warm side of the Brazil Current between 32°S and 25°S in the southwestern Atlantic Ocean; the area between Cape Blanc (21°N near northwest Africa) and the Canary Islands; near the Azores Islands; around the North sub-Arctic Frontal Zone in the North Atlantic Ocean.

Local Names: ARGENTINA: Calamar rojo; AUSTRALIA: Red ocean squid; CANADA: Red flying squid, Neon flying squid; CHINA: rÓu-yú, bá-shì-rÓu-yú, qíang-rÓu-yú; FRANCE: Encornets rouges, Calmars rouges; GERMANY: Pfeilkalmar, Flugkalmar; ITALY: Totano nero; JAPAN: Aka-ika (Red squid), Murasaki-ika (Purple squid), Baka-ika (shortened form of Baka ni ookii ika (very large squid), Kuro-ika, Goudou-ika; KOREA: Bbal-gang-O-jing-eo; PORTUGAL: Pota de orelhas, Pota saltadora; ROUMANIA: Calmarul zburator; RUSSIA: Kal’mar bartrama, Neonovyj kal’mar, Letaujschij kal’mar; SPAIN: Pota saltadora; TAIWAN PROVINCE OF CHINA: Chì-yÓu; UK: Large squid; URUGUAY: Calamar rojo; USA: Neon flying squid, Red flying squid, Webbed flying squid.

Remarks: Three subspecies of ***Ommastrephes bartramii*** inhabit the North Atlantic, the North Pacific and the circumglobal Southern Hemisphere, but they have not yet been formerly described. These 3 geographically isolated populations are differentiated by spermatophore morphology, by their size structure (Zalygalin *et al.*, 1983; Nigmatullin *et al.*, 2003) and by substrate-inhibitory traits of optic ganglia cholinesterases (Shevtsova *et al.*, 1979). It is critically necessary that a special taxonomic revision of this species be undertaken in order for the 3 subspecies to be officially established and named, based on well-founded systematic analyses and descriptions. This is necessary not only for systematic and nomenclatural purposes, but it is important for biological and, especially, fishery-oriented management reasons.

Literature: Wormuth (1976), Roper *et al.* (1984), Dunning (1998a,b,f), Yatsu and Mori (2000), Bower and Ichii (2005), Brunetti *et al.* (2006), Wakabayashi *et al.* (2006).

Dosidicus Steenstrup, 1857

Dosidicus Steenstrup, 1857a, *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobenhavn*, 1856–1857: 120–121. [120].

Type Species: *Dosidicus gigas* (d’Orbigny, 1835).

Diagnostic Features: Funnel groove deeply excavated in **foveola**, rounded anteriorly, **with average of 7 longitudinal ridges and 4 or 5 side pockets**; carpal-locking apparatus present on tentacular club; medial suckers on manus with 4 large teeth, 1 in each quadrant; dactylus of tentacular club with suckers in 4 longitudinal rows; **small subcutaneous photophores on ventral surface of mantle, head and arms III and IV**, 2 intestinal photophores (in juveniles/subadults); photophore present on ventral surface of eyeballs (in juveniles/subadults); no large mantle photophores; **right or left arm IV hectocotylized, modified section smooth**; **tips of all arms in adults very attenuate, thin**, with numerous, minute, densely-packed suckers; longitudinal ridge of mantle component of locking cartilage with anterior bifurcation; cross-section A of gladius with 3 lateral lobes.

Remarks: Monotypic.

Dosidicus gigas (d'Orbigny 1835)

Fig. 293; Plate IX, 54

Ommastrephes gigas d'Orbigny 1835, in 1834–1847, *Voyage dans l'Amerique.Meridionale*, 5(3): 1–758 [50, pl 4]. [Type locality: 40°S to 60°S Valparaiso, eastern South Pacific Ocean].

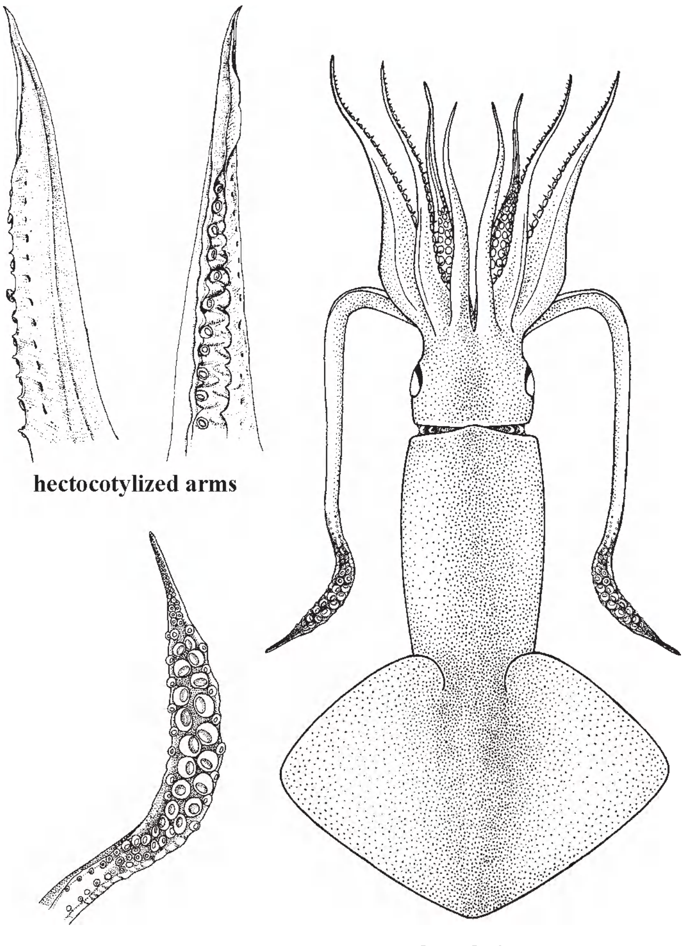
Frequent Synonymys: *Ommastrephes gigas* d'Orbigny 1835; *O. giganteus* d'Orbigny, 1839–1842, *in* Ferussac and d'Orbigny, 1834–1848; *O. giganteus*, Gray, 1849; *Dosidicus eschrichti* Steenstrup, 1857a; *D. steenstrupi* Pfeffer, 1884.

FAO Names: En – Jumbo flying squid; **Fr** – Encornet géant; **Sp** – Jibia gigante.

Diagnostic Features: The mantle is large, robust, thick-walled. The **fins are rhomboidal, very muscular**, broad, **width 56% of mantle length (49 to 65%), length 45% (41 to 49%) of mantle length, single fin angle 57° (50° to 65°)**. **The funnel groove is deeply excavated in the foveola, rounded anteriorly, with an average of 7 cutaneous longitudinal ridges and 4 or 5 lateral side pockets**. The dactylus of the tentacular club has suckers in 4 longitudinal rows. The carpal-locking apparatus has 1 to several knobs that alternate with smooth-suckered rings. The largest suckers on the manus of club have 1 enlarged central tooth distally and 3 smaller enlarged teeth in the other quadrants. Small subcutaneous photophores occur on the ventral surfaces of the mantle, head and arms III and IV; **2 small intestinal photophores** exist. These are **visible in juveniles and young individuals but are obscure in adults**. The longitudinal ridge of the mantle component of the locking cartilage has an anterior bifurcation. The distal tips of the arms, especially in adults, are drawn out into very long, attenuate tips **with 100 to 200 minute, closely packed suckers**; dorsal protective membrane on arms very weakly developed, but the trabeculae are well developed, muscular, exposed papillae; **either right or left arm IV is hectocotylized** (not both on the same specimen) **by absence of suckers and stalks at arm tip, and expanded and perforated protective membranes**. The anterior section of the gladius is tri-lobed or A-shaped in cross-section; the gladius lacks vanes, is very narrow, rod-like, then widens slightly posteriorly into a small terminal conus.

Size: Large-sized species: maximum total length approaches 2.5 m, with a maximum mantle length of 1.2 m (off Chile); maximum weight to 50 kg. Attains about 1 m mantle length in the northern population; common mantle length to about 500 to 800 mm; common weight to about 20 to 30 kg.

Geographical Distribution: ***Dosidicus gigas*** exhibits a broad and variable range in the eastern Pacific Ocean: from approximately 22ºN to 22ºS, limited approximately by the 20ºC isotherm. Unusual periodic extensions of range reach into the 50º North and South regions; records are confirmed from 59ºN in Alaska, and from 53ºS, approaching Tierra del Fuego. The longitudinal range westward into the open equatorial Pacific Ocean probably extends to 125ºW, but the full extent is not clearly known (fishing has been successful in waters 1 000 km off the Peruvian coast) (Fig. 294).


hectocotylized arms

tentacular club

dorsal view

Fig. 293 *Dosidicus gigas*

Fig. 294 *Dosidicus gigas*

🟥 Known distribution

Habitat and Biology: ***Dosidicus gigas*** is one of the largest and most abundant nektonic squids in the epipelagic zone of the world oceans; it is endemic to the eastern Pacific Ocean and its distribution seems to be limited by the isoline of phosphate of 0.8 mg. concentration and by the 20ºC surface isotherm. During the El Niño event of 1997–1998 that affected coastal oceanographic conditions as far north as northern California and Oregon, associated with the advection of anomalously warm water into inshore waters, ***D. gigas*** was reported in Oregon for the first time and was caught in large numbers. A similar, though much more wide-spread and invasive El Niño event in 2002–2006 carried ***D. gigas*** into Alaskan waters for the first reported time as far north as 59ºN. This species has undergone a sustained range extension into central and northern California waters. This invasion has impacted the ecosystem dynamics in Monterey Bay where it has established permanent residence since 2002 in coincidence with climate-linked oceanographic conditions and a consequent reduction in competing top-level predators. The abundance of Pacific hake (*Merluccious productus*), a principal prey of the Humboldt squid and the most important commercial groundfish species, has declined markedly in coincidence of the establishment of ***D. gigas*** in the region.

The jumbo flying squid is known to descend to depths in excess of 1 000 m. An ultrasonic telemetry system was employed to track vertical and horizontal movements of 3 ***D. gigas*** off the Costa Rica Dome and in Peruvian waters. Squid were tagged and released after sunset and tracked for 8 to 14 hours. Swimming activity generally was above 200 m at night; then the squids dived to bathypelagic depths (greater than 1 000 m) during the day. Most daytime hours were spent deeper than 250 m in the oxygen minimum layer (OML) or hypoxic zone; then the squid migrated to near-surface waters at night. Feeding occurs both at night and during the day in the OML below 300 m.

During El Niño years ***D. gigas*** exhibits a high abundance in association with the well-developed countercurrent “ridge”, or upwelling, off the Costa Rica Dome, but during La Niña years when the upwelling is less developed, abundance is low. Two factors associated with the well-developed upwelling probably account for the higher abundance of ***D. gigas***: 1) subsurface phytoplankton, *Chlorophylla maxima*, form there to provide high productivity, many species of which become prey for jumbo flying squid; 2) a strong salinity front forms along the North Equatorial Countercurrent to serve as a barrier to entrain the squid. The abundance of ***D. gigas*** in the eastern central Pacific during October to December is higher in areas of upwelling. Squids migrate periodically northwest to southeast and back, in association with the changing divergence zones. Off Peru where a significant fishery occurs, adult squid abundance is positively associated with sea surface temperatures (SST) of 17º to 22ºC in July, the peak of the fishery season. In the presumptive hatching area off the Costa Rica Dome high abundance is associated with SST of 24º to 28ºC. These patterns are associated with the mesoscale variability of the El Niño Southern Oscillation (ENSO).

The size at first maturity for females in Peruvian waters is 240 to 320 mm mantle length; mature adults occur throughout the year but the principal spawning period is spring/summer (October to January), with a secondary peak in July/August. Spawning occurs along the entire coast of Peru with greatest concentrations in the north between 03°S to 08ºS and in the central zone between 12°S and 17°S.

A large-scale artisanal fishery for ***D. gigas*** occurs in the central Gulf of California in 2 areas of alternate seasonal upwelling. Two distinct cohorts of ***D. gigas*** occur in that area: a large, late-maturing cohort and a medium-sized early-maturing cohort. Large females mature late at age 1 year and 730 mm mantle length, large males mature at 10 months and 600 mm mantle length. Females of the medium-sized cohort mature at 7 months, 370mm mantle length and males at 7 months and 340 mm. Predominant catches consist of large mature females, 750 mm mantle length and males, between 530 and 670 mm mantle length. The intra-annual cohorts of ***D. gigas*** forage in alternate upwelling seasonal areas during their respective life histories.

Growth of ***D. gigas*** in equatorial waters is rapid and the life span of most is about 1 year; however the largest specimens of the large cohort probably live to 2 years.

Reproduction takes place year-round. Spermatophore total and component lengths, and sperm volume increase remarkably with growth of the male. Female ***D. gigas*** have the highest potential fecundity known among cephalopods, up to 32 million oocytes.

Mature eggs from oviducts of females are transparent, amber-yellow, slightly ovoid, 0.9 mm to 1.1 mm long. The hatchlings are about 1 mm mantle length The paralarva is a typical rhynchoteuthion type with a well-developed tentacular proboscis that is quite thick and much longer than the arms in the early stages; eventually it can be up to 80% of mantle length. The process of separation of the proboscis begins at 5 to 6 mm mantle length and is complete by about 10 mm mantle length.

Paralarvae are planktonic and the smallest ones (1.2 to 1.6 mm mantle length) normally are found over the continental slope and up to about 300 nautical miles offshore in the epipelagic waters, mostly from the surface to 100 m. However, extraordinarily high abundance of ***D. gigas*** rhynchoteuthion paralarvae have been caught in a band parallel to the coast, 740 to 900 km offshore from Central America. Captures were coincident with the 29°C surface isotherm and maximum abundance (>12 000 rhynchoteuthions per 15-minute tow) was 4 orders of magnitude greater than any other report of paralarval cephalopod abundance. This extraordinary abundance may have been created by the interactions of warm El Niño waters and the aggregation by convergence of surface currents. Paralarval and juvenile ***D. gigas*** (1 to 10 mm mantle length) have been positively identified, using mitochondrial gene sequencing, in the central Gulf of California, Mexico. Since the smallest paralarvae of 1 mm mantle length are the size expected for ***D. gigas*** hatchlings, spawning must take place in the area of San Pedro Martin Basin.

Artificial fertilization of ***D. gigas*** eggs from Peruvian waters produced 167 hatchlings that were maintained at 18°C. Hatching occurred 6 to 9 days after fertilization and the rhynchoteuthion paralarvae survived for up to 10 days following hatching. Size at hatching was 0.9 to 1.3 mm mantle length (mean 1.1 mm) and mantle length increased to 1.1 to 1.5 mm (mean 1.4 mm) 7 days post-hatching.

Dosidicus gigas progresses through a spectrum of prey organisms during ontogenesis. Ontogenetic stages alternate with critical transitional periods during which squids change their mode of life and progress to the next higher trophic level. A principal prey of adults is the California sardine (*Sardinops sagex caerulea*) and in years of high population density the squid consume up to 60 000 tonnes of sardines during their 9-month residence in the Gulf. Such an intense predation, when 80% of the squid diet is sardines, negatively impacts the landings in the sardine fishery. Also in the Gulf of California, as well as in the open ocean, large and medium-sized ***D. gigas*** prey significantly on epipelagic/mesopelagic fishes, principally myctophids, e.g. *Hygophum atratum*, *Myctophum aurolaternatum*, *Lampanyctus parvicauda*, *Diogenichthys laternatum*, *Benthosema panamense*, *Triphoturus mexicanus*; also *Vinciguerria lucetia*, *Symbolophorus* spp. and other small pelagic fishes (e.g. northern anchovy and Pacific sardine species, saury-pike (*Scomberesox saurus*), flying fishes (Exocoetidae). Secondary, though significant, prey consists of micronektonic squids (principally ommastrephids, including cannibalism on smaller conspecific specimens), pelagic red crab (*Pleuroncodes planipes*), pteropods, megalopae and euphausids. In its expanded range in the California Current off Monterey, California, ***D. gigas*** feeds on Pacific hake (*Merluccius productus*), shortbelly rockfish (*Sebastes jordani*) and other species with semi-pelagic life histories. Large migratory squids off the coast of Chile consume congrijo (*Genypterus*), hake (*Merluccius gayi*), sardines, squids, decapod and stomatopod crustaceans. A dramatic decrease in catch of hake, the main demersal fishery resource in central Chilean waters, resulted in a total allowable catch in 2005 of 70 000 tonnes, about one-half that of 2004. Since ***D. gigas*** is a known major predator on hake, a multispecies model was conducted which estimated that the Humboldt squid biomass of 300 000 tonnes removed a biomass of hake of 150 000 tonnes, slightly in excess of the total commercial hake landings in 2004. Coupled with estimates of overfishing, squid predation is the principal cause of the serious hake decline.

Adult ***D. gigas*** squid were observed to attack captive skipjack tuna (*Katsuwanus pelamus*) and yellowfin tuna (*Thunnus albacores*) when inside the purse seine, causing significant bite damage. This unnatural condition begs the question of which species is predator and which is prey. Normally, ***D. gigas*** hunts in near-surface waters with peak intensity at dawn and a secondary peak in the evening. While they probably prey on small tunas, it seems most likely that the netted tunas prey on the aggregated squid, and bite damage on the fish is the result of opportunism or defense by the squid. The adult ***D. gigas*** occasionally is captured in the purse-seine fishery for tunas in only about 2% of the sets. The interactions between tunas and ***D. gigas*** demonstrate considerable plasticity in the schooling behaviour of the squid. ***Dosidicus gigas*** is very aggressive and cannibalistic on smaller individuals and readily attacks conspecific individuals that have been captured on jigs. Occasionally the attack behaviour is so strong that many individuals will attack others that have attacked jigged specimens, so that a large “squid ball” is formed. Several reports exist of attacks on humans by large ***D. gigas***, including at least one death. Scuba divers working among large feeding ***D. gigas***, usually at night and separated from dive buddies, have been attacked by single or multiple individuals, that sometimes attempt to pull them into deeper water, or sometimes inflict deep lacerations through wet suits and dive skins.

A major prey of sperm whales stranded in Peru and Chile, ***Dosidicus gigas*** was the second most important species in terms of weight, 32% in one study. Abundance of sperm whales in Peruvian waters is positively associated with high CPUE in the ***D. gigas*** fishery. In the Humboldt Current sperm whales (*Physeter macrocephalus*) prey almost exclusively on ***D. gigas***, consuming what was estimated between 6.7 and 20.1 million tonnes per year, which represented 34 times the highest catch of squid reported in the Peruvian fishery. Sperm whales in the Gulf of California prey extensively on ***D. gigas*** every spring/summer season, regardless of the inter-annual variations in squid populations. Various species of beaked whales also prey on ***D. gigas***, as do the inshore and offshore forms of bottlenose dolphin in the Gulf of California, Mexico. ***Dosidicus gigas*** is among the 3 most-captured prey species that constitute 90% of the diet of blue marlin (*Makaira nigrecans*) caught off Cabo San Lucas, Gulf of California, Mexico; it is prey of the striped marlin (*Tetrapturus andax*) in southern Gulf of California, Mexico and it constitutes the principal prey of swordfish (*Xiphias gladius*) and sailfish (*Istiophorus platypterus*) al lover its distributional range. Other pelagic fish predators include the dolphinfish or mahi mahi (*Coryphaena hippuris*), the yellowfin tuna (*Thunnus albacares*), juvenile hammerhead shark (*Sphyrna lewini*) and silky sharks (*Cercharhinus falcifermis*).

The jumbo flying squid releases prodigious quantities of ink when threatened by potential predators. The ink contains free amino acids and ammonium which serve as a chemical defense by disrupting sensory detection and by phagomimicry.

The parasites of ***D. gigas*** include 9 to 12 species of nematodes, cestodes, trematodes and the ciliate, *Chromidina*. All parasites occur in their larval stages. Infection rates and species compositions are similar for males and females of similar mantle length, as well as geographically across the sampling range. Parasites are acquired progressively during ontogeny and the formation of the helminth fauna proceeds in definite ecological patterns typical for particular size-age groups of hosts.

Interest to Fisheries: The significant fishery for ***D. gigas*** is linked to the major coastal upwelling ecosystem associated with the low velocity eastern boundary current system, the Peru or Humboldt Current. Exploratory fishing for this species was initiated in the early 1970s in several Pacific areas off the western Americas. Most of the fishery was carried out by Japanese jigger boats under a joint venture scheme and by Mexican shrimp fishermen that switch to squid fishing during the closed season for shrimp fishing. The best catches are obtained during the summer months, but the season has been progressively expanded, so that fishing now occurs throughout the year. Reduced catches in some areas coincide with increased catches in other parts of the species range: so a decreased abundance in Peruvian waters coincided with increased catches principally in the Gulf of California, Mexico and off Central America, in the Costa Rica Dome region.

The fishery for ***D. gigas*** in the Gulf of California developed very rapidly during 1978–1980, attaining 22 400 tonnes; it collapsed entirely for several years after 1981, then it rebounded again in the 1990s.

In Chilean waters catches of ***D. gigas*** occur year-round, concentrated mainly off central Chile. Chinese jigging vessels in offshore waters of Chile recorded maximum catches concentrated around 28°30'S, 76°78'W; average CPUE was in excess of 10 tonnes/day, with sea surface temperatures mainly 17° to 19°C. The principal gear for the ***D. gigas*** fishery is the jigging machine.

Jigging is the main fishing activity in Peruan waters as well. The multinational jigging fleet active off Peru is so extensive and concentrated, that the light emission from the jigging vessels is detectable from space via satellite imagery. Fishing grounds are concentrated off the coast of Peru at 02ºS to 10ºS; jigging grounds on the high seas were located off Peru at 03ºS to 18ºS and off Central America at 05ºN to 10ºN. These localities were associated with areas of upwelling events in the eastern Pacific rather than with bathymetry or proximity to coastal regions, and they occurred over depths of 200 to 4 500 m between 30 and 400 nautical miles offshore.

With extensive knowledge of the El Niño/southern oscillation cycle and increasing knowledge of the life cycle of ***D. gigas***, recruitment can be predicted and appropriate management schemes can be applied.

The total instantaneous biomass of ***D. gigas*** is estimated to be 7 million to 10 million tonnes, of which 2 million to 4 million tonnes occur in the open ocean, beyond the EEZs (Exclusive Economic Zones). With catches values close to 700 000 tonnes in 2007, this species alone accounted for about 21% ot the total squid world catch in that year.

Dosidicus gigas tissues are rich in essential amino acids and the species is consumed fresh and frozen. Hydrolyzed protein of ***D. gigas*** is an excellent supplement to the feed of farmed shrimps. Squid meal made from different body parts were tested as food for cultured shrimp, with positive results.

Local Names: JAPAN: Amerika-ooakaika, Amerika-oosurume, Jumbo squid; MEXICO: Pota; USA: Humboldt squid.

Literature: Nesis (1983), Roper *et al.* (1984), Ehrhardt *et al.* (1986), Roper *et al.* (1995), Hernandez-Herrera *et al.* (1998), Wormuth (1998), Nigmatullin *et al.* (2001), Nigmatullin *et al.* (2002a), Markaida (2006a,b), Rodhouse *et al.* (2006), Waluda *et al.* (2006), Gilly *et al.* (2006a,b), Field *et al.* (2007b).

Eucleoteuthis Berry, 1916

Eucleoteuthis Berry, 1916, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68: 45–66. 4 plates. [60].

Type Species: *Eucleoteuthis luminosa* (Sasaki, 1915).

Diagnostic Features: The funnel groove has **foveola with 4 to 9 longitudinal folds and 1 to 3 side pockets**, often obscure. **External photophores include** small, scattered, subcutaneous photophores on mantle, head, arms and tentacles and **large cutaneous mantle photophores that consist of a pair of long yellowish strips** that extend **along the ventral surface of the mantle**, one on each side of the midline; each strip interrupted posteriorly by a gap at the level of maximum fin width; **2 oval bioluminescent patches near anterior margin of mantle** anterior to each strip; 2 patch-like photophores at base and in middle on ventral surface of each ventral arm. **A single, round photophore on ventral surface of each eye and 1 round photophore on intestine**. Dactylus of tentacular club with 4 series of small suckers; carpal-locking apparatus on tentacular stalk with 1 to 4 knobs and 1 to 3 smooth-ringed suckers. Two to 4 suckers with denticulate rings are located on carpus proximal to first knob. Largest medial suckers on manus of club with 1 large, pointed tooth at distal margin of ring. Tips of all arms not attenuate. Arms have 19 to 32 pairs of suckers. **Left ventral arm hectocotylized by smooth type (suckers absent)**. Fins heart-shaped with attenuate tail; fin length 41 to 50% and width 50 to 65% of mantle length; fin angle 35° to 50°. **Mantle-funnel locking cartilage fused after paralarval stage**. The cone flags of the gladius are short, rhomboidal, with distinct radial creases. The greatest width of the cone flags is about 56% of that of the rachis. Marginal rigid ribs of the rachis are simple; axial rigidity rib of the rachis is trapezoid-like in cross-section. Lateral plates of the gladius do not adhere to the dorsal surface of the rachis but form wide free folds over the rachis. The stem is short, reminiscent of a mammalian vertebra in cross-section. Width of the stem is approximately equal to its thickness. Cone is short, flattened laterally. Rostrum is drop-shaped, its apex is curved ventrally. Alveola is thin; its ventral and lateral walls are thin, smooth, while the dorsal wall is ribbed. Spermatozoa with 1 flagellum.

Geographical Distribution: High tropical and subtropical areas in the southern sectors of the Atlantic, Indian and Pacific oceans and northern sector of the Pacific Ocean.

Remarks: Monotypic genus that contains 1 oceanic species. Restriction profiles of 2 endonucleases, AluI and Tsp509I are diagnostic for species identification.

Eucleoteuthis luminosa (Sasaki, 1915)

Fig. 295

Symplectoteuthis luminosa Sasaki, 1915b, *Journal of College of Agriculture, Tohoku Imperial University, Sapporo*, 6(6): 131–150. [144, fig. 4, pl. 4, figs 7–13]. [Type locality: Sagami Bay, Japan, western Pacific Ocean].

Frequent Synonyms: *Symplectoteuthis luminosa* Sasaki, 1915b.

FAO Names: En – Luminous flying squid; **Fr** – Encornet lumineux; **Sp** – Pota luminosa.

Diagnostic Features: The same as those given for the genus.

Size: Maximum mantle length 227 mm and body weight about 235 g.

Geographical Distribution: True bi-peripheral oceanic species with ranges in the North Pacific Ocean and the Southern Hemisphere. Distributed in the North Pacific Ocean from the southern Kurile Islands and Japan (from 25°N to 45°N) to California and western Mexico (from 10°N to 40°N); in the southern South Pacific Ocean between 20°S and 35°S in the west and between 13°S and 43°S in the east; in the southern Indian Ocean between 15°S and 34°S and in the southern Atlantic Ocean between 10°S and 36°S. Absent in the North Atlantic Ocean (Fig. 296).

Habitat and Biology: *Eucleoteuthis luminosa* is the least studied species among ommastrephids. It is an epipelagic and upper mesopelagic species distributed from the surface to 400 m. It inhabits open waters mostly over great depths of more than 200 m, and it is neither associated with the bottom nor slope habitats. Subadult and adult squids can be observed at the surface at night, but only infrequently. During the day they inhabit the depths greater than 50 to 100 m. The abundance is low or moderate locally (especially in the South Pacific Ocean between 30°S and 40°S). The maximum mantle length in males is 207 mm and in females 227 mm. Males reach maturity at 95 to 185 mm mantle length (age 180 to 270 days), and females mature at 102 to 200 mm mantle length (age 220 to 240 days). Geographical variability of size at maturity and size morphology is pronounced. Maximum size and size at maturity increases from the low latitudes to the high latitudes. Life span is a maximum of 1 year. In the lower latitudes spawning occurs throughout most of the year, and in the higher latitudes spawning occurs in the spring and summer seasons. Spermatophore lengths are 11.2 to 15.8 mm, and their numbers in Needham's sac of mature males reach up to 150, mostly between 70 and 100. Egg size is 0.8 to 1.0 mm, and potential fecundity of mature females varies between 300 000 and 625 000 ova. The oviducts of mature females contain about 17 000 ripe eggs, probably more.

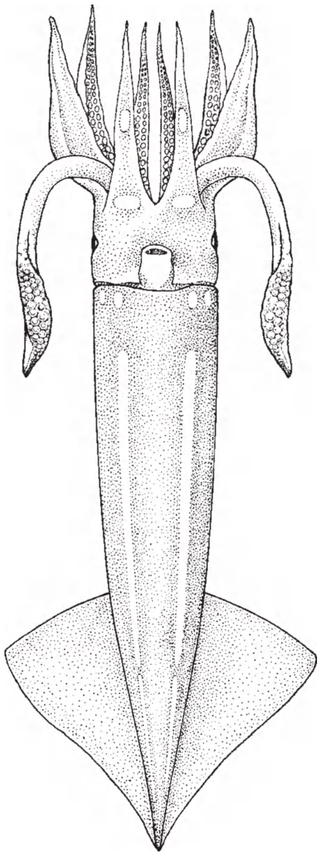


Fig. 295 ***Eucleoteuthis luminosa***

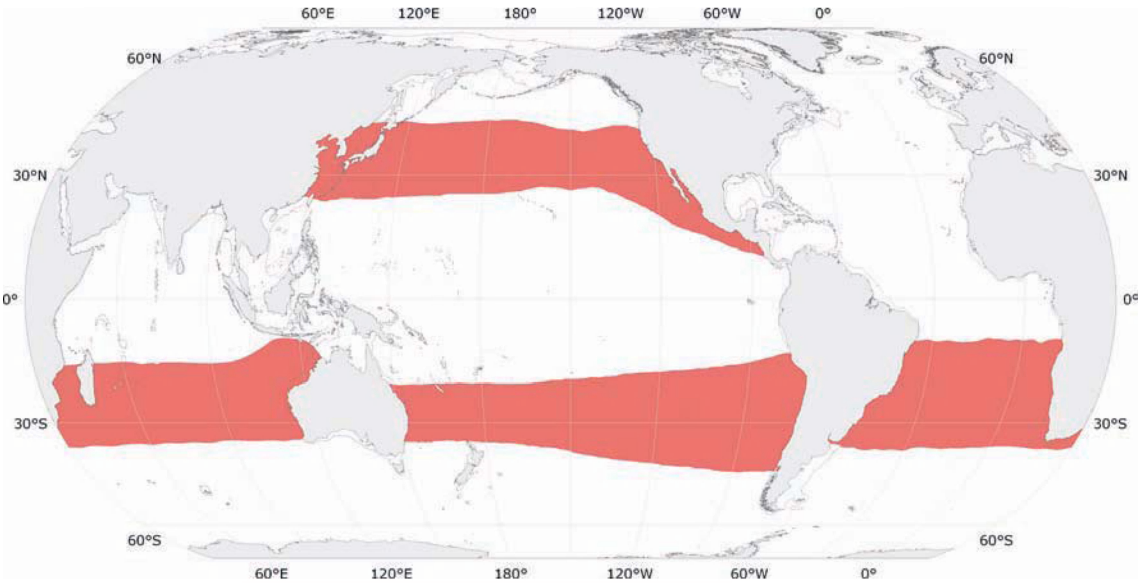


Fig. 296 ***Eucleoteuthis luminosa***

🟥 Known distribution

This species is an intermittent, multibatch spawner. Paralarvae can be distinguished from other confamilial paralarvae by their specific chromatophore pattern on the surface of the mantle and head.

Prey organisms for ***Eucleoteuthis luminosa*** include many species of pelagic crustaceans, heteropod molluscs and larvae and juveniles of teleost fishes and squids. The known predators include lancetfish (*Alepisarus ferox*), shark (*Sphyrna zygaena*), different species of tunas, the trichichthyid fish, orange roughy (*Haplostethus atlanticus*), sea birds and northern fur seal. Off eastern Australia ***E. luminosa*** is preyed upon by yellowfin tuna (*Thunnus albacares*) and swordfish (*Xiphias gladius*) in the warmer surface waters associated with the East Australia Current. Most subadult and adult squids are infested with helminth parasites: larvae of nematodes and cestodes and metacercariae of trematodes of the family Didymozoidae. All forms of parasites mainly are localized on the inner wall of the stomach.

Interest to Fisheries: The species is not fished commercially due to its low abundance and widespread population structure. However, in Japanese waters from time to time it may be captured as bycatch during the jigging fishery for ***Todarodes pacificus***.

Local Names: AUSTRALIA: Striped squid; JAPAN: Suji-ika; RUSSIA: Kal'mar-ljuminosa, Polosatyj kal'mar; TAIWAN PROVINCE OF CHINA: Guang-tiáo -yóu; USA: Luminous flying squid.

Literature: Young (1972a), Zuev *et al*. (1975), Alexeyev (1994a), Roper *et al.* (1995), Mori *et al.* (2002), Okutani (2005).

Hyaloteuthis Gray, 1849

Hyaloteuthis Gray, 1849: *Catalogue of the Molluska in the British Museum*. I. Cephalopoda Artepedia, pp. 164 London [63].

Type Species: *Hyaloteuthis pelagica* (Bosc, 1802).

Diagnostic Features: The funnel groove has a **foveola with 7 to 9 longitudinal folds and 0 to 3 side pockets**, often obscure. **Large cutaneous photophores present** on the ventral surface of the mantle and arms in the form of round, yellow, reflective patches: **3 situated along each ventral arm and 19 arranged in a fixed pattern on the ventral surface of the mantle**, where they form pairs, either closely set or well-separated. **A single, round photophore on ventral surface of each eye and 1 round photophore on the intestine**. Dactylus of tentacular club with 4 series of small suckers. Carpal-locking apparatus on tentacular stalk with 1 knob and 1 smooth-ringed sucker. Largest medial suckers on manus of club with 1 large, pointed tooth at distal margin. Protective membrane of tentacular club very poorly developed. Tips of all arms not attenuate. Arms have 15 to 22 pairs of suckers. **Right, or rarely left, ventral arm has a hectocotylus of the smooth type**, with the absence of suckers on the modified portion. Fins rhomboidal with straight or very slightly convex posterior edges. Fin length 35 to 40% and fin width 55 to 62% of mantle length; fin angle 45° to 55°. Mantle-funnel locking cartilage not fused. The cone flags of the gladius are short, rhomboidal, with minute radial creases. The greatest width of the cone flags comprises 57 to 87% of that of the rachis. Marginal rigid ribs of the rachis are simple, and the axial rigid rib of the rachis is low, rounded in cross-section. Lateral plates of the gladius adhere to the dorsal surface of the rachis. The stem is roughly triangular in cross-section; width of the stem is slightly greater than its thickness. The cone is short, rounded in cross-section. Rostrum is absent. Alveola is very thin and smooth. Spermatozoa with 1 flagellum.

Geographical Distribution: Tropical waters in the Atlantic and Pacific Oceans.

Remarks: ***Hyaloteuthis*** is monotypic, comprised of 1 oceanic species. The restriction profiles of 2 endonucleases, AluI and Tsp509I, are diagnostic for species identification.

Hyaloteuthis pelagica (Bosc, 1802)

Fig. 297

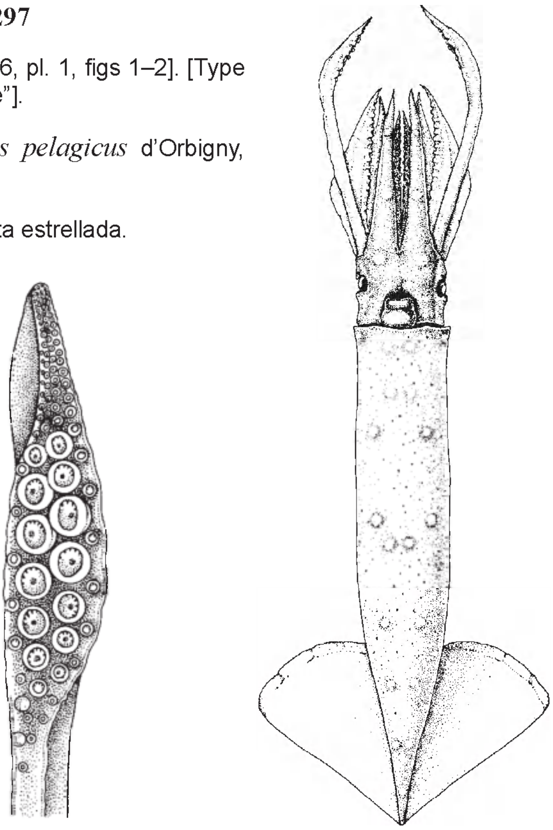


Fig. 297 ***Hyaloteuthis pelagica***

Sepia pelagica Bosc, 1802, *Histoire Naturelle Coquilles*, I: pp. 324. [46, pl. 1, figs 1–2]. [Type locality: “Trouvee en pleine mer, par Bosc dans l’estomac d’une dorade”].

Frequent Synonyms: *Sepia pelagica* Bosc, 1802; *Ommastrephes pelagicus* d’Orbigny, 1834–1848; *Ommatostrephes pelagicus* Steenstrup, 1880.

FAO Names: En – Glassy flying squid; **Fr** – Encornet vitreux; **Sp** – Pota estrellada.

Diagnostic Features: The same as those given for the genus.

Size: Maximum mantle length 105 mm and body weight 35 g.

Geographical Distribution: A truly bicentral oceanic species; in the north Atlantic Ocean from 10°N to 28° N in the eastern part and to 40°N in the western part; in the South Atlantic Ocean from 5°S to 15°S in the eastern part and to 23°S in the western sector; in the North Pacific Ocean from 10°N to 35°N off Japan and to 25°N off California; its range in the South Pacific Ocean includes oceanic waters from 0°S to 36°S off Australia and to 20°S off southern Chile; mostly absent from the equatorial zones of both oceans. It was not found to occur in the open waters of the Indian Ocean (Fig. 298).

Habitat and Biology: ***Hyaloteuthis pelagica*** is distributed mainly in zones of trade-wind currents and adjoining parts of the central waters of the cyclonic circulations; it is absent from zones of equatorial divergence. This epipelagic to mesopelagic and upper bathypelagic species inhabits open waters over great depths of more than 400 m, and it is not related in any biological or oceanographic way to bottom and slope waters. Paralarvae and juveniles inhabit the upper 50 m at night and from 100 to 200 m during the day. Subadult and adult squids inhabit subsurface layers from 15 or 20 m to 150 m at night. They also have been observed at night at the surface but only infrequently. During daytime they inhabit the depths from 200 to 800 m. The population numbers are low or moderate locally. The maximum male mantle length is 81 mm and the maximum female mantle length is 105 mm. Males reach maturity at 50 to 65 mm mantle length (age 80 to 100 days), and females mature at from 50 to 90 mm (age 80 to 135 days). No pronounced geographical variability exists for size at maturity or size morphology. The life span is half a year. Spawning occurs throughout the year with some seasonal variability in activity. Spermatophores attain lengths of 5 to 11.5 mm, and their numbers in Needham’s sac of mature males reach a maximum of 120, but normally they vary between 50 and 80 total. Egg size is 0.9 to 1.0 mm, and female potential fecundity varies between 30 000 and 100 000 ova. Oviducts of mature females contain a

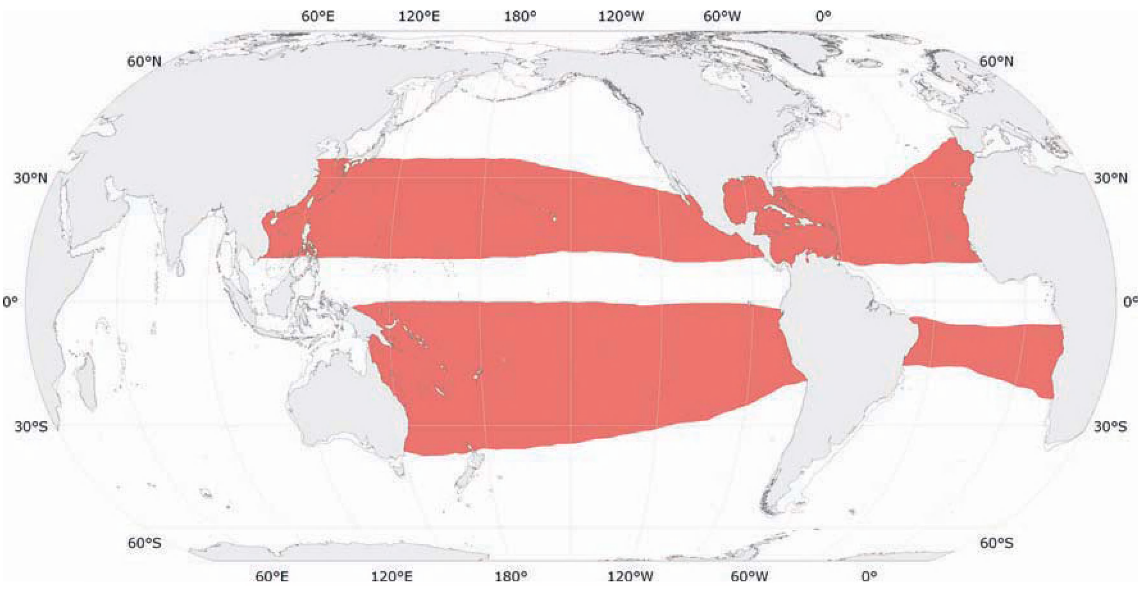


Fig. 298 ***Hyaloteuthis pelagica***

🟥 Known distribution

maximum of 500 ripe eggs. The species is an intermittent, multibatch spawner. It feeds mainly on juvenile teleosts and squid, hypereid amphipods, crab larvae, chaetognathes and to a lesser degree on copepods, shrimps, euphausiids and teleost larvae. Its predators include several oceanic species of ommastrephid squids, dolphinfish (*Coryphaena*), lancet fish (*Alepisarus*), bonito (*Sarda*), different species of tunas and sea birds. ***Hyaloteuthis pelagica*** is preyed upon by yellowfin tuna (*Thunnus albacares*) off eastern Australia and it is an important prey of several fishes in the tropical Atlantic Ocean, such as albacore (*Thunnus alalunga*), yellow fin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), sailfish (*Istiophorus albicans*), blue marlin (*Makira nigricans*), white marlin (*Tetrapturus albidus*) and longbill spearfish (*Tetrapturus pfluegeri*). Most subadult and adult squids are infested by helminth parasites, principally metacercariae of trematodes of the family Didymozoidae, that are localized in cysts on the inner wall of the stomach.

Interest to Fisheries: The species is not fished commercially due to its small size and low, local area abundance.

Local Names: JAPAN: Shirahoshi-ika; RUSSIA: Kal'mar-gialotevtis, Kal'mar-svetljach'ek.

Literature: Wormuth (1976), Nesis and Nigmatullin (1979), Young and Hirota (1990), Roper *et al.* (1995), Vecchione *et al.* (1998a), Okutani (2005).

Ornithoteuthis Okada, 1927

Ornithoteuthis Okada, 1927c, *Bulletin de l'Institut Oceanographique de Monaco,* 494: 13–16. [15].

Type Species: *Ornithoteus volatilis* (Sasaki, 1915b).

Frequent Synonyms: *Ommastrephes* Sasaki, 1915b.

Diagnostic Features: Mantle narrow, drawn out posteriorly into long, pointed tail; **fins long, narrow, strongly pointed posteriorly, their length 50 to 60% and width about 45 to 52% of mantle length**; **fin angle 20° to 35º; funnel groove smooth with foveola with 7 to 9 longitudinal folds and a few side pockets** (often obscure); small tetraserial suckers on dactylus of tentacular club; **tentacular club moderately expanded but without carpal-locking apparatus**; carpal sucker area reduced, tubercle-like knobs absent; largest medial suckers on manus with 15 to 25 equal-sized pointed teeth; no enlarged teeth; **no external photophores, nor subcutaneous photophores exist**; a single, round photophore evident on ventral surface of each eye and 2 round photophores on ventral surface of intestine in paralarvae and a narrow, pinkish photogenic strip, with 2 interruptions, extends along the ventral midline of viscera in adults; **right (or very rarely left) arm IV hectocotylized** in mature males with papillose type (distal modified section bears papillae formed from sucker stalks) and with a honey-comb sculptural formation along the midpart of ventral surface of arm. Protective membranes of arms and tentacles normally developed. Cone flags of the gladius very long (about 25% of the gladius length), without radial creases; greatest width of the cone flags about two-thirds that of the rachis. Marginal rigidity ribs of rachis simple; axial rigidity rib rounded-rectangular in cross-section. Lateral plates of gladius adhere to dorsal surface of rachis by their proximal parts. Distal parts of lateral plates free, form longitudinal fold over hanging rachis. Ventral stem very long, with high dorsal keel, anchor-like in cross-section; stem width less than its thickness. Cone very short, round in cross-section; rostrum absent. Alveola thin, film-like, smooth. Spermatozoa with 1 flagellum.

Size: Small- to medium-sized squid; maximum reported mantle length 310 mm.

Geographical Distribution: Indo-West Pacific and tropical-subtropical Atlantic Ocean.

Habitat and Biology: Epi-mesopelagic, lower sublittoral and bathyal squids. Adults occur in the lower epipelagic and mesopelagic zones and to the bottom in the bathyal realm. Paralarvae and juveniles occur in midwater and into the near-surface epipelagic waters.

Remarks: The 2 nerito-oceanic species in the genus are quite similar in appearance and habitat in their respective oceans, the Indo-West Pacific (***Ornithoteuthis volatilis***) and the tropical-subtropical Atlantic (***O. antillarum***). Historically the distributional ranges of these 2 now-distinct species probably were continuous, but biogeographic divergence resulted in the formation of the separate, closely-related species recognized currently. The 5 syntype specimens from Sagami Bay and off Atami are extant in the Museum of Tokyo University, Zoology Department.

Literature: Nesis (1979a,c), Nesis and Nigmatullin (1979), Hochberg (1983), Bizikov (1996), Dunning (1998b,c), Nesis (2003), Nigmatullin *et al.* (2003).

Key to the species of *Ornithoteuthis*

1a. Sessile arm sucker ring dentition without sexual dimorphism on arms II; hectocotylized right arm IV with honeycomb-like cutaneous sculpturing on the midventral surface comprised of 2 or 3 longitudinal rows of small depressions, with 10 to 15 depressions (pits or pores) in each row . . . . ***Ornithoteuthis volatilis***

1b. Sessile arm sucker ring dentition with sexual dimorphism on arms II; rings on dorsal row with 2 small plate-like lateral teeth and 1 distal, central, sharply pointed, enlarged tooth; rings on ventral row with 2 small, medial plate-like distal teeth and 2 small plate-like lateral teeth; hectocotylized right arm IV with honeycomb-like cutaneous sculpturing on the midventral surface comprised of 4 or 5 longitudinal rows of depressions, with 20 to 25 depressions (pits or pores) in each row . . . . ***Ornithoteuthis antillarum***

Ornithoteuthis volatilis (Sasaki, 1915)

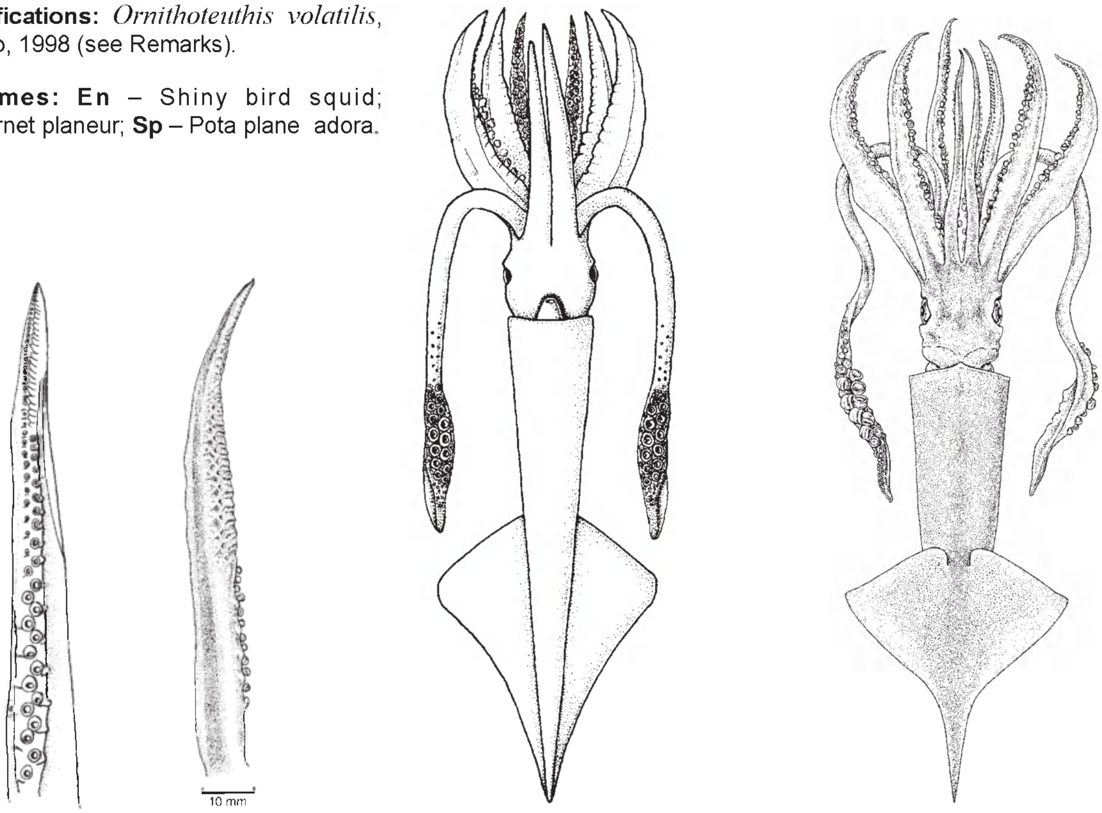
Fig. 299

Ommastrephes volatilis Sasaki, 1915b, *Journal of the College of Agriculture, Tohoku Imperial University, Sapporo*, 6(6): 131–150. [138, text fig. 3, pl. 4, figs 1–6]. [Type locality: off Atami, Sagami Province, Japan, western Pacific Ocean].

Frequent Synonyms: *Ommastrephes volatilis* Sasaki, 1915.

Misidentifications: *Ornithoteuthis volatilis*, Silva-Mello, 1998 (see Remarks).

FAO Names: En – Shiny bird squid; **Fr** – Encornet planeur; **Sp** – Pota plane adora.



hectocotylus arms **ventral view** **dorsal view**

Fig. 299 ***Ornithoteuthis volatilis***

Diagnostic Features: Mantle very narrow, muscular, drawn out posteriorly into a long pointed tail. Fins long, sagittate, sharply lanceolate posteriorly, posterior margins concave; fin length 55% (51 to 59%) of mantle length; fin width 47% (45 to 51%) of mantle length; single fin angle 27% (20 to 35%). **Head broad, considerably broader than mantle width. Tentacular club expanded with very large medial manal suckers**, their rings with 18 to 21 evenly-spaced, equal-sized (not enlarged), sharply-pointed teeth, occasionally interspersed with low, flat platelets. Arm sucker rings with 10 to 14 sharp teeth on distal margin and with smooth proximal rim; rings without sexual dimorphism. **Right arm IV hectocotylized with papillose type modification**; distal half with reduced-sized suckers, sucker stalks modified into papillae, particularly in dorsal row, and a honeycomb sculpturing with lateral pores along the midventral surface with 2 or 3 longitudinal columns of depressions and swollen ridges, and with 10 to 15 depressions (pits or pores) in each column. **A single, round photophore patch occurs on the ventral surface of each eye**; **on viscera one large, round photophore occurs near the anus and one small oval photophore occurs at the posterior end of the intestine**; a narrow strip of pinkish bioluminescent tissue extends from the small photophore to the posterior tip of the mantle cavity, interrupted by 2 gaps where arteries intervene. These round photophores persist from the paralarval stage to fully mature adults.

Paralarvae with 2 round, unequal-sized intestinal photophores that are evident at about 3.5 mm mantle length; the larger, anterior one ventral to the intestine near the anus; the smaller, posterior one ventral to the intestine just anterior to its descent from the ceacum; a single, ovoid photophore patch on the ventral surface of each eye at about 4.0 mm mantle length; a proboscis typical of the ommastrephid rhynchoteuthion-stage with a length of 50 to 75% of the mantle length at less than 4.0 mm mantle length; proboscis length approximately equal to longest arms; the 2 lateral distal suckers on tip of proboscis up to 150% larger than remaining 6 suckers; dorsal mantle chromatophore pattern of 5 oblong chromatophores in a +-shape and a single small chromatophore between the minute fins; ventral mantle chromatophore pattern form a side-to-side oblong of 6 rectangular chromatophores and 2 very small, roundish chromatophres at the posterior tip of the mantle.

Size: The maximum mantle length reported is 250 mm in females and 310 mm in males.

Geographical Distribution: Indo-West Pacific, tropical to subtropical oceans. In the western Pacific from 36°15'N to 40°S; off southwestern Japan, the Ogasawara Islands, off Sanriku and Joban districts, northeastern Japan, and in the South China Sea; New Caledonia; eastward to the Line Islands, to 140°W, where its latitudinal range is quite restricted, roughly 5°N to 15°S. In the Indian Ocean ***O. volatilis*** occurs from the Arabian Sea to south of Madagascar in the west to about 30°S, and eastward into the Timor Sea; Coral Sea. Off the eastern Australian coast its distribution extends to 40°S, off the northwestern Australian coast it occurs in continental slope waters between 13°50'S and 18°37'S. The species apparently does not occur in the central and eastern North Pacific and it is absent from Hawaiian waters. ***Ornithoteuthis volatilis*** has been reported in the far southeastern Atlantic off South Africa and Namibia, but whether a permanent, self-perpetuating population exists in the Benguela Current presently is not verified (Fig. 300).

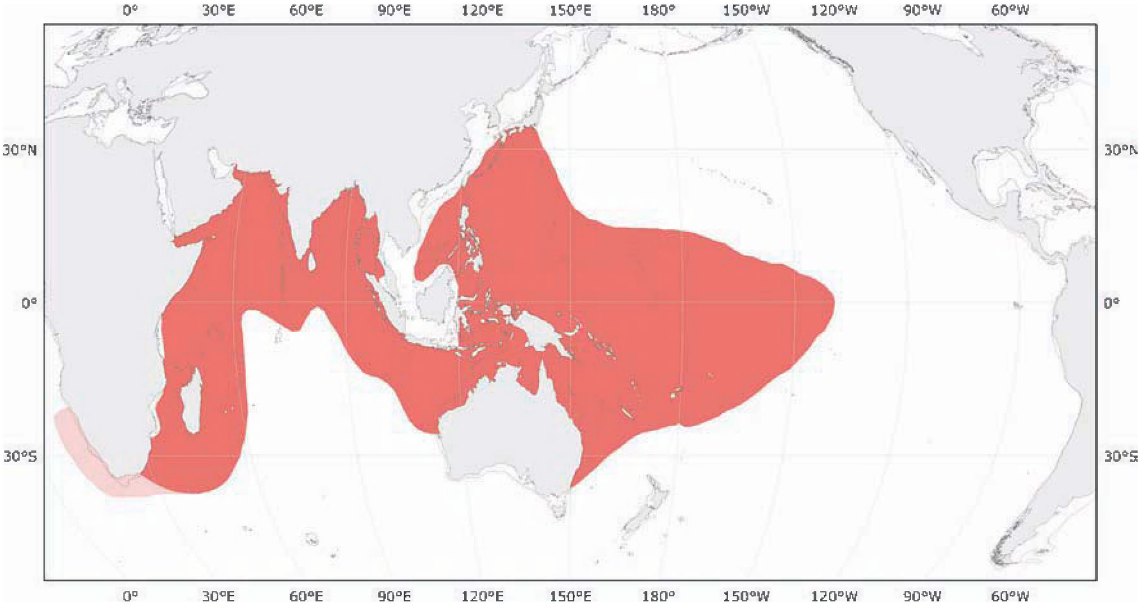


Fig. 300 ***Ornithoteuthis volatilis***

🟥 Known distribution ▨ Probable presence

Habitat and Biology: ***Ornithoteuthis volatilis*** is a tropical/subtropical species, widely distributed in the Indo-Pacific Ocean. It occupies tropical slope and oceanic waters from the surface (paralarvae; adults at night) to moderate depths, at the bottom in bathyal zone and in midwater above the slope (lower epipelagic, mesopelagic). Paralarvae and juveniles also occur in the equatorial zone in midwater above great oceanic depths. Specimens of 180 to 200 mm mantle length have been captured in trawls fished at 500 to 770 m in the South China Sea. The abundance (density index) on the continental slope of the South China Sea is highest at 400 to 600 m. In the western Indian Ocean the species is recorded off Kenya (1°S to 6°S, 46°E to 52°E) and around Saya-de-Malha Bank (8°30'S to 11°S, and 56°E to 60°E). ***Ornithoteuthis volatilis*** is commonly captured in trawl catches in Australian slope waters. While identification of adults is relatively easy because of the slender body and long, attenuate fins, traditionally the identification of ommastrephid paralarvae has been challenging in areas where multiple species co-occur. Recent studies, however, have demonstrated positive identification techniques using chromatophore patterns. The colour of the mantle of live adults is dark reddish brown, with a bright strip along the ventral midline produced from the intestinal photophores. Adults are captured principally in midwater and demersal trawls in continental slope waters and near seamounts but rarely are caught at the surface. On the other hand, several specimens have been inadvertently captured when they broke the sea surface and “flew” aboard vessels. It has been suggested that ***O. volatilis*** undergoes diel vertical migrations, just as its congener, ***O. antillarum***, does in the North Atlantic.

In the South China Sea ***O. volatilis*** is most abundant in May and June and during the day than at night. Size at maturity varies significantly in both sexes, depending on season and locality. For example, mature females have been observed at 150 mm mantle length, while other females up to 270 mm mantle length were still maturing in winter. Also, mature males were caught in southeastern Australia in summer, at 160 to 240 mm mantle length, while other males were still immature at 180 to 200 mm mantle length.

The reproductive strategy of ***O. volatilis*** adheres to the "***Sthenoteuthis***-type" for r-strategists. They have very small eggs (0.7 to 1.0 mm, mostly 0.75 to 0.85 mm), and the total of vitelline oocytes in the ovary plus ripe eggs in the oviducts usually represents 10 to 15% of the potential fecundity. Females have an asynchronous type of oocyte stock (fecundity) formation by which oogenesis occurs by continuous asynchrony. Spawning is intermittent (batch, pulse) with several egg masses produced over a more or less extended period of time. The intensity of spawning and average egg numbers in these sequential egg masses is approximately constant during the spawning period. Spermatophores from a mature male of 93 mm mantle length from the western Indian Ocean averaged 9.6 mm long, about 10.3% of mantle length; the number of spermatophores (fecundity) was about 100 with a total sperm reservoir volume of 0.1 cm^3. The reproductive strategy of males belongs to the "intermediate type" for effective sperm production in which there is an ontogenetic increase in the volumes of both the Needham's Sac and the seminal reservoirs of the spermatophores.

As a nerito-oceanic species, ***O. volatilis*** lives near or over slopes; paralarvae, juveniles and subadults live in midwater in the epi- and mesopelagic zones over the slopes and oceanic depths, as well as above the tops and slopes of seamounts and midocean ridges; they spawn near the bottom around seamounts and ridges, some after long migrations to these localities. Spawning of ***O. volatilis*** off southeastern Australia occurs in the deeper shelf and upper continental slope waters that comprise the warm East Australian Current of tropical origin. Size distribution analysis of paralarvae and adults suggests that spawning in this region occurs year-round. In the northern South China Sea the spawning season is from June to October. In the western North Pacific Ocean ***O. volatilis*** spawns in the summer and its paralarvae are distributed in the Kuroshio Current off Japan. Division of proboscis begins at about 4.0 to 5.0 mm mantle length and separation of tentacles is complete by about 6.5 to 7.0 mm mantle length. The hunting strategy of ***O. volatilis*** is the actively browsing predator type in which prey consists of many different food component species, each of relatively small individual size and weight. Predators of ***O. volatilis*** include yellowfin tunas (*Thunnus albacares*), longnose lancetfishes (*Alepisaurus ferox*), dolphinfishes (*Coryphaena hyppurus*), swordfish (*Xiphias gladius*) and numerous other species of pelagic fishes throughout the tropical Indo-Pacific and eastern Pacific Oceans; also, sperm whales prey extensively on this species, as do the South African fur seals (*Arctocephalus pusillus pusillus*) and several shark species, such as the tiger shark (*Galeocerdo cuvier*), the scalloped hammerhead shark (*Syphrna lewini*) and the smooth hammerhead shark (*Syphrna zygaena*). ***Ornithoteuthis*** species are host to the diagenetic trematode parasites.

Interest to Fisheries: While ***O. volatilis*** is a widely distributed species in tropical/ subtropical Indo-West Pacific waters, to date adults have not been captured in large numbers. The mean instantaneous biomass for harvest-sized ***O. volatilis*** is estimated to be 1 million tonnes. However, if concentrations of this species can be found, they will provide a potentially desirable product because both the size and texture of the flesh are suitable. In the northern South China Sea, a study indicated that the stock was over 550 tonnes in the survey area. The same study also determined that the nutrient composition of the flesh will make a fishery worth developing.

Local Names: AUSTRALIA: Long-tailed flying squid; JAPAN: Tobi-ika, yase-tobi-ika; RUSSIA: Letajuschij kal'marptica.

Remarks: The reference to ***O. volatilis*** by Silva-Mello (1998) from pelagic fish stomach contents is considered a misidentification. ***Ornithoteuthis volatilis*** never has been reported in the western Atlantic Ocean, and the very few records in the far southeastern Atlantic Ocean are considered incidental occurrences, not established populations. ***Ornithoteuthis antillarum*** is the only Atlantic species in the genus and it is common in the tropical/subtropical western Atlantic, as identified in Silva-Mello's report. Consequently, Silva-Mello's reference to ***O. volatilis*** is a misidentification.

Literature: Nesis (1993a), Dunning (1998b,c), Nesis (2002), Okutani (2005).

Ornithoteuthis antillarum Adam, 1957

Fig. 301; Plate IX, 55–57

Ornithoteuthis antillarum Adam, 1957, *Bulletin de Institut Royal Science Naturelle Belgique*, 33(7): 1–10. [3, pl. 1 figs 1–4]. [Type locality: Basse Terre (Guadeloupe), Antilles, West Indies, western central Atlantic Ocean].

Frequent Synonyms: None.

Misidentifications: *Ornithoteuthis volatilis*, Silva-Mello, 1998.

FAO Names: En – Atlantic bird squid; **Fr** – Encornet oiseau; **Sp** – Pota pajaro.

Diagnostic Features: Mantle muscular, very narrow, drawn out posteriorly into a long, thinly-pointed tail. Fins elongate, sagittate to lanceolate, very sharply pointed posteriorly; **posterior margins concave; anterior margins convex**; **fin length greater than 50% of mantle length**. Head broad, equal to or greater than maximum mantle width. Funnel groove with **foveola with 7 to 12 indistinct folds, side pockets frequently obscure or absent**. Tentacular club moderately expanded with **12 to 14 enlarged medial club suckers**; sucker rings with about 20 nearly equal-sized, sharp teeth, occasionally interposed with low, flat platelets; no enlarged teeth. Carpal-locking apparatus weakly developed with few suckers and without knobs. Arm sucker rings with 15 sharply-pointed teeth; sexual dimorphism on rings of arms II: rings on dorsal row have 2 small plate-like lateral teeth and 1 distal, central, sharply-pointed enlarged tooth; rings on the ventral sucker row have 2 small, medial, pointed distal teeth and 2 small plate-like lateral teeth on each side. **Right arm IV hectocotylized** with reduced distal suckers and honeycomb-like cutaneous sculpturing on the midventral surface comprised of **4 or 5 longitudinal columns of depressions with 20 to 25 pits or pores in each column**. **A single elongate photophore patch** occurs on the **ventral surface of each eye**. In the mantle cavity **1 relatively large round photophore lies near the anus and 1 smaller oval photophore lies on the posterior end of the intestine**. **A narrow strip of pinkish bioluminescent tissue** extends along the ventral midline from the posterior oval photophore to the posterior tip of the mantle cavity. The morphology of the gladius at various growth stages also may be diagnostic. Proboscis length in paralarvae is 25 to 50% of mantle length, thick and longer than the arms at less than 4 mm mantle length. Then they become equal to or shorter than the arms for a period of time. The 2 lateral (distal) suckers on the tip of the proboscis are 2 times larger than the remaining 6 suckers. A single, oblong photophore occurs on the ventral surface of each eye, developed at 4.0 to 4.5 mm mantle length, and 2 unequal-sized, round photophores are on the ventral surface of the intestine: the anterior one larger, near the anus, yellowish, developed at 3.0 to 3.5 mm mantle length; the posterior one, smaller, later-developing, whitish, developed at 8 mm mantle length. A visceral luminous strip develops on juveniles larger than 30 mm mantle length. Mantle covered with densely crowded, large brown chromatophores.

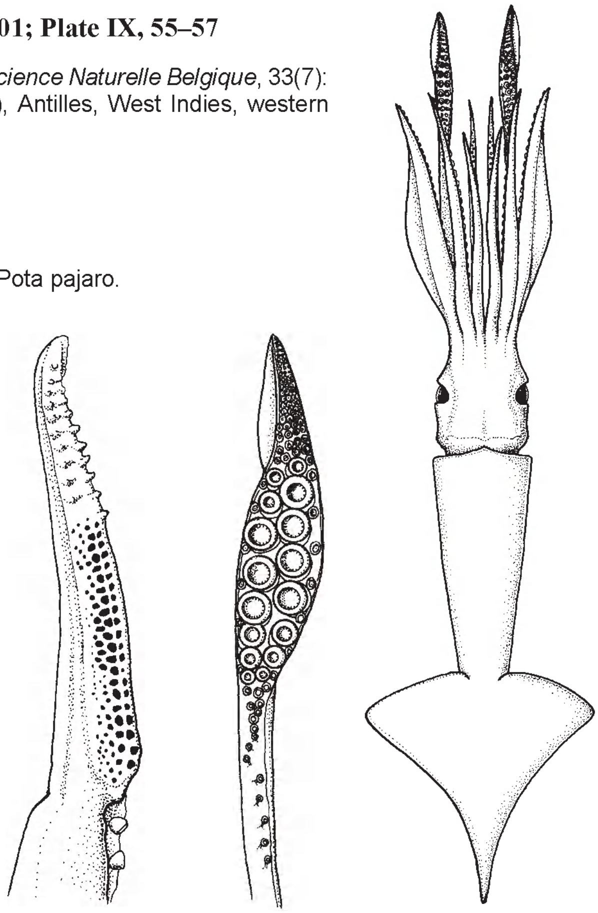

hectocotylus arm tentacular club dorsal view

Fig. 301 *Ornithoteuthis antillarum*

Size: The maximum mantle length recorded is 300 mm on a specimen from the northern end of the species' distributional range.

Geographical Distribution: An amphi-Atlantic tropical/subtropical species that has been recorded in the eastern Atlantic Ocean from 20°N to 28°S and in the western Atlantic Ocean from 45°N to 40°S (Fig. 302).

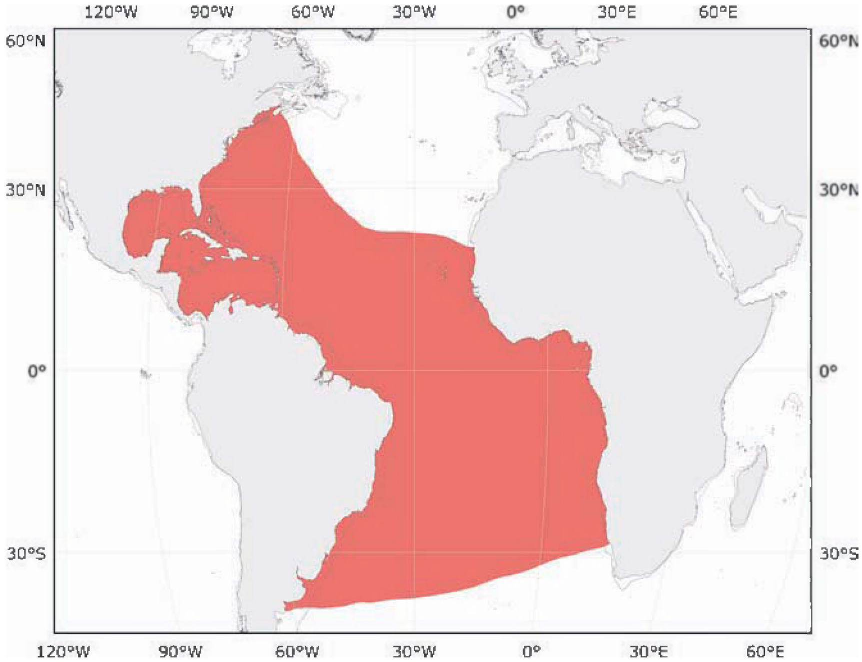


Fig. 302 *Ornithoteuthis antillarum*

🟥 Known distribution

Habitat and Biology: This species is a nerito-oceanic form that occurs throughout the water column over slope and oceanic depths. In the western North Atlantic it is common in slope waters off New England and southeastern Canada. Paralarvae and adults are relatively abundant in the Gulf of Mexico, the Straits of Florida and the Gulf Stream, as well as southward into the Caribbean and further southward into slope waters off Brazil. While it appears not to be a schooling species, experimental trawling in the western Atlantic Ocean off northern New England, as well as numerous observations from submersibles, indicate that it is common in midwater to just above the bottom. It has never been observed sitting on the bottom. It has been reported at the surface at night in the Caribbean, and many specimens were captured at night over deep bottom depths in large midwater Engel trawls in the eastern South Atlantic at 100 to 600 m. In the eastern Gulf of Mexico (27°N 86'W) extensive opening-closing net (Tucker trawl) samples determined the diurnal vertical distribution of micronektonic ***O. antillarum*** to be only 200 to 400 m during the day, with a few specimens at 100 to 200 m. The population occurred at 0 to 100 m exclusively at night, while some were at 100 to 200 m. The significant preponderance of captures from daytime bottom trawls versus night trawls and the occurrence in midwater and at the surface at night suggests that ***O. antillarum*** is a modified diel migrator that lives above the bottom during the day and disperses into mid-depths at night. Daytime depths of capture on the slope range from 450 to 1 100 m.

This species is a fast swimmer, so frequently is able to avoid capture by nets. Observations and video imagery from submersibles are recorded from off Key West, Florida, the Lesser Antilles, the Louisiana/Texas slope, the Northwest Providence Channel, Bahamas, and off New England where it was captured at depths of 100 to 893 m, water temperatures of 7.4 to 15°C, and with mantle lengths of 90 to 153 mm. On dives in the Bahamas in 2 consecutive years during autumn, ***O. antillarum*** was the most commonly observed squid. A typical position in the water column observed for this species at rest is the "J" posture, in which the animal hangs roughly head-down with the arms and tentacles curled and slightly splayed dorsally back over the head and anterodorsal mantle. This behaviour has been observed in several ommastrephid species.

Maximum mantle length of mature adults varies over the range of the species. In tropical waters some specimens of both sexes mature at 80 to 90 mm mantle length, while further north and south some specimens are still immature at greater than 100 mm mantle length.

Statolith analysis of a population of small-sized, early-maturing squids from the tropical central-east Atlantic Ocean indicates the species is fast-growing and does not exceed 182 days old. Growth rates for juvenile and immature individuals are high but decrease significantly with onset of maturity. It is thought that spawning migrations occur as populations mature and move into waters associated with sea mounts. Paralarvae, juveniles and subadults occupy midwater in epipelagic to mesopelagic zones over slopes, tops and oceanic depths, then with onset of maturity migrate to seamounts and ridges to spawn on or near the bottom, for example on the equatorial Atlantic seamounts along the mid-Atlantic Ridge.

Maturation of males follows the intermediate strategy of simultaneous ontogenetic increase in the volumes of both Needham's sac and the seminal reservoirs of spermatophores. Spermatophore length averages 9.0 mm, or about 6% of mantle length and the fecundity is quite low for a nerito-oceanic ommastrephid, about 100. The mean volume of seminal reservoirs is 0.15 mm^3, while the volume of the total sperm reservoirs is 0.1 cm^3. Reproduction-type in ***O. antillarum*** is the r-strategy, characterized by very small eggs (0.7 to 1.0 mm, mainly 0.75 to 0.85 mm). The total of vitellin oocytes in the ovary and ripe eggs in the oviducts generally represents 10 to 15% of potential fecundity in pre-spawning females. Oocyte stock formation (fecundity) is asynchronous, where oogenesis occurs by continuous asynchrony.

Spawning is intermittent (pulse, batch) with several egg masses spawned over an extended time; the intensity of spawning and the average number of eggs per mass are approximately constant during the spawning period. Females from a small-sized, early maturing population from the tropical central-east Atlantic have a potential fecundity of 50 000 to 220 000 oocytes and is a multiple (intermittent) spawner and frequently releases small egg masses of fewer than 1 500 eggs.

Young paralarvae can retract completely into their mantle cavity. Proboscis fusion begins to separate at about 4 mm mantle length and division into 2 separate tentacles is complete at 6 mm mantle length. Paralarvae are abundant in the summer in Gulf Stream waters from west of Key West, Florida northwards, concentrating along the Gulf Stream front at 75 to 100 m.

Ornithoteuthis antillarum exhibits the actively browsing type of hunting strategy in which prey represents many different species, each with low individual weight. As a browsing predator it feeds on all available small prey, principally on amphipods, as well as on larvae and fry of carnivorous fishes and on small squids, both in and below the thermocline. One specimen of 140 mm mantle length was observed and photographed from a submersible at 684 m (10.7°C) in the Bahamas feeding on an adult midwater fish, *Gonostoma elongata*. The prey of micronektonic ***O. antillarum*** in the eastern Gulf of Mexico (27°N 86'W) changes during ontogeny.

While copepods are numerically dominant at the smaller size classes (less than 4.0 mm mantle length) (of these the metridiid *Pleuromamma* is the major prey item), the less frequent euphausids probably are more important energetically because of their larger size and morphology; decapod crustaceans and cephalopods are the most abundant prey at larger size classes (more than 4.0 mm mantle length).

Predators on ***O. antillarum*** include epipelagic and mesopelagic fishes. A study off northeastern Brazil revealed that the diet of 4 species of billfishes, Istiophoridae, consisted mainly of ***O. antillarum*** and the ocean pomfret (*Brama brama*). In upper slope and adjacent oceanic waters off Brazil ***O. antillarum*** and ***Illex argentinus*** are the most important links in the trophic relations, the former a major component in the diets of the smaller tunas (*Thunnus alalunga* and *T. albacares*), as well as billfishes. Other species of fishes and cetaceans predators on ***O. antillarum*** include: common dolphinfishes (*Coryphaena hyppurus*), Atlantic sailfishes (*Istiophorus albicans*), skipjack tunas (*Katsuwonus pelamus*), white marlins (*Tetrapturus albidus*), albacore tunas (*Thunnus alalunga*), yellowfin tunas (*Thunnus albacares*), bigeye tunas (*Thunnus obesus*), swordfishes (*Xiphias gladius*), pygmy sperm whales (*Kogia breviceps*) and orca whales (*Orcinus orca*). A seasonal study on yellowfin tuna (*Thunnus albacares*) off southern Brazil showed that ***O. antillarum*** and teleost fishes are the most important dietary components in winter. The parasites of ***O. antillarum*** are primarily didymozoid trematodes, at infection intensity of 10 to 50 times less than in same-sized specimens of ***Sthenoteuthis pteropus***.

Interest to Fisheries: ***Ornithoteuthis antillarum*** is similar to all other species of ommastrephids in that its flesh is firm, muscular and palatable. Tests on its congener, ***O. volatilis***, have confirmed its qualities and acceptability as a potentially viable commodity. Its size of 80 to 120 mm mantle length is adequate for fishery purposes. In the higher latitudes of its range, ***O. antillarum*** attains a very desirable size of 250 to 300 mm mantle length. Observations from submersibles indicate it is a common species in slope waters of the tropical/subtropical western Atlantic. Its abundance in stomach contents of many species of large oceanic and neritic predatory fishes and cetaceans also suggests an abundant resource. However, it does not appear to assemble in large schools, as do ***Illex*** species, and it never has been observed to rest or reside on the bottom, where it would be more readily available to commercial trawls. An approximation of the instantaneous biomass of ***O. antillarum*** suggests a value of 500 000 tonnes. If an efficient fishing technique can be developed, this species could provide an important fishery product.

Local Names: USA: Atlantic bird squid.

Remarks: This species was misidentified as ***O. volatilis*** (Silva-Mello, 1998) in stomach contents of pelagic fishes from the southwestern equatorial Atlantic Ocean. ***Ornithoteuthis antillarum*** is a very abundant prey in this region and ***O. volatilis*** does not occur in these waters.

Literature: Roper and Young (1975), Vecchione and Roper (1992 [1991]), Passarella and Hopkins (1992 [1991]), Arkhipkin *et al.* (1998c), Dunning (1998b,c), Vecchione *et al.* (2001), Nesis (2002, 2003).

Sthenoteuthis Verrill, 1880

Sthenoteuthis Verrill, 1880, *Transactions of the Connecticut Academy of Sciences*, 5(5): 177–257. [222].

Type Species: *Sthenoteuthis oualaniensis* (Lesson, 1830)

Diagnostic Features: Funnel groove has a **foveola with 5 to 9 longitudinal folds and 4 to 6 distinct side pockets**. The **external light organs present**, including small subcutaneous photophores, are scattered on mantle, head and ventral arms. Large dorsal mantle photophores present: **large, yellow, oval photophore located anteriorly on dorsal part of mantle in squid greater than 140 mm mantle length** (observed to shine constantly in live squid). The photophore consists of numerous, densely packed, small, yellow, subcutaneous photophores, 1.0 to 2.5 mm in diameter, embedded in the mantle musculature, beneath which is a white reflective layer. **A single round photophore occurs on the ventral surface of each eye and 2 round photophores occur on the ventral surface of the intestine**. The dactylus of the tentacular club has 4 rows of small suckers. Carpal-locking apparatus on tentacular stalk with 2 to 5 knobs and an equivalent number of alternating smooth-ringed suckers. Zero to 2 suckers with denticulate rings occur on the carpus proximal to the first knob. **The largest medial suckers on the manus have 4 large, pointed teeth, one at each quadrant**. **Tips** of all arms **not attenuate.** Arms have 26 to 35 pairs of suckers. Tips of trabeculae of protective membranes do not project beyond the edge of the membrane. Ventral protective membranes of arms III subequal to arm width. Right or left ventral arm hectocotylized by smooth type. Fins rhomboidal, not attenuate posteriorly. Fin length 40 to 50% and fin width 70 to 88% of mantle length; fin angle is 58° to 72°. Mantle funnel-locking cartilage may be fused or not fused. The cone flags of the gladius are short, rhomboidal, with distinct radial creases. The greatest width of the cone flags ranges between 55 and 60% of the width of the rachis. The marginal rigid ribs of the rachis are doubled (with the exception of the giant form of ***Sthenoteuthis oualaniensis***), axial rigid rib of the rachis is wide, rounded-rectangular in cross-section. The lateral plates of the gladius do not adhere to the dorsal surface of the rachis, but form wide, free folds over the rachis. The anterior stem is short, reminiscent of a mammalian vertebra in cross-section. The width of the stem is equal to, or slightly greater than, its thickness. The cone is short, compressed laterally. The rostrum is absent. The alveola of the gladius is thick, covered with tiny ribs and thorns. Spermatozoa have 1 flagellum.

Size: Large-sized squid; mantle length up to 650 mm.

Geographical Distribution: It occurs in tropical and partly subtropical waters of the Atlantic, Indian and Pacific Oceans.

Remarks: ***Sthenoteuthis*** includes 2 oceanic species. Two endonucleases, AluI and Tsp509I, are diagnostic for species identification.

Literature: See species accounts.

Key to the species of *Sthenoteuthis*

1a. Mantle and funnel cartilages fused at post-paralarval stages; 6 to 8 pairs of suckers on hectocotylized arm; distributed in the Pacific and Indian Oceans . . . . ***Sthenoteuthis oualaniensis***

1b. Mantle and funnel cartilages not fused; 11 to13 pairs of suckers on hectocotylized arm; distributed in the Atlantic Ocean . . . . ***Sthenoteuthis pteropus***

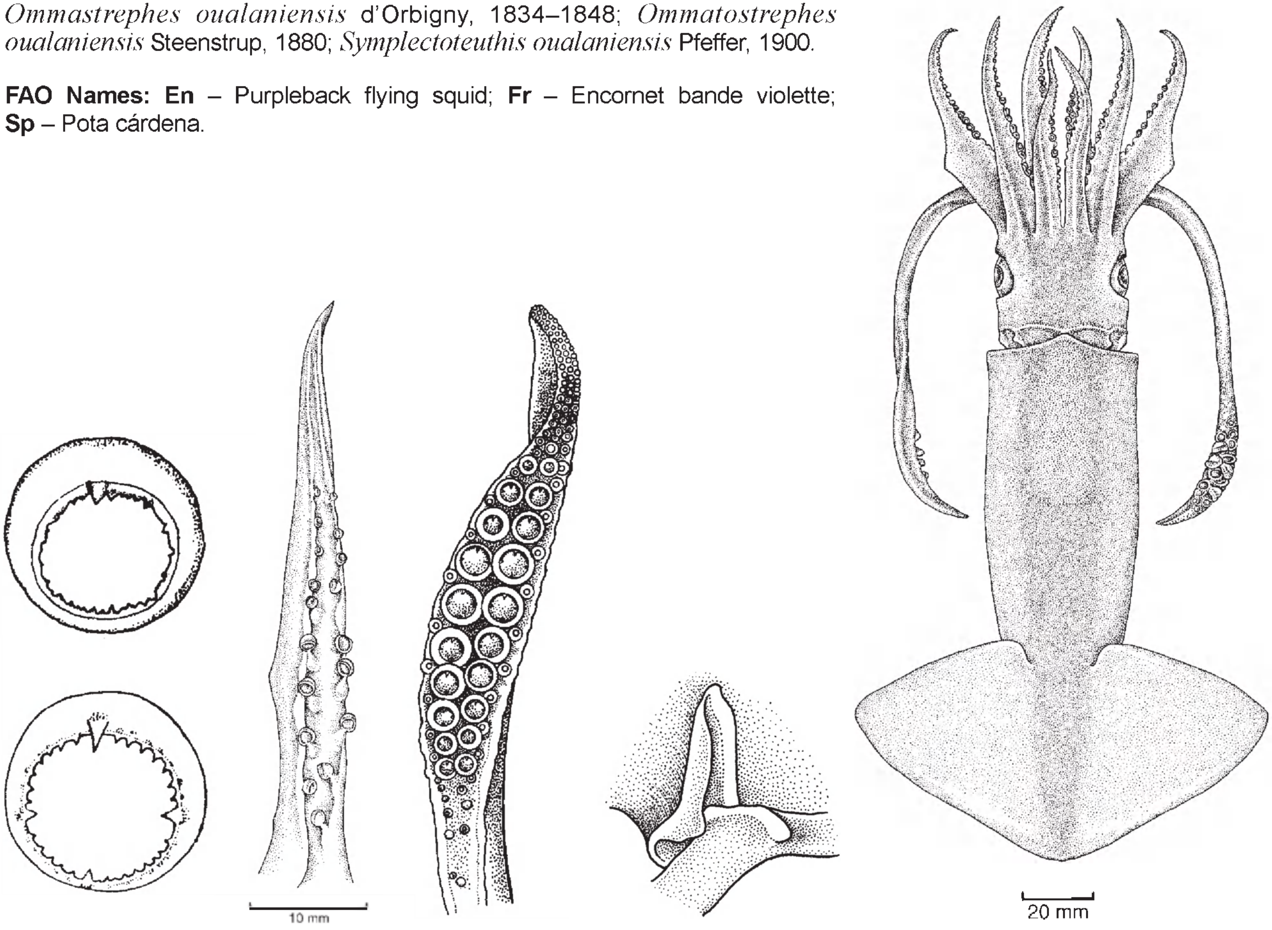
Sthenoteuthis oualaniensis (Lesson, 1830)

Fig. 303; Plate X, 58

Loligo oualaniensis Lesson, 1830, *In* 1830–1831, *Zoologie*, 2(1): 471 pp. [24, pl. I, fig. 2]. [Type locality: Oualan Island, Caroline Archipelago, Micronesia, western Central Pacific Ocean].

Frequent Synonyms: *Loligo oualaniensis* Lesson, 1830; *L. vanicoriensis* Quoy and Gaimard, 1832; *L. brevitentaculata* Quoy and Gaimard, 1832; *Ommastrephes oualaniensis* d'Orbigny, 1834–1848; *Ommatostrephes oualaniensis* Steenstrup, 1880; *Symplectoteuthis oualaniensis* Pfeffer, 1900.

FAO Names: En – Purpleback flying squid; **Fr** – Encornet bande violette; **Sp** – Pota cárdena.



sucker **hectocotylus arm** **tentacular club** **mantle button** **dorsal view**

Fig. 303 ***Sthenoteuthis oulaniensis***

Diagnostic Features: Mantle and funnel cartilage fused at post-paralarval stage by 9 to 12 mm mantle length. The large dorsal mantle photophore begins to develop in immature squid of 100 to 120 mm mantle length, but in maturing and mature squid of this same size it is not quite developed; **6 to 8 pairs of suckers occur on the hectocotylized arm of mature males**.

Size: Maximum mantle length 650 mm and body weight 8.5 kg.

Geographical Distribution: Indo-Pacific, tropical, oceanic species; its range extends in a broad band that stretches throughout the open waters of the tropical zone of the Indian and Pacific oceans and the Red Sea, generally where bottom depths exceed 200 m. It enters into subtropical zones where warm currents occur near Japan, the eastern Australian coast and South Africa (Fig. 304).

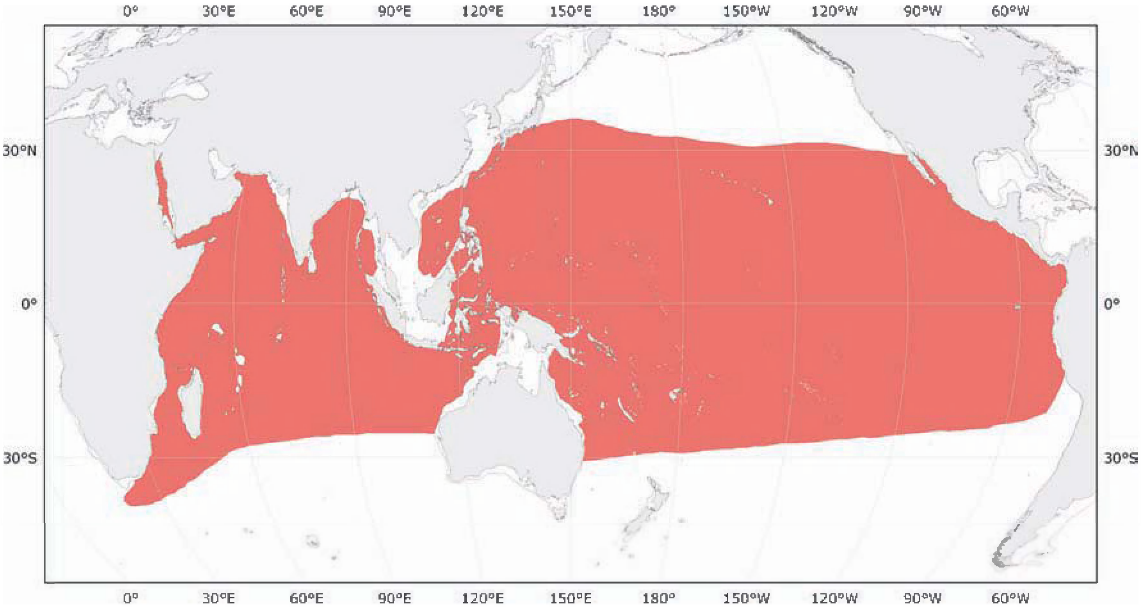


Fig. 304 ***Sthenoteuthis oulaniensis***

🟥 Known distribution

Habitat and Biology: ***Sthenoteuthis oualaniensis*** is a widely distributed, abundant and highly productive, epipelagic to mesopelagic and upper bathypelagic species that inhabits open waters over great depths of more than 200 to 400 m, at sea surface temperatures from 16° to 32°C, but usually above 20° to 22°C.

The Asian continent limits the northern boundary of its range in the Indian Ocean. The southern boundary reaches to the southernmost point of Africa to about 35°S, and in some years even to 39°S (commonly it is located in the Natal area and in some warm years even up to the Agulhas Bank); then it continues eastward approximately along the longitudes 25°S to 30°S, then to 35°S near the western Australia coast. In the Pacific Ocean it is widely distributed from the Pacific coast of central Honshu, Japan (about 36°N to 38°N) to the central part of the California Peninsula (about 25°N); in the Southern Hemisphere it extends from the southern part of the Australian coast (38°40'S) eastward to northern Chile (18°S to 22°S). The reproductive area of the species is located in the Indian Ocean northward of 18°S to 22°S, in the North Pacific Ocean between 20°N to 25°N and in the South Pacific Ocean from 16°S to 25°S. The more high-latitude areas of the species range is used by migrant squid as foraging zones, mainly by the females of the middle-sized form. Squid migrate to high latitudes with seasonal warming during summer in their appropriate hemisphere along the shift of surface isotherms of 20° to 22°C; then they move to lower latitudes with the seasonal autumn of water temperature. This species is truly pelagic, not associated with the bottom.

The planktonic paralarvae and juveniles usually live in the homogenous surface layer above and near the gradient layer (0 to 75 m and 100 m). Diurnal vertical migrations by paralarvae and juveniles are absent or very short in distance. During daytime the main bulk of juveniles occurs near the surface from 0 to 30 m, while at night they descend deeper, between 25 and 75 m, moving out of the zone of maximum numbers of conspecific predatory adult squids. Subadult and adult squids are interzonal animals. At night they inhabit surface and subsurface layers from 0 to 150 m to feed, with maximum numbers between the surface and about 25 m. In the morning they descend to depths of 200 to 1 100 m and remain there during the day.

The species is in the process of intensive adaptive radiation. On the basis of size differences of mature squid, as well as dorsal photophore and gladius morphology, 5 forms of undetermined status are distinguishable. At least the dwarf (1), middle-sized (3) and giant (5) forms probably are species in *statu nascendi*. **1) The dwarf form without a dorsal photophore**; the morphology of the gladius is variable. It is a common inhabitant of the equatorial waters of the Indian and Pacific Oceans mainly between 15°N and 15°S, but with locally warm currents it extends to 20°N to 26°N and 20°S to 27°S. The mantle length of mature males is 75 to 130 mm and of mature females 80 to 150 mm. The life cycle is about a half-year. **2) The dwarf form with a dorsal photophore**; the morphology of the gladius is unknown. The abundance of this form is very low. It has been recorded in the Red Sea, Mozambique Channel and Costa Rica Dome area. The mantle length of mature females is 90 to 150 mm. Duration of the life cycle is unknown. Probably this form is not a separate group, but, rather, it may represent the earliest maturing stage of both middle-sized groups (3 and 4). **3) The middle-sized, typical form** has a **dorsal photophore and double axes on the gladius**. This is the most abundant and widely distributed form. Its range coincides with the range of ***S. oualaniensis*** except it is absent in the Red and Arabian Seas and the Gulf of Aden. The mantle length of mature males is 120 to 240 mm and of females

150 to 400 mm. The life cycle is 1 year. **4) The middle-sized not typical form** has a **dorsal photophore and a single axis on the gladius**. This form is relatively abundant but it is narrowly distributed in the Red and Arabian Seas and the Gulf of Aden. The mantle length of mature males is 160 to 260 mm and of females 200 to 320 mm. The life cycle is 1 year. Probably this form and the giant form are parts of a united stock. **5) The giant form** has a **dorsal photophore and a single axis on the gladius**. This form is very abundant, an inhabitant of the Red Sea, the Arabian Sea and the Gulf of Aden northward of 12°N, but 2 large mature females of 725 and 820 mm mantle length were captured in an equatorial area (5 September 1991; 00°58'8"N, 2°06'8"E). The mantle length of mature males is 240 to 320 mm and of females it is 360 to 650 mm and even to 820 mm. The life cycle is 1 year, but its duration in very large specimens (greater than 700 mm mantle length) is unknown.

The species is very fast growing: by the age of 300 days specimens can reach 550 to 600 mm mantle length and 8 to 9 kg body weight; the largest daily increment in length is 1.0 mm for dwarf and middle-sized forms and 3.8 mm for the giant form. ***Sthenoteuthis oualaniensis*** is a typical monocyclic r-strategist. Potential fecundity varies from 300 000 to 350 000 oocytes in the dwarf form, from 0.7 to 8.5 million in the middle-sized form and from 6 to 22 million in the giant form. The relative fecundity is 3 000 to 7 000 oocytes per gram. The ripe eggs are small, 0.75 to 1.0 mm in diameter. Spermatophore lengths depend on the mantle length of mature males, and it varies from 8.8 to 11.7 mm in the dwarf form, from 16 to 32 mm in the middle-sized form, and from 40 to 50 mm in the giant form. The number of spermatophores in the Needham's sac of mature males can reach 300, but mainly it varies between 100 and 200. Mating occurs in surface layers at night in the "head to head" position without preliminary rituals; probably promiscuity is common. Duration of copulation is short, only 0.5 to 2 minutes. Copulation results in up to 150 spermatangia being attached to the buccal cone and membrane of females, and then the viable sperm are stored in 70 to 120 seminal receptacles that are situated on the buccal membrane. At the species level, spawning takes place all year round, with the duration of the spawning season for individual females up to 1 to 3 months. The spawning peak of the dwarf form is in the summer, of the middle-sized form in the northern part of its range it is in autumn to winter and in its southeastern Pacific range it is during the warm season (December to February); the spawning season of the giant Arabian form is in the spring. Spawning takes place in the epipelagic zone at night. This squid is an intermittent, multibatch spawner. After spawning once, females continue to feed and grow, while the next portion of oocytes matures; then spawning begins again. Each subsequent batch is quasi-equal in number of eggs. In the giant form, the maximum measured volume of egg mass is about 25 litres with a density of about 1 or 2 eggs per cubic centimetre. Egg masses are pelagic, and they float above the upper pycnocline layer. The duration of embryogenesis in water temperatures of 20° to 25°C is 3 to 6 days. Hatching size is about 1.0 mm mantle length. Paralarvae have the typical ommastrephid rhynchoteuthion-stage defined by the tentacles being fused into a trunk-like proboscis. During growth the proboscis gradually separates and in ***S. oualaniensis*** this separation is complete by 7.0 to 8.0 mm mantle length, signalling the end of the rhynchoteuthion-stage. Molecular genetics sequencing of the mitochondrial gene cytochrome c oxidase I discriminates 1 to 10 mm mantle length paralarvae from other rhynchoteuthions, e.g. ***Dosidicus gigas***.

Sthenoteuthis oualaniensis is a fast-swimming, highly manoeuvrable nektonic squid that reacts very quickly to any change in its surroundings. Juveniles are capable of "flying" during daytime. Under threat from pursuit of predators they can reach a high speed and then glide above the surface of the sea some tens of meters. The cruising speed of adult squid is about 3 to 10 km per hour, but the burst speed reaches greater than 25 to 35 km per hour. During the day at depth, squids are nearly non-active, and either "hang" in the water or move slowly with a speed of only 1 to 1.5 km per hour, propelled by the undulating fins. The species is an obligate shoaling (schooling) squid throughout ontogenesis. Usually, shoals consist of squid of uniform size. Shoal size is highly variable and depends on the productivity of the area and the density of the squid population: it varies from 2 to about 800 individuals, occasionally more. At the periphery of its geographical range, this species may form joint schools with same-sized ***Dosidicus gigas*** and ***Ommastrephes bartramii***.

Sthenoteuthis oualaniensis is an active predator with a very wide spectrum of food organisms. Paralarvae feed on micro- and mainly mesozooplankton (copepods, amphipods, etc). Post-paralarvae and juveniles (10 to 80 mm mantle length) feed on meso- and macroplanktonic invertebrates, mainly copepods, euphausids, amphipods and chaetognaths, as well as on juvenile fishes and squids. In squid from 90 to 150 mm mantle length, the role of fishes and squids increases as food preference. Active feeding of middle-sized squid (150 to 350 mm mantle length) takes place in the evening, night and early morning at the surface, and to 50 and 75 m. The middle-sized squid feed predominantly on micronektonic plankton-eating fishes (mainly myctophids, juveniles of flying fishes and the oceanic lightfish *Vinciguerria nimbaria*), juveniles of predatory fishes (paralepidids, gempylids, etc), squids (mainly the common clubhook squid ***Onychoteuthis banksii***, different species of enoploteuthids and conspecific juveniles) and pelagic shrimps and crabs. The adult females of the giant form (greater than 400 mm mantle length) in the Arabian Sea feed mainly on myctophids, that occur in very dense concentrations in the layer of 100 to 200 m. The duration for complete digestion of food is 3 to 6 hours in juveniles and 5 to 8 hours in adult middle-sized squid.

The predators of this species (all forms) are very diverse. For paralarvae and juveniles they include large chaetognaths, jellyfishes, small squids, planktivorous and small carnivorous teleosts. Juveniles (3 to 12 mm mantle length) are the prey for large squids (conspecific adults and the Humboldt squid ***Dosidicus gigas***), both species of dolphinfishes (*Coryphaena hippurus*, *C. equisetis*), snake mackerel (*Gempylus serpens*), lancet fish (*Alepisaurus ferox*), and different species of tunas (*Thunnus alalunga*, *T. obesus*, *T. albacares*, etc). Off eastern Australia, *S. oualaniensis* is common prey of yellowfin tuna (*T. albacares*) and swordfish (*Xiphias gladius*). Many species of sea birds are significant predators on juveniles, especially around the numerous oceanic islands. The main predators of middle-sized and large squid include swordfishes (*Xiphias gladius*), striped marlins (*Tetrapterus audax*), several species of sharks, such as the frill shark (*Chlamydoselachus anguineus*), the blue shark (*Prionace glauca*), the dusky shark (*Carcharhinus obscurus*), the oceanic whitetip shark (*Carcharhinus longimanus*), the smooth hammerhead (*Sphyrna zygaena*, etc), marime mammals such as the striped and the spotted dolphins (*Stenella caeruleoalba*, *S. attenuata*), the sperm whale (*Physeter macrocephalus*) and, locally, the Galapagos fur seal (*Arctocephalus galapagoensis*). In the Arabian Sea, adults of the giant form are their principal predator.

The helminth fauna of this squid consists of 12 species of larvae of trematodes, cestodes, nematodes and acanthocephalans, among which are 2 representatives of nematodes that have significant negative impact on the commercial importance of the species. Larvae of *Anisakis* sp. are a mortal danger to humans, but they are localized in the ovaries and encysted in the coelomic membranes, neither of which is used for human food. Larvae of *Porrocaecum* sp. are encysted on the internal mantle wall and they may significantly degrade the quality of the marketable components of the infested squid.

The total instantaneous biomass of ***S. oualaniensis*** is estimated to be at the level of 8 to 11.2 million tonnes, including 3 to 4.2 million tonnes in the Indian Ocean and 5 to 7 million tonnes in the Pacific Ocean. In general, the areas of dense concentrations coincide with dynamically active feeding zones and oceanographic fronts. In the open waters of the Peruvian region (5°S to 25°S and from the Exclusive Economic Zone (EEZ) boundary to 95°W) it forms dense concentrations together with ***Dosidicus gigas***.

Interest to Fisheries: ***Sthenoteuthis oualaniensis*** is not fished commercially on an industrial level mainly due to the absence of effective fishery methods and to the relatively poor quality of the meat (at least for Asian consumers in comparison with ***Todarodes pacificus***). Local artisanal fisheries for this species carried out in the last 40 years by dipnet and hand jigs were conducted from near Okinawa, Taiwan Province of China and Hawaii. The catches are used mainly as bait for the tuna fishery. Many attempts to use jigging machines to fish for the species in different parts of the species range were not effective. However, this species has great potential for a future significant fishery with about 3 million tonnes of stock in dense concentrations and a potential catch on the level of about 300 000 to 500 000 tonnes or more. The main prospective areas for fishery development are the Arabian Sea, the Gulf of Aden and the adjacent open waters to 12°N; the southern part of the equatorial zone of the Indian Ocean between 4°S and 10°S and between 65°E and 95°E; the area of Mozambique between Madagascar and the edge of the Mozambique shelf; the equatorial zone of the Pacific Ocean between 2°N and 2°S and between 95°W and 110°W; the oceanic part along the Peruvian Exclusive Economic Zone (EEZ) boundary between 6°S and 18°S (mixed concentrations with ***Dosidicus gigas***); and areas near the Hawaiian Islands, Taiwan Province of China and Okinawa. The most promising area for the development of a large-scale fishery for ***S. oualaniensis*** is the Arabian Sea. The giant form of this species of 300 to 650 mm mantle length (mode 480 to 540 mm mantle length) inhabits this area. More than 200 000 tonnes were captured in the northwestern part of the Arabian Sea in dense concentrations of more than 10 tonnes per square km. The potential average catch is estimated at about 100 000 tonnes. The optimal fishing season for this squid is September to May, with the peak in March to May. The most effective gears are the wide-cut pelagic trawl and the mechanized vertical lines with large blinking jigs. The meat of the giant form of greater than 350 mm mantle length tastes acidic because of the presence of large quantities of urea (49.1±1.52 mg/100 g); special treatment with citric acid is required for this species to be utilized as food.

Local Names: AUSTRALIA: Yellow-backed squid; CHINA: Yuán-wū-zēi; JAPAN: Tobi-ika; PERU: Pota cárdena; RUSSIA: Kal'mar-ualanienis, Purpurnyj kal'mar (purple squid); TAIWAN PROVINCE OF CHINA: Nán-yóu; USA: Purpleback flying squid.

Literature: Zuev *et al.* (1975), Wormuth (1976), Roper *et al.* (1984), Nigmatullin *et al.* (1991b), Nesis (1993b), Roper *et al.* (1995), Bower *et al.* (1999c), Nigmatullin *et al.* (2002c), Zuev *et al.* (2002), Nixon and Young (2003), Okutani (2005), Gilly *et al.* (2006b), Parry (2006), Wakabayashi *et al.* (2006).

Sthenoteuthis pteropus (Steenstrup, 1855)

Fig. 305

Ommastrephes pteropus Steenstrup, 1855, *in Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1855(5/6): 199–200. [199]. [Type locality: St Croix Island, Caribbean Sea, western Central Atlantic].

Frequent Synonyms: *Ommatostrephes pteropus* Steenstrup, 1855; *Architeuthis megaptera* Verrill, 1878; *Sthenoteuthis megaptera* Verrill, 1880.

FAO Names: En – Orangeback flying squid; **Fr** – Encornet orange; **Sp** – Pota naranja.

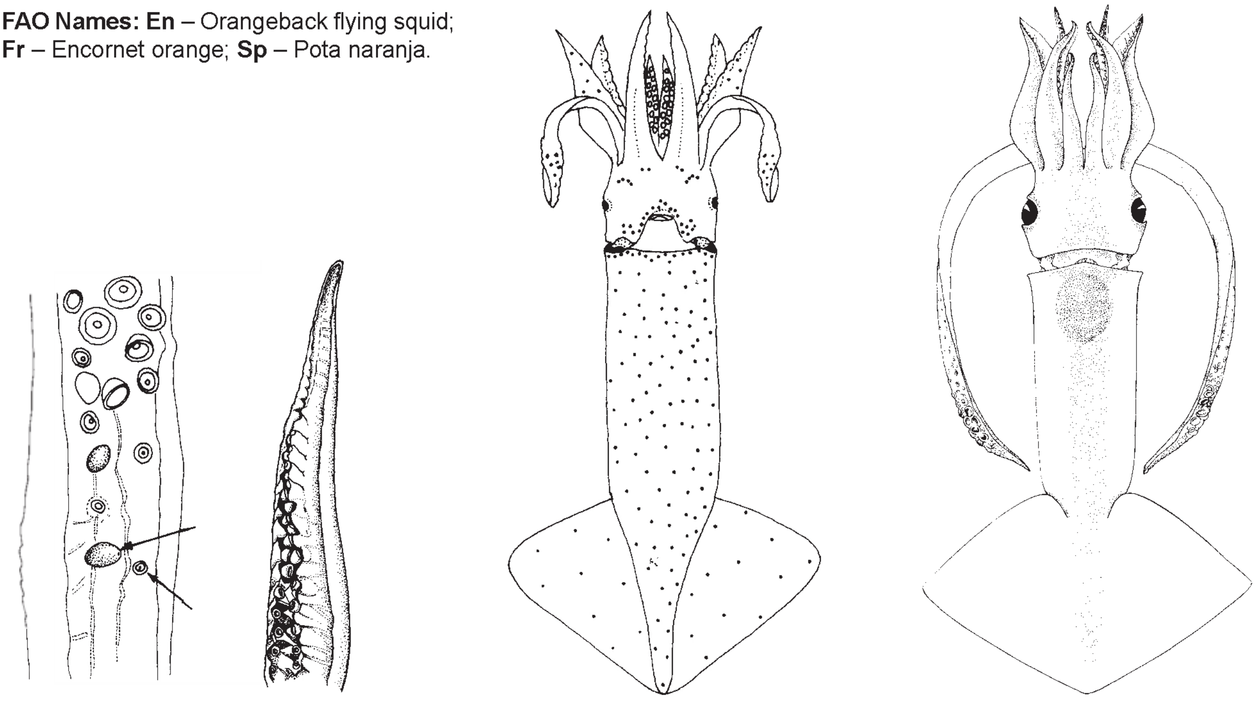

sucker tentacular club ventral view dorsal view

Fig. 305 *Sthenoteuthis pteropus*

Diagnostic Features: Mantle and funnel cartilage not fused during entire ontogenesis (only 2 specimens recorded with fused funnel cartilage among many thousands studied). Large dorsal mantle photophore begins to develop in immature and maturing squid of 90 to 110 mm mantle length; all adult specimens have this photophore; **11 to 13 pairs of suckers** on **hectocotylized arm**.

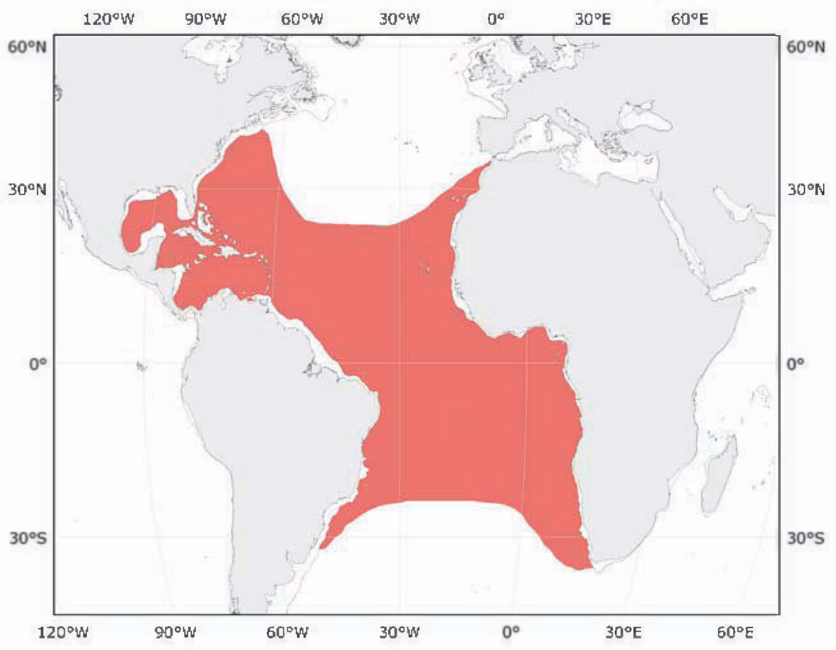


Fig. 306 *Sthenoteuthis pteropus*

🟥 Known distribution

Size: Maximum mantle length 650 mm; body weight 7 kg.

Geographical Distribution: Tropical Atlantic Ocean. The extreme limits of its northern distribution lie at the latitude of New York (42°N) and Madeira (34°N); in some years north to 36°N near the Strait of Gibraltar. Its southernmost limits extend to southern Brazil (30°S to 32°S) and South Africa (36°S). The boundaries of the species range in the central part of the ocean coincide approximately with the Tropics of Cancer and of Capricorn (Fig. 306).

Habitat and Biology: ***Sthenoteuthis pteropus*** occurs at sea surface temperatures from 16° to 32°C, usually above 20° to 22°C. Squid migrate to high latitudes with seasonal warming of the appropriate hemisphere in harmony with the shift of the surface isotherms of 20° to 22°C; then they return to lower latitudes in the autumn in coincidence with the seasonal drop in water temperature. Significant seasonal shifts occur at the boundaries of the range. During summer in the Northern Hemisphere (July to October) the northern boundary is displaced to the northern limits of the species distribution, whereas the southern boundary displaces approximately to 23°S near Brazil and Namibia and about 10°S in the central part of ocean. During winter (February to March) the northern boundary shifts to the south to about 20°N to 22°N near Cuba and northern Mauritania, while the southern boundary is displaced to the southern limits of the species range. The reproductive region occupies the equatorial zone, including the Caribbean Sea and Gulf of Mexico between 20°N and 20°S near the continents and between 10°N and 10°S in the central part of the ocean. The higher latitudes in both hemispheres are the principal feeding zones of the species range; they also are occupied seasonally, mainly by immature females of the large form.

Sthenoteuthis pteropus is an abundant, highly productive species that dwells in epipelagic to mesopelagic and upper bathypelagic zones. It inhabits open waters over great depths in excess of 200 to 400 m, and this species is not associated with the bottom. In general, squid of this species live in the oceanic pelagic zone from the surface to 1 200 m. Paralarvae, post-paralarvae and early juveniles up to 90 mm mantle length as a rule live in the homogenous surface layer from the surface to between 50 and 75 m. Diurnal vertical migration in paralarvae and post-paralarvae is minimal to absent, and in juveniles it is a very short range. During daytime, juveniles principally inhabit the surface layer from the surface to about 30 m, and at night their habitat extends to depths of 30 m to between 75 and 100 m. Squids larger than 120 to 150 mm mantle length undergo the typical diurnal vertical migration: they rise to the surface layers at night for active feeding, then descend to daytime depths in the morning. On moonless nights most squids are concentrated near the surface between 0 and 30 m, while on moonlit nights they are more widely dispersed in somewhat deeper water, between 10 and 50 m. During about a 1-hour period at dawn, squid descend to the depth of their daily habitation, with the maximum concentration at depths of 600 to 850 m. In the twilight crepuscular period – before sunrise and sunset-squid occur in the 150 to 400 m range.

Sthenoteuthis pteropus is represented **by 2 intraspecific forms** of undetermined systematic status. 1) **A small, early-maturing, equatorial form**; it lives only in the equatorial zone and its most adjacent waters between 10°N to 15°N and 8°S to 15°S in the eastern Atlantic, while it occupies nearly the entire range of the species distribution (*sensu lato*) in the central and western Atlantic, including the Caribbean Sea and the Gulf of Mexico. These squids are relatively stable in that they do not undergo long distance migrations at any time during their life cycle. Spawning takes place all year round. The mantle length of the mature male of the small form is 110 to 200 mm and of the mature female 150 to 320 mm (mode 210 to 250 mm). **2) A large, late-maturing, mostly peripheral form**; this is distributed throughout the entire range of the species (*sensu lato*) in the eastern Atlantic, less broadly in the central part of the ocean to 20°W to 25°W; probably it occurs in the peripheral parts of the species range (*sensu lato*) in the western Atlantic. In the eastern Atlantic the main concentrations of this large form of squid are distributed in waters to the north of 8°N to 12°N and to the south of 6°S to 10°S, as well as along the south tropical front. Two allopatric populations occur in the open waters along the African coast; they differ by distribution, spawning season and direction of ontogenetic migrations. These squids are northern and southern populations that are confined to northern and southern African upwelling zones respectively. These populations spawn in the equatorial zone. Then the developing immature females greater than 200 to 250 mm mantle length migrate during the warm season in their given hemisphere, to the north (northern population) and the south (southern population) to foraging grounds that are located in both peripheral zones of the species range (*sensu lato*). After active feeding and somatic growth they migrate back to the equatorial zone to complete maturation and to spawn. However, no morphological differences exist to differentiate between these forms.

Spawning is seasonal, and it takes place in the autumn period of each particular hemisphere. The mantle length of the mature male of the large form is 180 to 280 mm and of the female 300 to 650 mm.

In the most intensively studied area, the eastern Atlantic, ***S. pteropus*** appears to be subdivided into 3 groups that probably have populational status: the northern large squid, the equatorial small squid and the southern large squid. They differ ecologically and genetically, and their ranges overlap to a small degree (the 2 populations of the large form) or to a considerable degree (both large squid populations with the equatorial form).

The reproductive biology of ***S. pteropus*** is very similar to that of ***S. oualaniensis***. The potential fecundity of mature pre-spawning females varies from 0.5 to 1.5 million oocytes at 160 to 180 mm mantle length and from 6 to 18 million oocytes at 400 to 540 mm mantle length. These same mean values for females of the small early-maturing form are about 2 to 3 million oocytes, and for the large late-maturing females it is 8 to 10 million oocytes. The relative fecundity is 2 000 to 5 200 oocytes per gram.

Ripe eggs are small, 0.75 to 1.0 mm in diameter. The oviducts contain from thousands to 1 million eggs depending on the size of mature female and the stage of the infilling process. Spermatophore lengths are proportional to the mantle length of the mature male and they vary from 15 at 107 mm mantle length to 42 at 240 mm mantle length. The number of spermatophores in the Needham's sac of mature males less than 160 mm mantle length is 100 to 300, while at greater than 170 mm mantle length there are 200 to 500 spermatophores. Promiscuous mating takes place in the surface layers at night in the "head to head" position. The duration of copulation is 0.5 to1 minute. Each copulation results in up to 180 spermatangia being attached to the buccal cone and buccal membrane of females, and then the viable sperm are stored in 57 to 154 seminal receptacles that are situated on the buccal membrane.

Spawning occurs in the epipelagic zone at night. ***Sthenoteuthis pteropus*** is an intermittent, multibatch spawner. After the first spawning, females continue to feed and grow, while the next portion of oocytes matures; then they spawn again. Each subsequently spawned batch of eggs is subequal in number of eggs. Large females presumably release at least more than 50% of their total oocyte stock.

In total, during the individual spawning period of at least the large females, 5 or 6, and probably more, egg masses are produced. Egg masses are pelagic, and they float above the upper pycnocline layer. The size of embryos at hatching is about 1.0 mm mantle length. The duration of the paralarval stage is 32 to 38 days.

The majority of males become mature at 120 to 150 days, and almost all males older than 180 days are fully mature. The life span of males is completed by age 270 to 280 days. Females begin to mature at the age of 200 to 220 days, and the maximum maturation takes place at 240 to 300 days. All females are in full spawning condition at ages over 300 to 320 days. The maximum age of a spent male is 305 days and of a spawned-out female it is 372 days. The life cycle of females of both small and large forms seldom exceeds 1 year, and the life cycle of males is 1 to 2 months shorter.

This species is a very fast-swimming and highly manoeuvrable nektonic squid that reacts very quickly to any change in its surroundings. Occasionally, under threat from potential predators, juveniles may break through the sea surface and soar into the air for some tens of metres. The cruising speed of adult squid is about 3 to 10 km per hour, and burst speed is more than 30 km per hour. During the day at depth these squid are nearly inactive, and they either “hang” or move very slowly with undulating fins at a speed of about 1.5 km per hour. Throughout ontogenesis, shoaling (schooling) is the obligate behaviour of this squid. Usually, shoals consist of uniform-sized individuals. The size of shoals is highly variable, from 2 to about 1 000 specimens. At the periphery of its distributional range, ***S. pteropus*** may form joint feeding schools with same-sized ***Ommastrephes bartramii***.

Sthenoteuthis pteropus is an active predator that undergoes gradual changes in its food spectrum during ontogenesis. Paralarvae feed on micro- and mainly mesozooplankton (copepods, juveniles of euphausiids and larvae of fishes and squids). Post-paralarvae and juveniles (10 to 80 mm mantle length) feed on meso- and macroplanktonic invertebrates, mainly copepods, euphausids, amphipods and chaetognaths, as well as juvenile fishes and squids. In squid from 90 to 150 mm mantle length, the role of myctophid fishes and small squids as food sharply increases, while the role of crustaceans is minimized. Active feeding of subadult and adult specimens takes place in the evening, night and early morning hours at the surface down to 50 to 75 m. Squid 150 to 350 mm mantle length feed predominantly on micronektonic plankton-eating fishes. These are mainly myctophids (principally species of *Myctophum*, *Hygophum* and *Vinciguerria nimbaria*) and to a lesser degree juveniles of predatory fishes (paralepidids, gempylids, etc), as well as flying fishes, squids (mainly ***Onychoteuthis banksii***, different species of enoploteuthids and juveniles of their own species) and pelagic shrimps. Large females of 360 to 650 mm mantle length feed mainly on squids (mostly ***Onychoteuthis banksii*** and their own species) and to a lesser degree on flying fishes and middle-sized predatory fishes. The duration for full digestion of food is 3 to 6 hours in juveniles and 5 to 8 hours in adults. Correspondingly, the values of daily food ration for these 2 ontogenetic groups is 8 to 27% of body weight and 7 to 10% of body weight, respectively.

The known predators of this squid include the following groups: paralarval and post-paralarval predators include jellyfishes, small squids, plankton-eating and small carnivorous teleosts; juveniles (3 to 14 mm mantle length) are the prey for large squids (mainly conspecific adults), dolphinfishes (*Coryphaena hippurus*, *C. equisetis*), snake mackerel (*Gempylus serpens*), lancet fishes (*Alepisaurus ferox*, *A. brevirostris*), and several species of tunas (e.g. *Thunnus alalunga*, *T. obesus*, *T. Albacares*); locally, sea birds also are predators on juveniles; the main predators of subadult and adult ***S. pteropus*** are swordfishes (especially important is *Xiphias gladius*), some active species of pelagic sharks, such as the blue shark (*Prionace glauca*), the bigeye thresher (*Alopias superciliosus*), the great white shark (*Carcharadon carcharias*), hammerheads (*Sphyrna* spp.) and requiem sharks (*Carcharhinus* spp), dolphins (including *Steno bredanensis*) and very rarely, sperm whales.

The parasitic helminth fauna of this squid consists of 13 species of larvae of trematodes, cestodes, nematodes and acanthocephalans. Two nematode species have negative implication for the commercial importance of ***S. pteropus***. The larvae of *Anisakis* sp. cause death to humans, but they are localized in the ovaries and encysted in coelomic membranes that are not used for food. The larvae of *Porrocaecum* sp. are encysted locally on the internal mantle wall; they may reduce the quality and value of the marketable product of infested squids.

The total instantaneous biomass of ***S. pteropus*** is estimated at the level of 4.2 to 6.5 million tonnes. More than half of this standing stock is concentrated in the eastern tropical Atlantic Ocean in 3 macroscale areas of dense concentrations (see below). The annual total biomass production for ***S. pteropus*** is estimated at 34 to 52 million tonnes.

Interest to Fisheries: ***Sthenoteuthis pteropus*** currently is not intensively fished commercially, but it represents a significant potentially valuable fishery resource in the open Atlantic Ocean. The mantle and the appendages are well suited for human consumption, and the viscera are excellent raw materials for the production of biologically active substances. A seasonal, artisanal fishery occurs near Madeira with very small catches. In the 1970s to 1980s Soviet investigators attempted to develop commercial exploitation of this species in the eastern tropical Atlantic Ocean, experimenting with wide-cut pelagic trawls, twin trawls, automatic jigging machines and mainly individual hand jigs. Jigging machines were not effective because the feeding behaviour of this oceanic squid is more complicated in comparison with that of inshore and neritic species of ***Illex***, ***Todarodes*** and ***Nototodarus*** that are very efficiently fished by this gear. To increase the fishing efficiency for this species, the complicated lifting movement of a longline is required. The use of the wide-cut pelagic trawl from large-capacity trawlers also was unsuccessful. The catches did not exceed tens of kilograms. Likewise, the catches of twin trawls in surface waters (0 to 15 m) in the equatorial eastern Atlantic Ocean, as a rule, did not exceed 200 kg. At some lighted drift stations where dense concentrations of large squid (280 to 450 mm mantle length) occurred in areas near the Angola and Namibia Exclusive Economic Zone (EEZ) boundaries, catches were on the level of 3 to 8 tonnes. Collectively, these data are evidence of the potential for a viable fishery for this species. The total annual fishery potential is 1.9 to 2.9 million tonnes. The possible annual potential catch inside Exclusive Economic Zones (EEZs) is about 0.5 to 0.8 million tonnes. The 3 principal potential fishery grounds are located in the eastern Atlantic Ocean eastwards from 20°W between 15°N and 22°N and 25°S: 1) northeast area between 10°N and 20°N, from the African coast to 25°W; 2) equatorial area between 5°N and 10°S and from 0° to 20°W; 3) Angolan area between 5°S and 20°S, from the African coast to 5°E. Two smaller areas of high squid concentrations occur in the open waters of the Gulf of Guinea between 2°N and 3°S, and in the Caribbean Sea and western Atlantic near the Lesser Antilles. Because ***S. pteropus*** is so widely distributed and is subdivided into geographic populations that undergo sequential seasonality of growth and reproduction, it is possible to maintain a year-round fishery. The main impediment to the development of a viable commercial fishery for this species is the development of optimal fishing gear and the establishment of consistent, reliable fishery methods.

Local Names: COLUMBIA, CUBA, MEXICO, VENEZUELA: Lomo aranjado; JAPAN: Nise-akaika; MADEIRA: Pota de limao, Lula de limao; PORTUGAL: Pota laranja, Pota limão; RUSSIA: Krylorukij kal’mar (wing-armed squid), Kal’mar pteropus; USA: Orangeback flying squid, Yellowback squid.

Literature: Roper (1963), Roper *et al.* (1984), Arkhipkin *et al.* (1988), Zuev *et al.* (1992 [1991]), Dunning (1998b), Nigmatullin (2002a), Zuev *et al.* (2002), Laptikovsky and Nigmatollin (2005), Okutani (2005).

2.22.3 Subfamily **TODARODINAE** Adam, 1960

Todarodinae Adam, 1960b, *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 36(19): 1–10 [2].

Type Genus: *Todarodes* Steenstrup, 1880.

Diagnostic Features: Ommastrephids with **funnel groove and foveola present** (except ***Todaropsis***), **side pockets absent**; left tentacular club with 2 pairs of carpal suckers; tentacles without carpal-locking apparatus; **suckers on dactylus of tentacular club quadriserial**; medial manus sucker rings with 20 or fewer long, pointed teeth, with single, large, pointed tooth distally (in some species); right or left or both arm(s) IV hectocotylized in mature males; ocular, visceral and mantle photophores absent.

Table 12

Comparison of genera of Todarodinae[1/]

	Hectocotylus	Funnel groove with foveola	Tentacular stalks with free trabeculae	Largest manus sucker with teeth	Largest manus sucker with teeth
Martialia	left or right arm IV	Yes	Yes	1 tooth enlarged	linked by intermediate ridges or plates
Nototodarus	both arms IV	Yes	No	1 tooth enlarged or subequal teeth	linked by intermediate ridges or plated
Todarodes	right arm IV	Yes	No	generally subequal teeth	linked by intermediate ridges or plated
Todaropsis	both arms IV	No	No	subequal teeth	without intermediate ridges of plates

[1/] From Young and Vecchione (2008k).

Todarodes Steenstrup, 1880

Todarodes Steenstrup, 1880, *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1880: 73 –110, 12 figs, 1 pl. [83].

Type Species: *Todarodes sagittatus* (Lamarck, 1798).

Diagnostic Features: Funnel grove with foveola, side pockets absent. Tentacular club with 2 pairs of carpal suckers, tentacles without fixing apparatus; suckers on dactylus of tentacular club quadriserial; medial manus sucker rings with 20 or fewer long, pointed teeth with a single larger tooth distally in some species. **Only right arm IV hectocotylized** in mature males. **Ocular, visceral and mantle photophores absent**.

Remarks: The genus ***Todarodes*** is represented in the Mediterranean Sea, the North and South Atlantic Ocean, the northwestern and southwestern Pacific Ocean, Indo-Pacific waters, northeastern Indian Ocean, and the Southern Ocean and its northern meanders. Traditionally, the genus consists of 4 species, one of which, ***T. pacificus***, contained 2 subspecies. While these former subspecies of ***T. pacificus***, namely ***pacificus*** and ***pusillus***, are similar in several respects, it is now considered that their morphological differences are sufficiently broad as to consider them separate species. This distinction has been recognized by Okutani (2005), a designation with which we concur. Some species of ***Todarodes***, particularly ***T. pacificus*** and less so ***T. sagittatus***, support among the largest fisheries in the world.

Todarodes sagittatus (Lamarck, 1798) **Fig. 307**

Loligo sagittata Lamarck, 1798, *Bulletin des Sciences par la Société Philomatique de Paris*, 2(5): 129–131. [130]. [Type locality: "sur les côtes de l'Ocean de l'Europe et de l'Amerique", fide Lamarck (1799: 14)].

Frequent Synonyms: *Loligo sagittata* Lamarck, 1798; *Ommastrephes sagittatus* Lamarck, 1798; *Ommatostrephes sagittatus* Lamarck, 1798; *Loligo todarus* Verany, 1851; *L. aequipoda* Rüppell, 1844; *Sepia media* Barbut, 1783; *Loligo brasiliensis* Férussac, 1823; *Sepia loligo* Gmelin, 1789.

Misidentifications: None.

FAO Names: En – European flying squid; **Fr** – Toutenon commun; **Sp** – Pota europea.

Diagnostic Features: Mantle strong, muscular, long and slender; fins wide and strong, fin length up to 45% mantle length. Funnel groove with foveola, without side pockets. Entire **club** relatively **very long, extends along stalk**; **club suckers** on elongate carpus in **10 to 12 pairs**; **medial manus sucker rings with 17 to 20 long pointed teeth**; **manus with 14 to 18 quadriserial sucker rows**; club suckers on dactylus in 4 rows. Arm suckers with enlarged central tooth, 7 to 9 regular teeth and virtually no small alternating teeth. No light organs on viscera. **Right arm IV hectocotylized in males**, by the modification of terminal suckers into fleshy papillae. Dark purplish in colour.

Geographical Distribution: Eastern North and South Atlantic Ocean: from the lower Barents and Kara Sea (Arctic Ocean) southward to about 13°S (south of the Gulf of Guinea), including the North Sea, the Mediterranean Sea and the Marmara Sea. In the North Atlantic it extends to the mid-Atlantic Ridge (Fig. 308).

Size: Large-sized species: maximum reported size 750 mm mantle length for an unsexed specimen, probably a female, 640 mm mantle length for a male, both in North Atlantic waters. Common size between 250 to 350 mm mantle length.

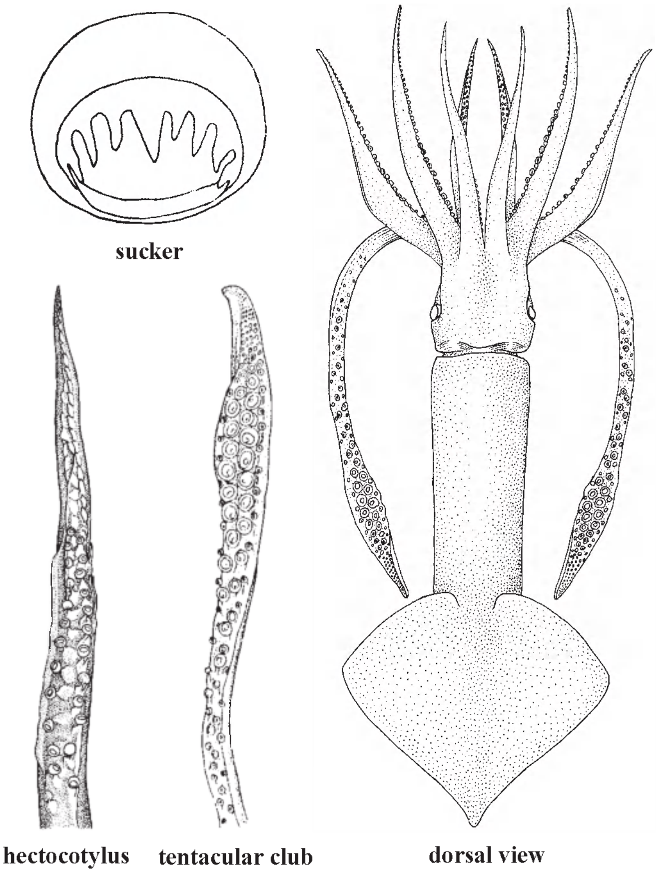


Fig. 307 *Todarodes sagittatus*

Habitat and Biology: A neritic and oceanic species that occurs from the surface to well over 1 000 m, having been captured in British waters to a depth of 4 595 m. Occasionally associated with the shelf and upper slope bottom communities, e.g. North African population, typically it inhabits lower slope waters, between 350 and 700 m. ***Todarodes sagittatus*** undergoes important trophic and ontogenetic migrations in the North Atlantic Ocean. In early summer large schools appear off the south and southwest coast of Iceland, the Faeroe Islands, Norway and, in some years, Scotland, where they remain until the beginning of winter. Coastal strandings of great numbers of squid are relatively common during this period. As winter arrives, the squid migrate into deeper offshore watersfor the duration of winter. The populations of the northwestern African waters and the western Mediterranean are rather stationary in comparison. This species is found in large numbers from March to May on the fishing grounds around Madeira and other parts of the eastern central Atlantic Ocean. Here ontogenetic movements occur as well, from the shelf to the slope and deep waters. ***Todarodes sagittatus*** is known to carry out diel vertical migrations between the surface and near-surface waters at night and in proximity to bottom waters during the day. However, night catches in deeper waters indicate that a portion of the population may not adhere to this general pattern. This species may occur alone or in small groups; then individuals form into very large congregations during its trophic movements on the North Atlantic and north African shelves.

With the exception of some geographic areas and seasons, the sex ratio is usually biased towards females in all the populations investigated to date, with relatively few, under-represented males in the captures. Numerous observations indicate that this is due mainly to ecological factors, since males and females inhabit different feeding grounds and get together during the mating/spawning seasons. Males may remain on the spawning grounds without

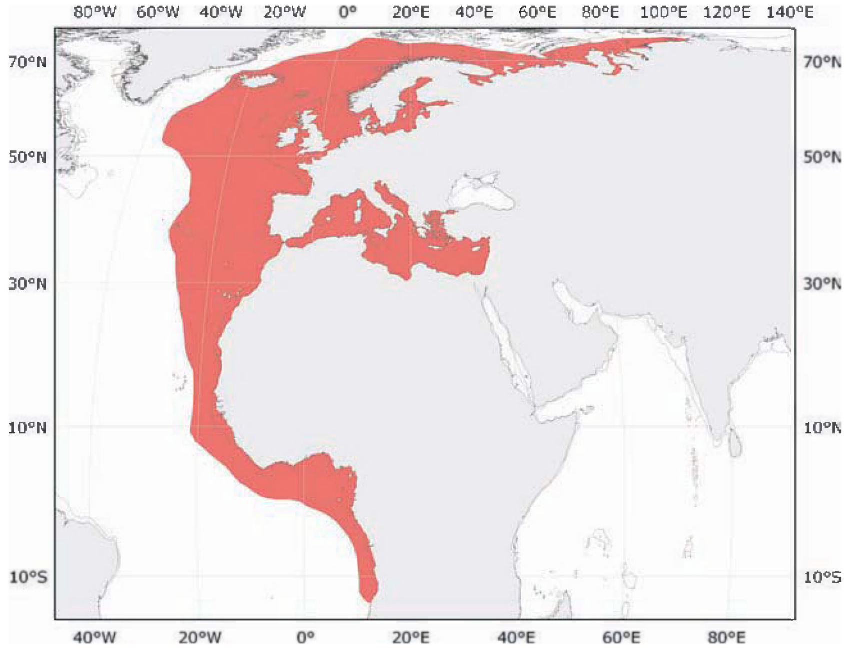


Fig. 308 *Todarodes sagittatus*

🟥 Known distribution

taking part in the feeding migrations, which may explain why they inhabit different depths than females and would account for their relative scarcity in the sampling captures. Males mature earlier and at smaller sizes than females. The smallest mature males from the northern African waters measured 170 to180 mm mantle length, while the smallest mature females were 200 to 210 mm mantle length. These sizes are comparatively smaller than those of squids in the Mediterranean Sea and in the North Atlantic Ocean. In the Mediterranean Sea, the smallest mature males measured 196 mm mantle length, but the bulk of the population matures at 230 mm mantle length; females start to mature from 300 mm mantle length onwards. In the North Atlantic, males start to mature at 280 mm mantle length and females (mantle length at 50% maturity between 460 and 480 mm) may remain immature until 500 mm mantle length. Spawning probably occurs throughout the year on the continental slope, with pronounced seasonal peaks that occur in late winter or early spring off northern Europe and North Africa, and between September and November in the western Mediterranean Sea (Catalan Sea and Balearic Islands). Spermatophore length varies depending on male size and geographic area; comparatively larger spermatophore sizes of 48 to 54 mm occur in squid from the Catalan Sea (western Mediterranean Sea), followed by North Atlantic males (38 to 44 mm) and North African populations (20 to 29 mm). Egg sizes also vary; with the exception of the Irish Sea populations (where mature eggs in female oviducts measure 1 to 4 mm; maximum diameter; preserved material), larger egg sizes are recorded in the North Atlantic and in the Mediterranean Sea (fresh material; 2.4 to 2.6 mm) than in the North African waters (preserved material; 1.0 to 1.2 mm). These differences may be related to the use of fresh material versus preserved samples, but this is not clear without additional observations. As in most ommastrephids, fecundity is high (up to several hundred thousand ova) and varies depending on the size of females; a potential fecundity up to 950 000 eggs was reported for females from northwestern African waters. ***Todarodes sagittatus*** females decrease feeding activity prior to spawning, and they are likely to undergo the “descending” type of spawning, characterized by intermittent activity, with a decrease of egg number per egg mass, as described for other members of the subfamilies Illicinae and Todarodinae. Spawning occurs in deep waters (200 to 800 m) apparently close to the bottom. No information is available on egg masses and embryonic development, nor are early life stages well known, partly because youngest paralarvae often are confused with or mixed with those of other ommastrephids. Observations on juveniles over the mid-Atlantic Ridge indicate that they are transported by currents and distributed in the upper layer of the water column (50 to 150 m), perhaps descending somewhat deeper during the day. Paralarvae off the North African coastal waters rise to the subsurface layers over the slope to forage, then they migrate later to the shelf edge as juveniles. Growth rate is high, especially in the early life phase, then slows with the onset of sexual maturity. A life cycle of about 1 year or slightly more is estimated based on statolith analysis after indirect validation, but a longer life span (from 1 and a half to 2 years) is considered likely for animals larger than 500 mm mantle length. Geographical area and environmental conditions *sensu lato* also may affect age and growth. A 600 mm mantle length female (plus several other specimens larger than the normal median size of 300 mm mantle length) was caught in the waters off Sardinia, central Mediterranean. Such records indicate that ***T. sagittatus*** in the Mediterranean can reach sizes comparable to the maximum reported size of the species in the North Atlantic waters. The peculiar small modal sizes of mature squid (250 to 300 mm mantle length) of the North African population off western Sahara, compared with those of their northern counterparts (350 to 420 mm mantle length), is thought to be caused by early maturation and subsequent decrease of somatic growth rates.

Todarodes sagittatus feeds on fishes, crustaceans and cephalopods, in decreasing order of importance; in northern waters the main prey are small herrings (*Clupea harenqus*) and cod (*Gadus morhua*). In turn, it is preyed upon by several top-level predators, such as tunas, swordfish, sharks, seals and cetaceans, both dolphins and whales, for which, in some species, ***T. sagittatus*** constitutes the most important food item. This is particularly relevant since ***T. sagittatus***, along with ***Illex coindetii*** and ***Todaropsis eblanae***, is the most important paratenic host for Anisakid nematods. A better understanding of parasitic transfer and parasite-induced diseases through the food web will aid the management of marine resources in general, as well as the safer human consumption of raw marine products in particular.

Interest to Fisheries: ***Todarodes sagittatus*** currently is taken mainly as a bycatch of trawl fisheries, but it may occur in sufficient densities in Norway to support a moderate, targeted fishery. In the Mediterranean, the main fishery is conducted by Italian vessels. A seasonal targeted fishery occurs during summer in southern Italy by commercial as well as sport fishermen; here, as in some other Mediterranean countries, the commercial value of this species is relatively high, although the flesh of large individuals is described as tough. This squid is consumed fresh or boiled and also it is marketed frozen, salted or dried, and it is used as bait in the cod and halibut fisheries. Apart from large-scale predation on commercial finfish species, occasionally it has been considered a nuisance because of its competition with finfishes in the baited hooks (long line) fisheries. Common fishing methods other than trawling are jigging and purse seining. Separate fishery statistics do exist, but the quality of fishery data reporting on this species is poor, since ***T. sagittatus*** often is mixed in catches with other short finned squid species.

Local Names: CYPRUS: Thrapsallo; FRANCE: Calmar; GREECE: Kalamari; ITALY: Totano viola, Totano selvaggio; JAPAN: Hokkaisurumeika, Taiseiyosurume, Yoroppasurumeika; MALTA: Totlu bajdani; MOROCCO: Passamar; RUSSIA: Kalmar; SPAIN: Pota; YUGOSLAVIA: Lignjun.

Remarks: Observations on several population parameters, along with peculiarities in the open-water distribution and certain morphological-ecological traits, support the existence of different populations in the Atlantic Ocean and the Mediterranean Sea (e.g. Nigmatullin, 1989b, Borges and Wallace, 1993, Borges, 1995, Nigmatullin *et al.*, 2002b). Further studies and observations are required, especially considering that such morphological and geographical differences are considered definitive at a subspecific level by some authors (i.e. Nigmatullin and Laptikhovsky, 1999). Mass strandings of the species have been observed in several areas of its distribution, e.g. Iceland, Scotland, Italy, but no sound explanation for these events is available to date.

Literature: Mangold-Wirz (1963), Clarke (1966), Wiborg and Gjøsæter (1981), Roper *et al.* (1984), Shimko (1984), Wiborg and Beck (1984), Guerra (1992), Piatkowski *et al.* (1998), Quetglas *et al.* (1998), Arkhipkin *et al.* (1999), Belcari (1999g), Lordan *et al.* (2001a), Nigmatulin *et al.* (2002b), Cuccu *et al.* (2005), Hastie *et al.* (2009).

Todarodes angolensis Adam, 1962

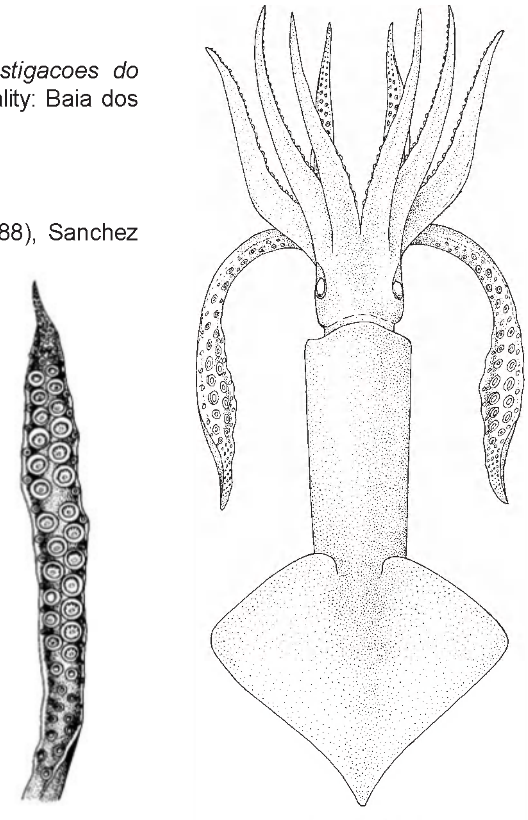
Fig. 309

Todarodes angolensis Adam, 1962, *Memorias da Junta de Investigacoes do Ultramar*, 2(33): 9–64, 2 pls. [32, text–fig 4, pl 2, figs 1–3]. [Type locality: Baia dos Elefantes, Angola, eastern South Atlantic Ocean].

Frequent Synonyms: None.

Misidentifications: *Todarodes sagittatus* Sanchez (1981, 1982, 1988), Sanchez and Moli (1984).

FAO Names: En – Angolan flying squid; **Fr** – Toutenon angolais; **Sp** – Pota angolense.


dorsal view

dorsal view

Fig. 309 ***Todarodes angolensis***

Diagnostic Features: Mantle cylindrical, typical for Todarodinae, fins sagittate. **Funnel groove with foveola, no side pockets**; no light organs on viscera. Carpal area of club very short; **4 pairs of suckers only (only 2 pairs in *Todarodes filippovae*, 10 to 12 in *T. sagittatus*)**; **medial manus sucker rings with 13 to 16 long, pointed teeth**; **largest sucker diameter <2.6% mantle length**; **manus with 14 to 18 quadriserial sucker rows**. Tentacular suckers in 4 rows; large sucker rings with 14 to 17 conical teeth alternating with square plates. Arm sucker rings with large distal teeth alternating with very small teeth; distal 40% of **right arm IV of male hectocotylized** with suckerless, thick pedicels nearly completely connected by the ventral protective membrane; dorsal row of pedicels flattened. Body dark purplish brown in colour.

Size: Large-sized squid; maximum mantle length 433 mm in females.

Geographical Distribution: Eastern South Atlantic Ocean, south of 13°S; occurs around South Africa and reaches into the Indian Ocean. Limits unknown (Fig. 310).

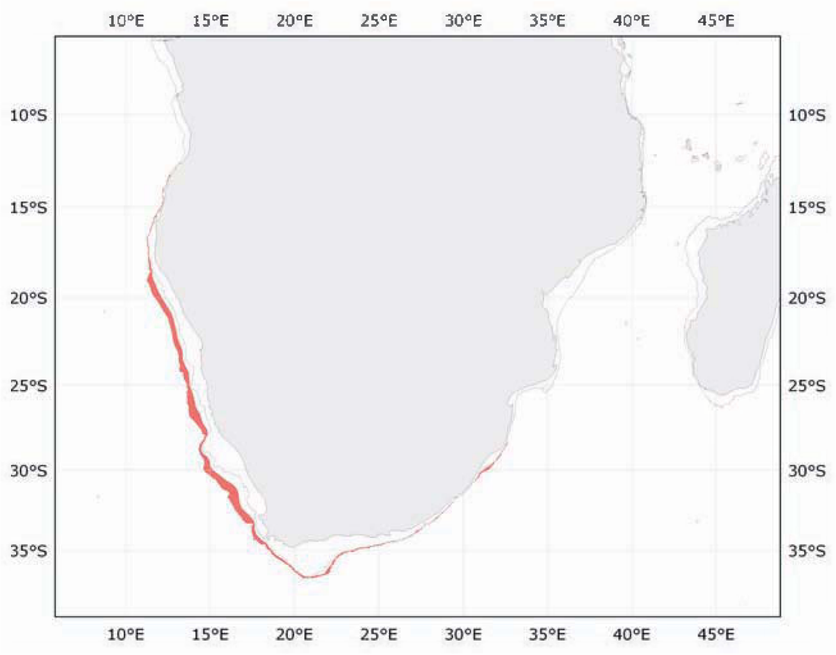


Fig. 310 ***Todarodes angolensis***

🟥 Known distribution

Habitat and Biology: On the South African continental slope, ***T. angolensis***, along with ***Todaropsis eblanae***, is an indicator species for the upper slope benthic habitat, from 300 to 500 m. During daylight adult squids occur only near the bottom, whereas juveniles occur in the water column but avoid the surface layer. At night, adult squids are dispersed throughout all the horizons except the surface layer, and juveniles are concentrated in the upper 60 to 80 m layer. Generally speaking, however, young squid prefer epipelagic waters, a habitus also reported for the Mediterranean ***T. sagittatus***. The sex ratio in the studied population of Namibian waters shows a clear predominance of females, as observed for the congener species ***T. sagittatus*** in other areas, a phenomenon explained by several authors with the assumption that females and males inhabit different grounds and depths except during the mating/spawning seasons. The smallest mature male measured 240 mm mantle length; the smallest mature female 250 mm mantle length. However, observations on the length and indices of the nidamental glands, the size-range of immature females (not exceeding 350 mm mantle length) and the presence of spermatangia on the buccal membrane of females of 300 mm mantle length, suggest that 300 to 350 mm is the size range corresponding to the onset of sexual maturity in the population. Southern Hemisphere spring (e.g. October to December) is the period of greatest abundance of maturing and mature squid. Growth studies based on statolith analysis indicate that the life span is about 1 year; however, a longer life span is possible, as hypothesized for its northern congener ***T. sagittatus***. Growth rates are subject to considerable individual variation and highly related to the environmental variability in the northern Benguela Upwelling System. The species feeds opportunistically on a variety of fishes and it is known to prey upon the Cape hake, *Merluccius capensis*, in the northern Benguela Current. In turn, it is preyed upon by several fishes, sharks and marine mammals, for some of which it constitutes the most common food item.

Interest to Fisheries: Currently there is no directed fishery for this species. It is caught as bycatch in otter trawl fisheries, but separate statistics are not reported.

Local Names: None available.

Remarks: The history of the nomenclature of ***T. angolensis*** and its congener, ***T. filippovae***, was outlined by Roeleveld (1989). ***Todarodes angolensis*** was first described by Adam (1962) as a subspecies of the northeastern Atlantic Ocean ***Todarodes sagittatus*** (Lamarck, 1798) and raised to the status of full species by Nesis (1973). In 1975, Adam described ***T. filippovae***, on the basis of the specimens first recorded by Filippova (1968b) from the southern Indian Ocean and originally identified as ***T. sagittatus angolensis***. Subsequently, Nesis (1979c) synonymised ***T. filippovae*** as described by Adam (1975) with ***T. angolensis***, on the basis of other specimens from the Australia-New Zealand region (2 immature females and 1 juvenile). Afterwards, Russian scientists referred all ***Todarodes*** (adults and paralarvae) caught in Southern Hemisphere waters to ***T. angolensis***. Therefore, the species is reported to occur from off New Zealand, the Auckland and Campbell Islands and in the area west and south of Tasmania. However, this synonymy was not generally accepted and other cephalopod systematists continued to treat the 2 species as distinct taxa (e.g. Okutani, 1980, 1990, 2005, Roper *et al.*, 1984, Dunning and Brandt, 1985). Further morphological and genetic studies fully supported the separation of the 2 species (e.g. Dunning and Wormuth, 1998, Roeleveld, 1989, Yokawa, 1994), which are clearly associated with different water masses in the Benguela system (Roeleveld, 1989). Okutani (2005), considered ***T. angolensis*** restricted to the South African coastal waters, while ***T. flippovae*** has a circum-subantarctic distribution. We support this view; however, further studies and observations are necessary to help clarify the status of the distribution of ***Todarodes*** species in the Southern Hemisphere. Special attention is necessary when species distribution is based on identification of stomach contents: due to the potential overlapping of ***Todarodes*** species in the area, identification to species level from beaks remains, especially in absence of flesh, must be considered with caution.

Literature: Adam (1962), Nesis (1973, 1979b), Roper *et al.* (1984), Roeleveld (1989), Villanueva and Sanchez (1989), Dunning and Wormuth (1998), Okutani (2005).

Todarodes filippovae Adam, 1975

Fig. 311

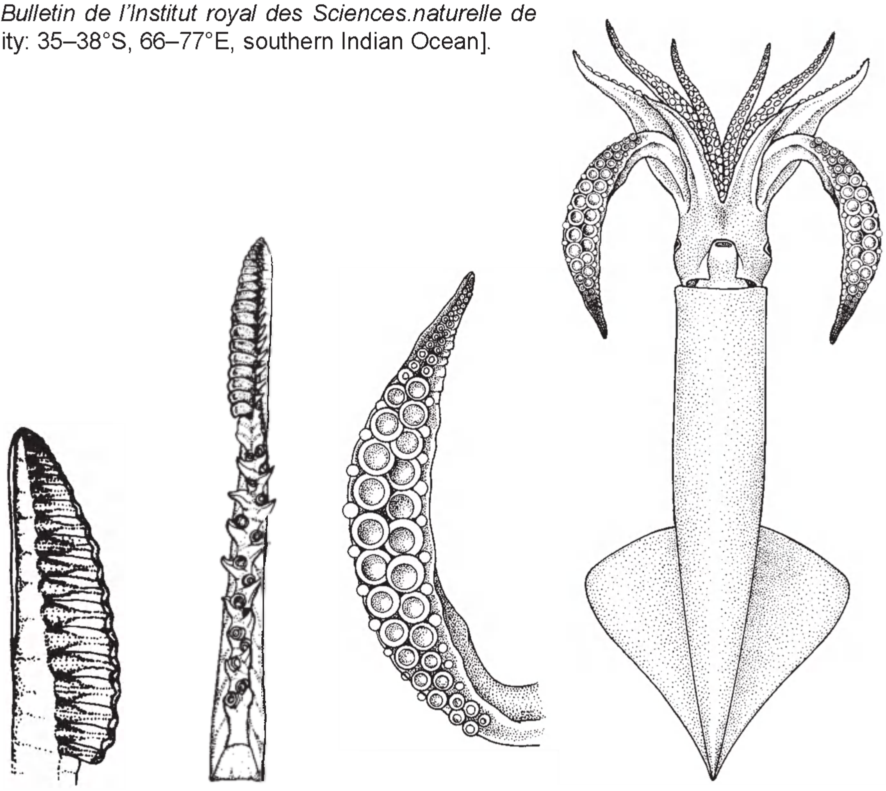
Todarodes filippovae, Adam 1975, *Bulletin de l'Institut royal des Sciences.naturelle de Belgique*, 50(9): 1–10. [3]. [Type locality: 35–38°S, 66–77°E, southern Indian Ocean].

Frequent Synonyms: None.

Misidentifications: None.

FAO Names: En – Antarctic flying squid; **Fr** – Toutenon antarctique; **Sp** – Jibia antártica.

Diagnostic Features: Mantle muscular, long, narrow (width 16 to 24% of mantle length); tapers to a pointed tail. Fins saggittate; length and width about 50% of mantle length; single fin angle about 30º to 35° (60° to 70° both fins). **Tentacles very large and robust. Clubs very expanded occupying nearly entire length of tentacles; only 2 pairs carpal suckers at base of club (4 pairs in *Todarodes angolensis*;** 10 to 12 pairs in ***T. sagittatus***); medial manus sucker rings with 7 to 13 long, pointed teeth; largest sucker diameter 2.7 to 4.5% mantle length manus with 12 to 14 quadriserial sucker rows. Arms relatively short; sucker rings with 10 sharp teeth; right



hectocotylus tip hectocotylus tentacular club ventral view

Fig. 311 *Todarodes fillippovae*

arm IV hectocotylized along the distal 21 to 36% (up to distal 60%, Dunning, 1993) of the arm, with suckers transformed to papillae and tubercles, with the ventral protective membrane and trabeculae very expansively developed.

Size: Large-sized squid; maximum reported size 540 mm mantle length, 4.7 kg for a female, about 400 mm mantle length for males; common between 200 and 400 mm mantle length.

Geographical Distribution: Circumpolar in the Southern Ocean; south of approximately 35°S; common in the Antarctic Convergence zone. The northernmost occurrence of the species is the record of 2 juveniles caught at 16°46' S, close to the economic zone of Peru, most likely as a result of the Peru Current transportation (Fig. 312).

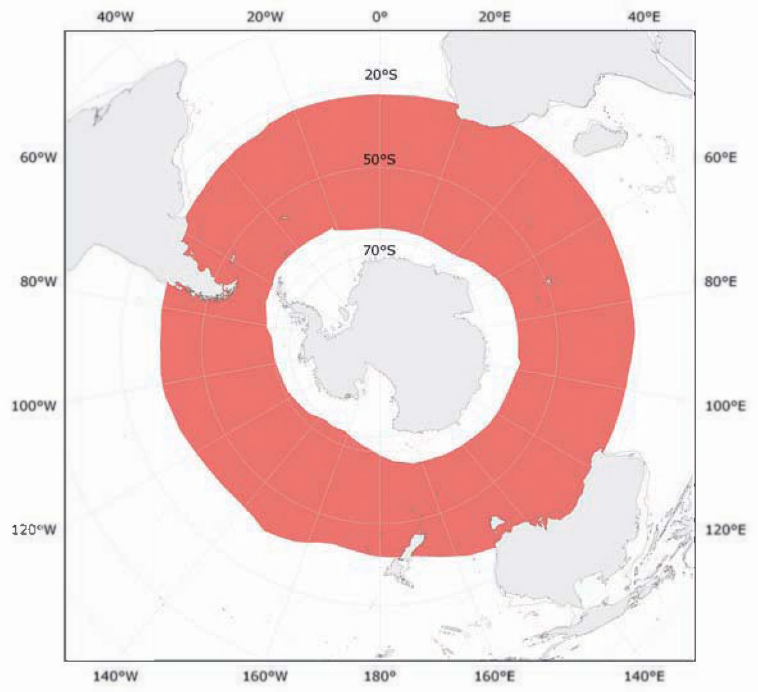


Fig. 312 ***Todarodes fillippovae***

🟥 Known distribution

Habitat and Biology: An oceanic species, ***Todarodes filippovae*** extends from the surface to about 1 200 m depth; it inhabits open waters or slope locations, very rarely, if ever, extending over the continental shelf. With the exception of the low velocity Peru Current off the southeastern Pacific coast of South America, all other areas where the species has been collected are associated with high velocity current systems, i.e. the Antarctic Circumpolar Current, the Falkland Current, the Benguela Current and the East Australia Current. Positive links between species life cycles and these high velocity systems are likely to occur, both in the transport of planktonic eggs and paralarval stages, as well as in the adult feeding ecology, as already described for other ommastrephids (e.g. ***Illex argentinus***).

No clear relationship is apparent between the species distribution and water temperature: ***T. filippovae*** is found associated with cold, Antarctic Intermediate Water (3° to 3.8°C), as well as warm superficial streams (up to 24°C). These observations suggest the presence of either a cryptic complex of species with different temperature requirements or a single, eurythermal species. While the species is widely distributed in the Southern Hemisphere, most information on its biology comes from the Tasman Sea (southern Australia) and South Africa. In Australian waters during summer ***T. filippovae*** occurs from central New South Wales to southwestern Western Australia and it is the most abundant ommastrephid squid in the subtropical convergence zone of the Tasman Sea and in the slope waters along the southeastern Australian coast. Juveniles as well as large adult individuals are most abundant in the upper, surface layer of the water column, where they are caught by jigs and driftnets in surface water temperatures between 11.5° and 24.7° C and at 250 m between 9.7°C and 11.9°C. No mass migration in a north-south direction nor across the Tasman Sea has been observed. However, mature specimens of both sexes move to the continental slope waters during summer months, prior to spawning. The spawning season occurs between December and August. Mature males represent a higher proportion of the population off southern New South Wales (38º to 32º S), suggesting that mating and spawning probably occur towards the northern boundary of the species distribution in this area. Spermatophores are evident in males at 260 mm mantle length, and at 320 mm mantle length all males have fully formed spermatophores. The smallest mature female observed with eggs in the oviduct was 380 mm mantle length. Observations from South African waters suggest a similarly long spawning period (February to August). Also, data on specimens from stomachs of commercially caught sperm whales off Durban suggest that these squid spawn off the southeast African coast. Few data exist on early life stages and rhynchoteuthion paralarvae are unknown. A few juveniles between 40 and 80 mm mantle length were caught off eastern Tasmania during midaustral summer and juveniles of unreported length were collected in the southern Pacific in autumn. Growth is rapid, as in most ommastrephids, with females generally growing faster than males and reaching larger sizes, while males mature earlier. Based on estimated growth rates of the summer Tasman Sea population, as well as on assumed daily periodicity in statolith increments, the life cycle is about 1 year or slightly more. In contrast with other ommastrephid species, but similar to its congener ***T. angolensis***, ***T. filippovae*** appear to grow faster in cooler oceanographic conditions. The species feeds on fishes, crustaceans and cephalopods. Crustaceans dominate in the diet of smaller squids (< 200 mm mantle length), while cephalopods are the more abundant prey items in stomachs of larger squids (>200 mm mantle length). In turn, ***T. filippovae*** is preyed upon by several fish species and top predators such as seals, albatrosses and sperm whales. Adults of this species may be infested with large numbers of encysted nematodes and cestodes in their mantle tissue.

Interest to Fisheries: This species is taken as bycatch to the jig fishery for ***Nototodarus sloanii*** off New Zealand and southern Australia; also it is caught as bycatch by trawlers around most of its distributional range. Listed among the 6 most abundant squid species in the South West Atlantic, it has been reported among the jig catches off the Falkland Islands, but there are no records of the species in the ***Illex argentinus*** or ***Loligo gahi*** squid fisheries on the shelf around the Falkland Islands since the establishment of the Falkland Islands Government Fisheries Department in 1987. Defined as 1 of the 2 "encroaching species" (along with *Martialia hyadesi*) of the targeted ommastrephid fisheries in the in the Southern Hemisphere, ***T. filippovae*** likely is a candidate for future exploitation.

Local Names: AUSTRALIA: Southern Ocean arrow squid.

Remarks: ***Todarodes filippovae*** was described by Adam (1975), on the basis of specimens from the southern Indian Ocean originally identified as ***T. sagittatus angolensis*** by Filippova (1968b). Subsequently, Nesis (1979b) synonymised ***T. filippovae*** with ***T. angolensis***, and most Russian scientists then referred all ***Todarodes*** (adults and paralarvae) caught in Southern Hemisphere waters to ***T. angolensis***. Therefore, many records of ***Todarodes*** squid off New Zealand, the Auckland and Campbell Islands and in the area west and south of Tasmania were considered to belong to ***T. angolensis*** (e.g. Korzun *et al.*, 1979, Nesis, 1979b, 1982, 1987). However, this synonymy was not widely accepted by the cephalopod community and other cephalopod systematists continued to treat the 2 species as distinct taxa (e.g. Okutani, 1980, 1990, 2005, Roper *et al.*, 1984, Dunning and Brandt, 1985). Additional morphological and genetic studies fully support the separation of the 2 species (e.g. Dunning and Wormuth, 1998, Roeleveld, 1989, Yokawa, 1994), which are clearly associated with different water masses in the Benguela system (Roeleveld, 1989). Okutani (1980), considered ***T. flippovae*** to have a circumsubantarctic distribution, potentially overlapping with that of ***T. angolensis*** in southern Africa waters. We support this view, while recognizing that further studies and observations are necessary to help clarify the status of the ***Todarodes*** species distributions in the Southern Hemisphere. Because of its broad circumpolar distributional range and the propensity for crypsis among ommastrephid and loliginid squid (e.g. Smith *et al.*, 1981, Brierley *et al.*, 1993, Yeatman and Benzie, 1993), possibly more than one species is represented by ***T. filippovae***. For example, Roeleveld, (1995) suggested that ***T. filippovae*** from off Chile is a distinct species. Consequently, the entity currently identified as one species, possibly represents a ***T. filippovae*** species complex (Rodhouse, 1998).

This species may prove to be important in the circumpolar Antarctic ecosystem, both because of its abundance and its trophic links with other organisms, as already evidenced for some areas of the distribution (e.g. the Benguela system Lipinski, 1992). When a fishery develops for this species, fundamental research focused on precise specific/subspecific/populational identification and stock structure will be required. Also, considering the role of ***T. filippovae*** in the food web, any future fishery will need to be rationally managed so that prey/predator relationships are not negatively impacted.

Literature: Adam (1975), Nesis (1979b), Roper *et al.* (1984), Dunning and Brandt (1985), Dunning (1998c), Roeleveld (1989), Dunning and Wormuth (1998), Rodhouse (1998), Jackson *et al.* (2007a).

Todarodes pacificus (Steenstrup, 1880) **Fig. 313**

Ommatostrephes pacificus (Steenstrup, 1880). *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1880: 73–110, 12 figs, 1 pl. [79]. [Type locality: Hakodate, Japan, western Pacific Ocean].

Fequent Synonyms/Misidentifications: *Ommatostrephes pacificus* Steenstrup, 1880: 79, fig. 5 (misspelling); *Ommastrephes sloani pacificus* Sasaki, 1929; *Nototodarus philippinensis* Voss, 1962a (= *N. hawaiiensis* (Berry, 1912)); *Todarodes pacificus pacificus* Dunning, 1988a.

FAO Names: En – Japanese flying squid; **Fr** – Toutenon japonais; **Sp** – Pota japonesa.

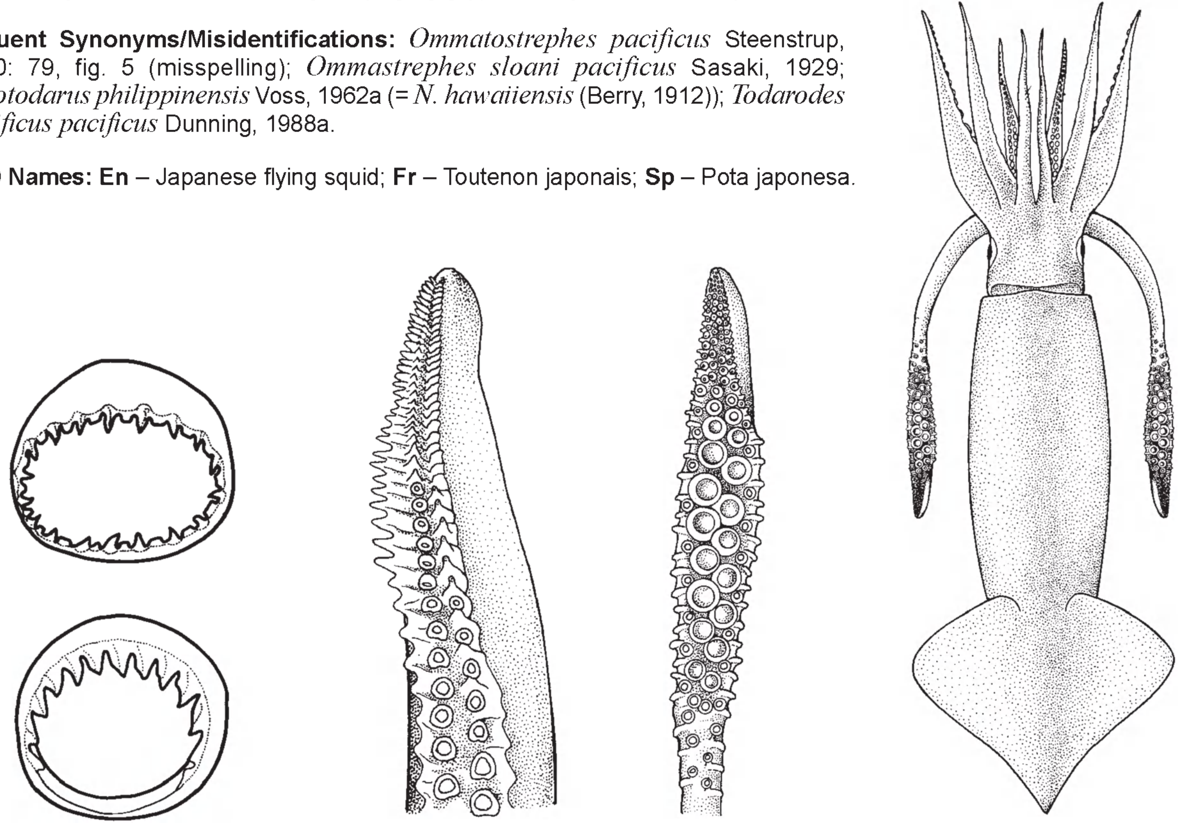

sucker hectocotylus tentacular club dorsal view

Fig. 313 ***Todarodes pacificus***

Diagnostic Features: Mantle cylindrical, slender, moderately muscular, with abrupt taper in the caudal area; **fins short, rhombic, sagittate; fin length 35 to 45% of mantle length**. Head large, only slightly narrower than mantle width. Mantle element of inverted T-shaped locking apparatus with straight ridge; no muscular fusion to funnel element of locking apparatus; funnel groove present with foveola but no side pockets. Arms subequal and long, the longest slightly less than half the mantle length; swimming keels well developed; largest arm sucker rings with 9 to 11 sharp, subequal, then somewhat flattened, teeth that gradually diminish in size to the smooth proximal rim; protective membranes and their supports (trabeculae) of uniform height, not higher than suckers. Only the **right ventral arm (IV) is hectocotylized in males**; right arm IV slightly thicker and shorter than left arm IV; 44 to 48 normal arm suckers present proximally; approximately 20 pairs of trabeculae present in the modified distal section that form an undulating spatula on the dorsal edge; the hectocotylized portion on the distal arm IV represents about 30% of the total arm length. Tentacular club long, expanded. Medial suckers on the tentacular club manus in 6 to 8 tetraserial, transverse rows; largest medial manus sucker rings with 16 to 28 moderately large, subequal, conical teeth interspersed with low, horny plates. **Light organs absent**. **Colour**: dorsal mantle brown with a distinct, deep blue-black stripe along the dorsal midline of the mantle that broadens on the dorsal surface of the head and extends anteriorly as thin stripes along the aboral edges of dorsal and dorsolateral arms (I and II). Rhynchoteuthion paralarvae have no ocular or visceral photophores; chromatophores on the ventral surface of the mantle are in 3 transverse rows of 4, with a single row of 2 at the posterior tip; a single small chromatophore lies at the posterior end of the dorsal mantle between the bases of the very small fins. The length of the proboscis usually is slightly longer than the longest arms, and the 8 minute suckers on the tip of the proboscis are nearly equal in size. The division of the proboscis begins at about 4 mm mantle length and the tentacles usually are separate 7 to 9 mm mantle length, occasionally up to 15 mm mantle length.

Size: The maximum mantle length of ***Todarodes pacificus*** is reported to be 500 mm, commonly 300 mm in temperate Japan, less than 200 mm off Hong Kong and in the South China Sea.

Geographical Distribution: This nerito-oceanic species is widespread in continental shelf and upper slope waters of the northwestern Pacific Ocean, from north of Japan into the Sea of Okhotsk at 52°N (reported to 60°N) and in the North Pacific to 49°N, eastward into the open Pacific to the region of about 45°N 170°E. The distribution continues southwestward through the western North Pacific, the Sea of Japan and the East China Sea to Hong Kong to around 18° to 19°N. Rarely, the species occurs in the eastern North Pacific to the northern coast of Canada, its northernmost record (Fig. 314).

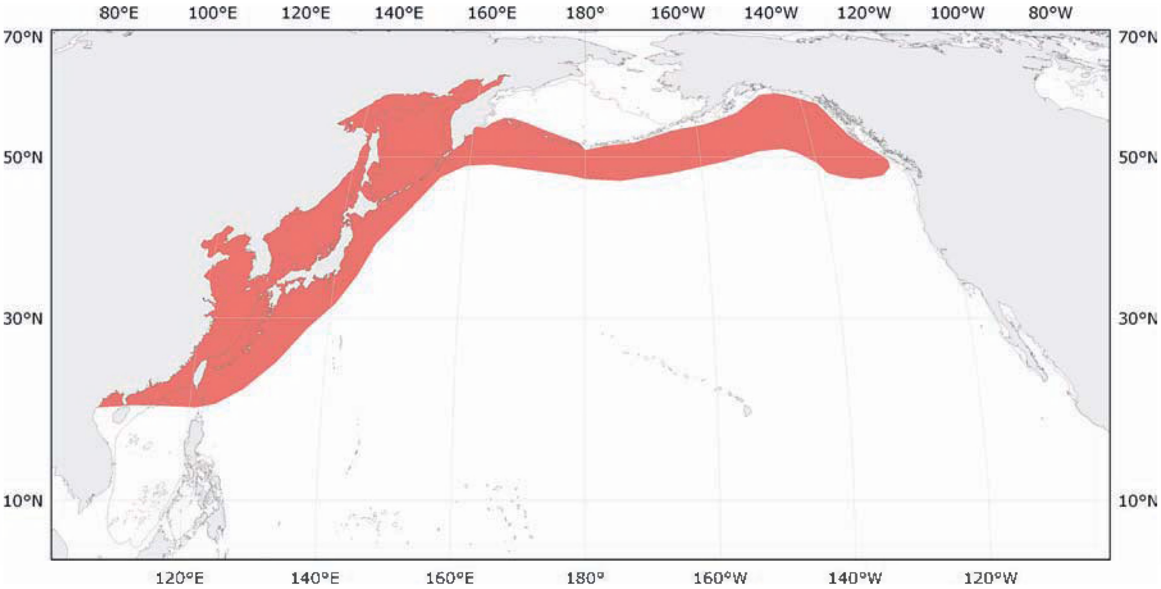


Fig. 314 ***Todarodes pacificus***

🟥 Known distribution

Habitat and Biology: ***Todarodes pacificus*** is a nerito-oceanic species in the low boreal to subtropical realm in the western North Pacific Ocean. It is a species characteristic of the high-velocity Western Boundary Current System with its nutrient-rich upwellings and vertical mixings in the continental shelf-slope zone. It inhabits the zoogeographic shelf provinces designated as north Japanese, south Japanese and Indo-Malayan. Populations are highly migratory and occur in large aggregations around oceanic fronts, seamounts and gyres where food is abundant. Three subpopulations, cohorts or stocks, defined by their spawning season, are recognized. The winter spawning population, with its centre of distribution north of 45°N, spawns from December to April, and the summer spawning population spawns from April to August. The autumn population usually is located south of 44°N and spawns from April to December.

The diel vertical distribution follows a typical nerito-oceanic species pattern. Both males and females inhabit the midwaters and near the bottom during the day, where they descend to or close to the bottom to feed on benthic and epibenthic prey at 150 to 200 m. At night the population ascends the water column to the upper 50 m and even to near the surface, principally to feed. While mating behaviour occurs above the bottom in midwater, the females descend to the bottom to rest, then to spawn on the continental shelf and upper slope at depths of 100 to 500 m. The sex ratio in exploited stocks is females greater than males, to a small degree. Sexual maturity in males usually occurs 4 to 6 months earlier than it does in females, so the males are considerably smaller at maturity than the females. Generally, females are slightly larger than the males.

Size differences occur between different geographical areas. The size at maturity for the summer spawning population is 230 to 270 mm mantle length, and that for the winter and autumn spawning populations is 240 to 330 mm mantle length. In immature females the GSI is <1.0% and *m* is <0.21; maturing females have a GSI of 1.0 to 2.6% and an *m* of 0.21 to 0.29, and mature females have a GSI of >2.6% and an *m* of >0.29. Oocyte development is asynchronous. Spermatophores are among the smallest in the Ommastrephidae, second only to those of ***Ornithoteuthis antillarum***.

In situ field observations and laboratory experiments have led to the proposal of a working hypothesis for the reproductive strategy of ***T. pacificus***. Eggs are laid into a gelatinous, balloon-shaped, nearly neutrally buoyant mass where they develop at 15 to 23°C for 4 to 9 and a half days. Hatchlings develop in water temperatures of 17° to 23°C. Spawning occurs on the bottom of the continental shelf and upper slope, where bottom trawls frequently collect exhausted, spent females at 100 to 500 m depth. ***Todarodes pacificus*** belongs to the offshore type (“type ***Illex***”) of reproductive strategy, which is evolutionarily less advanced than the oceanic strategy (“type ***Sthenoteuthis***”). Adult females of the offshore type have specific potential fecundity and growth rate characteristics that define their strategy as r-strategists: shelf-living species with very small eggs (0.70 to 0.95 mm); oocyte stock (fecundity) production is continuously asynchronous, where several egg masses are spawned intermittently over a period of time (also called pulse or batch spawning) and subsequent egg masses contain about the same number of eggs, rather than continuously diminish. These females continue to feed and grow during the intermittent spawning process, and they stop feeding only when an egg mass is being spawned; they do not undergo a gelatinous degeneration of muscular tissue, e.g. of mantle, arms, etc. The fecundity in the oviducts of pre-spawning females is between 320 000 and 470 000 ripe ova. Total fecundity, however, is much greater, because oocytes in all stages of development, from yolkless to mature stages, occur in the ovary of spawning females. Exhausted females with thin mantles have ovaries and oviducts that comprise 28% of the total body weight. Post-spawning, dead females have oviducts that still contain many ova, indicating that many more ova are produced than are laid. The reproductive strategy of male ***T. pacificus*** belongs to the “intermediate type” that is characterized by increased volumes of Needham’s sac and of the seminal reservoirs of spermatophores to insure the maximization of effective sperm production.

Mating and spawning have not been observed in nature, but a series of experiments and observations in the laboratory have been successful in defining these behaviours. Immature squid were captured in inshore waters off southern Hokkaido, Japan, and maintained in a large tank, where their maturation, mating and spawning were recorded. Males matured earlier than females, and they began mating with immature females about 2 to 3 weeks before the females matured, with ripe ova in their oviducts; after mating, the females spawned, then died. To mate, the male approaches the female rapidly from below and behind, grasps her around the head and mantle with his arms and tentacles; the hectocotylus (right arm IV) picks up a bundle of spermatophores as they are passed from the funnel opening, then quickly and firmly inserts them into the buccal membrane of the female. The spermatophores penetrate into the membrane tissue, now free of the ejaculatory apparatus, and the resulting sperm bulbs, or spermatangia, transfer spermatozoa into the seminal receptacles that encircle the buccal membrane of the female. Spermatozoa remain viable for several weeks until spawning takes place. In captive experiments females stop feeding and move to the bottom of the tank to rest about 2 days before spawning. The female supports herself on the bottom with the tips of the second and third pairs of arms, the tentacles and the posterior tip of the mantle. Once the female is at rest, the chromatophores begin to flash rapidly over the entire surface of her body, a signal that spawning is about to occur. While eggs have not been found in the natural habitat, eggs taken from the ripe ovary measure 0.78 mm in greatest diameter and 0.75 mm in smallest diameter, and up to 0.90–0.92 mm by 0.77–0.80 mm. Eggs are laid in a large gelatinous ball, up to at least 800 mm in diameter.

Just prior to spawning, the arms become flattened and lowered for about 1 minute, then they open gradually to envelop the small egg mass that is extruded through the funnel. The egg mass gradually swells into an enlarged mass, similar to a balloon being inflated, nearly neutrally buoyant, and requires about 7 minutes to be completed and then to be released and float near the surface. The external surface of the egg mass is formed by a thin layer of gelatinous, water-soluable mucosubstance, secreted by the nidamental glands, while the interior is another type of jelly with fibrils, an insoluable fraction of mucosubstance, presumably secreted by the nidamental glands (or the oviducal glands). The external layer serves as a protective shield that prevents crustaceans, protozoans and bacteria from invading and infecting the interior and the eggs and embryos. The mass contains about 200 000 eggs, each about 0.9 mm in diameter; greater than 90% of the eggs are fertilized. The chorion around each egg swells its diameter to 1.9 to 2.3 mm.

Paralarvae hatch in 4 to 6 days at 18° to 19°C and are immediately active, many swimming toward the surface. Once hatching is complete, the egg mass deteriorates. Hatchlings, at 0.95 mm mantle length, feed for about 7 days on the internal yolk until it is resorbed, then they begin to feed on their own, at 1.25 mm mantle length. The vertical distribution of hatchlings and paralarvae is associated with mantle length (age) and a general ontogenetic descent occurs. Most hatchlings (in the Sea of Japan near Oki Island) of less than 1.0 mm mantle length occur at 0 to 25 m; smallest paralarvae, 1 to 2 mm mantle length are concentrated at 0 to 50 m (90%); paralarvae of 2 to 3 mm mantle length (71%) concentrate at 25 to 75 m; and those paralarvae from >3 to 6.7 mm mantle length also occur principally at 25 to 75 m. The temperature range in the zone of capture is 15° to 22.3°C, conditions considered ideal for paralarval survival and development; the pychnocline occurs below 50 m, slightly deeper than the majority of paralarval captures. Largest catches are made in the frontal or mixing zone of cool water from the northwest and warm water in the Oki Strait.

Young juveniles are transported by oceanic currents from their hatching grounds to their feeding grounds. Their early distribution includes most of the waters that surround the Japanese Islands, except off the Pacific coast of northeastern Honshu and Hokkaido and the northernmost region of the Sea of Japan. The geographical and temporal distributions can vary significantly depending on the seasonal brood and the local subpopulation.

Paralarvae and juveniles of the autumn spawning population (the fishery for adults is mainly in the offshore waters in the Sea of Japan) are spawned principally in the area from the eastern East China Sea to the western sector of the Sea of Japan. Autumn-spawned juveniles are densely distributed during October through December, with peak abundance in November, along the west coast of Kyushu. Hatchlings and juveniles of the winter-spawned population (the fishery for adults occurs principally to the south of Kyushu) occur in abundance during November through April in waters to the south of Kyushu. Winter population juveniles are restricted to water temperatures above 18°C and over 19.20 parts per thousand chlorinity, with peak abundance at 20° to 22°C and 19.25 to 19.35 ppt chlorinity.

During the paralarval and juvenile periods, mortality is about 94%, caused by starvation, transport into unfavourable environmental conditions and predation, principally by scombroid fishes and later by tunas. The abundance of juveniles can predict the eventual stock size of adults. The values of strontium to calcium ratios (Sr:Ca) in the statoliths of ***T. pacificus*** can reveal the different spawning grounds and migration routes of the different populations of squid. Age data from statoliths analysis indicate that growth in ***T. pacificus*** can be represented by a sigmoid curve. The first 4 months after hatching are a relatively gentle slope, followed by a steep growth rate for the next 3 months and finally by a more gentle curve, to nearly flat, during the final 5 months of life. Growth rates can vary depending on the seasonal population and local environmental conditions, particularly the temperature regime. From hatching to 15 mm mantle length takes 0.5 months, to 120 mm mantle length requires 3 months, to 190 mm mantle length 6 months, and to 260 mm mantle length, about the maximum size, 12 months.

Recent research predicts the short- and long-term fluctuations in stock size by factors of wind stress, air temperature, sea surface temperature (SST), and mixed layer depth (MLD) during the spawning period (weak winds, warm air and SST positively affect recruitment and stock size). The spawning grounds are mapped with SST (19° to 23°C) over water depths of 100 to 500 m and the combination of factors determines stock success and abundance.

Years of poor recruitment correspond closely to years of lower than normal SST in the winter and spring, and cold winters influenced by strong northwesterly winds also are associated with lower recruitment levels. Significant changes in aspects of growth, size and maturity occur between the periods of high stock levels versus periods of low stock level. The mantle lengths of squid taken during the low stock period were smaller during June to early August than those taken during the high population period, but they were larger from mid-September to December. The mean proportions of mature males caught in low stock years sharply increased in mid-August and were consistently higher than the levels during high stock years, and gradually increased from mid-September onwards. Also, the squid matured earlier in low stock years than in high stock years. ***Todarodes pacificus*** life span is about 1 year.

Predators of ***T. pacificus*** are numerous, including many species of marine mammal such as the short-finned pilot whale (*Globicephala macrorhynchus*), other toothed whales, baleen whales, northern fur seal, rays, dolphin fish (*Coryphaena hippurus*), chub mackerel, jack mackerel (*Tracurus japaonicus*), skipjack tuna (*Katsuwonus pelamis*).

The prey of subadult and adult ***T. pacificus*** varies, depending on age and locality, as they tend to be opportunistic feeders, including on fishes and cephalopods when they are available. Juveniles and subadults feed mainly on planktonic crustaceans, notably euphausids (e.g. *Thermisto* sp.), gastropod larvae, chaetognaths and nectonic fishes, such as Myctophidae, sardines, anchovies (*Engraulis japonica*) and other small species and squids, including cannibalism. Adults prey mostly on nectonic species. When subadults and adults feed along the shelf-slope interface, they prey heavily on myctophid fishes. The feeding rate is greatest at around 18.00 to 20.00 hours, then gradually decreases towards dawn. Adults feed more actively during the daytime near the bottom than they do at night near the surface.

Niche separation occurs when the distributions of 2 ommastrephid species overlap; for example, ***T. pacificus*** and ***Ommastrephes bartramii*** are sympatric in some areas of their distributions, but in these areas ***T. pacificus*** preys on crustaceans, while ***O. bartramii*** feeds on fishes.

Experiments on the visual attack system of ***T. pacificus*** showed that attacks on slowly-introduced bait were made by the arms, not the tentacles; this conforms to observations on ***Loligo***, ***Illex*** and ***Sepia***. Similarly, slower moving hauling speeds on jigging machines catch more squid because the squid attack and are hooked by the arms, not the more fragile tentacles. Other behavioural experiments on visual discrimination revealed that ***T. pacificus*** can not discriminate between blue, green or white light. The positive cues for correct responses are intensity of the light, not the colour. This has important consequences for the fishery in eliminating the practice/expense of manufacturing and using coloured-lighted jigs, which are no more effective than white-lighted jigs.

Interest to Fisheries: For more than a century ***T. pacificus*** has supported a major fishery that nearly always has been in the top 2 or 3 in total annual landings of cephalopods in the world. It is the largest single cephalopod fishery resource over time on record. Fluctuations in landings are attributed to fluctuations in optimal oceanographic conditions as well as to over fishing. Estimates of instantaneous biomass, fishery production and potential catches are informative, both from the current levels as well as from anticipated future production. The estimated instantaneous biomass for ***T. pacificus*** is 2 to 5 million tonnes.

The fishery for ***T. pacificus*** has been conducted in Japanese waters for well over a century, and catch statistics have been compiled since prior to 1910. Since that time, fishery biology studies have been conducted, based on catch record analyses and exploratory fishing. The first comprehensive study on the life history of ***T. pacificus*** with an interest to the fishery was published in 1921. The earlier fishing grounds before the 1940s were centred in the neritic waters along the coasts of southern Hokkaido and northeastern Honshu. Following the second world war the fishery expanded dramatically with the development of technology and gear, the increase in the size of the jigging boats, and the expansion of the fishing grounds. So important were the general fisheries, including the squid fisheries, that at least 8 regional fisheries research laboratories were established in 1948. The fishery access to major concentrations of the squid occurs during the periods of their migrations to, at, and from the feeding grounds. Catches of ***T. pacificus*** climbed to a maximum of 768 000 tonnes in 1968. Even though new stocks and grounds have been discovered and developed since then, the catches remained in the 300 000 tonne range for many years. During the 1980s the annual catch averaged 267 000 tonnes. Then in the 1990s, with significantly increased effort and improved oceanographic conditions (a shift from a cool to a warm regime), the annual catches began to rise until 1996 when another peak catch was achieved (716 000 tonnes). Catches during the 1990s fluctuated between 280 000 tonnes to the peak in 1996, then dropped to 379 000 in 1998. Since then, through 2007, catches have averaged around 400 000 to 500 000 tonnes.

While purse seine and bottom trawl fisheries are conducted, the major portion of the fishery is conducted from jigging vessels using lights and continuous line jigging machines. Both the size and power of the boats, the intensity of the lights and the efficiency of the machines have increased drastically in recent years. With these increases, the costs of conducting the fishery have risen sharply. The concentration of vessels on the fishing grounds and the intensity of their lights are easily seen from satellites in space, a phenomenon that enables real-time knowledge of the spatial and temporal location of the fleet. This remote sensing technology also allows the repositioning of the fleet into water masses that influence the accumulation of the squid. The biomass of aggregations of squid on the continental shelf edge and the upper slope, as well as on any other potential fishing grounds, can be assessed directly by utilization of the echo integration method following rationalization with normalized target strength measurements and purse seine CPUE data. The fishing concentrations take place in the warm core eddies and streamers that spin off from the Kuroshio Current system at its confluence with the Oyashio Current off the east coast of Japan, as well as in mixed waters of the warm Tsushima Current and cold Liman Current in the Sea of Japan. Warm core rings can be up to 200 km in diameter and have a life span of a few months to 1 to 2 years. The squid fisheries always develop in the warm rings, never in the cold rings, and once started, productive jigging in the ring can last up to 2 months. The large autumn spawning population supports the major offshore fishery in the Sea of Japan. Many years of accumulated data from paralarval surveys show that when paralarval distributions are expanded over a broader geographic range, the resulting adult stock is high; conversely, a more restricted range of paralarval distribution results in a low population size in the adults from that brood. Thus, stock size can be predicted based on the extent of the distribution of the paralarvae that constitutes that year class.

Efforts to employ stock assessment models for management purposes have produced poor or inconsistent results. Clearly, when the spawning stock in any population gets too low, recruitment will be adversely affected. Most efforts at fishery management concentrate on limitation or control of the period and scale of fishing effort in an effort to be consistent with sustainable catch levels. However, in the case of the ***T. pacificus*** fishery, the prevention of fishing disputes and maintenance of catch prices also are objectives. Prior to 1998 fishing effort control was through vessel licensing. Then the Japanese government introduced a TAC (total allowable catch) system to manage the fishery based on an estimation of the allowable biological catch (ABC). Each of the 2 main stocks (spawning groups; Japan Sea, Pacific) is located in a separate area and fished at a different season (autumn, winter, respectively). Pre-season scientific surveys assess the distribution of the stocks, the number of recruits and specific biological parameters. Catches from previous years are used to calculate the allowable biological catch for the current year.

Squid are eaten in many different preparations as fresh, frozen, dried, fermented, etc. products. ***Todarodes pacificus*** often is eaten raw by humans as “sashimi” and “sushi”, and sometimes the squid are infected with helminth parasites that are pathogenic to humans. These parasites are 3 species of larval anisakid nematodes (*Anisakis simplex, A. physeteris and Pseudoterranova decipiens*) and 1 species of larval trypanorhynch cestode (*Nybelinia surmenicola*). Humans are not final or definitive hosts of these parasites, but they are considered as accidental hosts. In addition to the importance of squid as human food, it is important as bait for many species of fishes. Researchers have developed an artificial bait produced from the liver (digestive gland) retrieved from the waste products of processed squid. The artificial bait has the same hooking ratio as natural squid, but the bycatch of the artificial bait is much reduced.

Local Names: CHINA: Yat boon yau yue (Japanese softfish); JAPAN: Akaika, Ganzeki, Matsuika, Mugiika, Surumeika, Tonkyu.

Remarks: Despite clear differences in some morphological characters, genetic analyses indicate that the 3 seasonal groups are separate ecological populations that maintain genetic exchange (Kidokoro and Mori, 2004) Also, genetic analyses show that 2 major genetically distinct successive breeding groups exist in the Sea of Japan. One group consists of the squid from the autumn spawning aggregations, while the second group contains squid from the winter, summer and spring spawning cohorts (Kumagai *et al*., 2006). Analysis of 13 trace elements in squid tissues reveals that concentrations in ***T. pacificus*** were within international standards for 9 elements. In addition, Co, Zn, Ag and Cd (cobalt, zinc. silver, cadmium) were concentrated in the liver (digestive gland) at high levels (Oikawa *et al*., 2003). Mitochondrial DNA sequencing suggests that ***Nototodarus sloanii*** and ***N. gouldi*** are more closely related to ***T. pacificus*** than to ***N. hawaiiensis*** (Wakabayashi *et al*., 2006). The most effective preservatives for fixing and maintaining paralarval chromatophore patterns and mantle size are 5% hexamine-buffered formalin and 99% ethanol.

Literature: Roper *et al.* (1984), Okutani *et al.* (1993), Nigmatullin and Laptikhovsky (1999), Kidokoro and Mori (2004), Kumagai *et al.* (2006), Kishi *et al.* (2007), Sakurai and Kishi (2007).

Todarodes pusillus Dunning, 1988

Fig. 315

Todarodes pusillus Dunning, 1988b, *Memoirs of the Museum of Victoria*, 49(1):149–157, 4 figs. [149]. [Type locality: 13°48'S, 124°19'E, Timor Sea, northeast Indian Ocean].

Frequent Synonyms: *Todarodes pacificus pusillus* Dunning, 1988b.

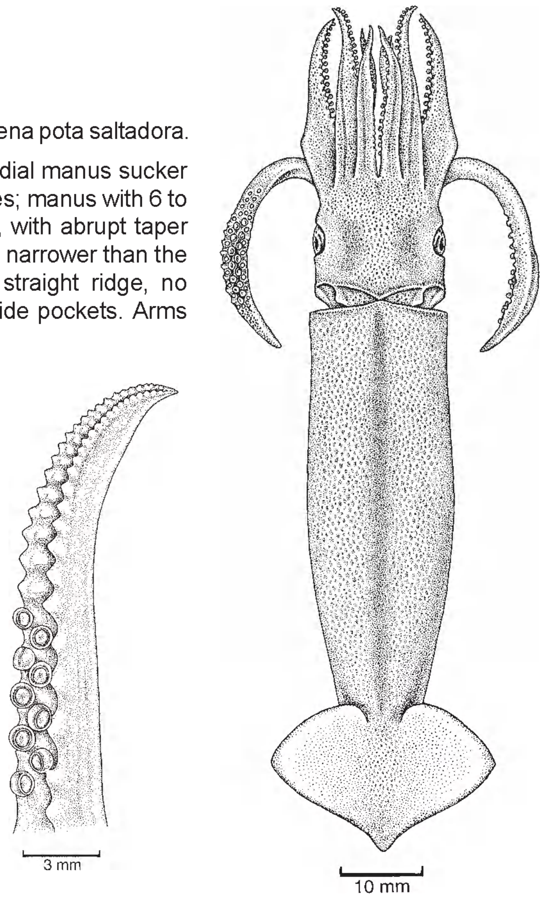
Misidentifications: None.

FAO Names: En – Little flying squid; **Fr** – Petit encornet volant; **Sp** – Pequena pota saltadora.

Diagnostic Features: Fin length 25 to 31% of mantle length; largest medial manus sucker rings with 16 to 18 long, pointed teeth interspersed with low chitinous plates; manus with 6 to 8 quadriserial sucker rows. The mantle is slender, moderately muscular, with abrupt taper posteriorly ventral to the fins; fins very short, small, rhombic; head slightly narrower than the mantle opening; mantle element of T-shaped locking apparatus with straight ridge, no muscular fusion to funnel element; funnel groove with foveola, but no side pockets. Arms subequal and large, the longest slightly less than 50% of the mantle length, with well-developed swimming keels. Largest arm sucker rings with 9 to 11 subequal, somewhat flattened teeth. Right ventral arm (IV) in males hectocotylized, slightly shorter and thicker than left ventral arm IV; 11 to 13 normal proximal arm suckers; about 20 pairs of trabeculae present on modified distal section that form an undulating spatula on the dorsal edge; hectocotylized portion occupies about 45 to 57% of the arm length. Arm I has 12 to 17 suckers. **Colour**: dorsal mantle dark to brown with a distinct blue-black stripe along the dorsal mantle midline that broadens on the head, then extends anteriorly along the dorsal surfaces of arms I and II.

Size: A very small-sized species: the largest female reported is 74 mm mantle length and the largest male is 68 mm mantle length. Maximum size certainly less than 100 mm mantle length.

Geographical Distribution: This species inhabits the continental shelf and upper continental slope of northern Australia, from the Timor Sea between 8°53'S and 19°31'S on the Northwest Shelf, and off the east coast of Australia, from the Torres Strait to off Brisbane. It also is reported in a narrow band from the Timor Sea through Indonesian waters to Mindanao in the southern Philippines (Fig. 316).



hectocotylus **dorsal view**

Fig. 315 ***Todarodes pusillus***

Habitat and Biology: To date, all recorded specimens were captured in demersal trawls at water depths between 78 and 357 m. The temperature at 50 m in the areas of capture is in excess of 23°C and surface temperatures reach 29°C in summertime. Up to 54 individuals have been caught in a single trawl tow, which suggests that this species is a schooling form. All females larger than 60 mm mantle length are sexually mature, with eggs in the oviducts; all males larger than 50 mm mantle length carried fully formed spermatophores.

Interest to Fisheries: None at present. Currently this species is so poorly known that it is difficult to predict its potential value in a fishery. While it is very small, with a maximum mantle length of perhaps 80 mm, its flesh seems to be a desirable consistency, comparable to juveniles of other todarodine species. If large concentrations occur, this species might support a limited fishery.

Local Names: None available.

Literature: Dunning (1988b), Dunning and Wormuth (1998), Okutani (2005).

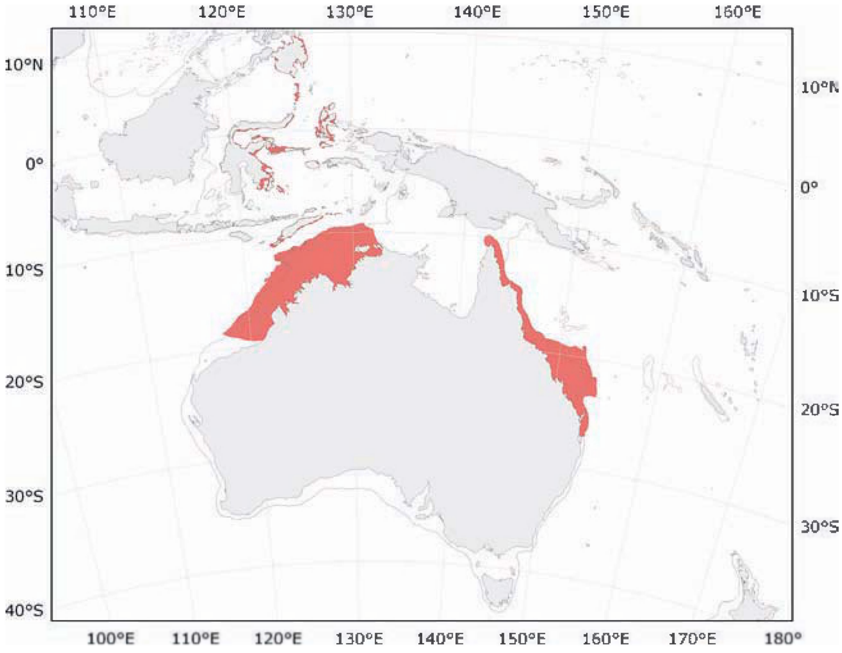


Fig. 316 ***Todarodes pusillus***

🟥 Known distribution

Martialia Rochebrune and Mabille, 1889

Martialia Rochebrune and Mabille, 1889, *Mission Scientifique du Cap Horn, 1882–1883*, 6(2) (*Zoologie*): H1–H143. [8].

Type Species: *Martialia hyadesi* Rochebrune and Mabille, 1889.

Diagnostic Features: Mantle robust, tapers to a somewhat elongated tail. Funnel groove with **foveola possesses 7 longitudinal folds**; **no side pockets**. **Photophores absent** throughout life cycle. T**entacular clubs occupy almost entire length of tentacles**; **not expanded**. **Carpal-locking apparatus absent** on tentacular club/stalk. Dactylus of tentacular club with 4 rows of small suckers. Largest medial suckers on manus with 15 relatively large, sharp teeth (1 conical tooth usually larger than others) alternate with 15 small flat plates or blunt teeth. Protective membranes of arms and tentacular clubs low, poorly developed; **trabeculae strongly developed, prominent, like cirri**. Arm suckers (stalks) attached at bases of trabeculae. Arm suckers proportionally small; rings with 5 pointed teeth in distal half, central 1 conical, lateral ones become truncated; proximal half of ring smooth. **Right (rarely left) ventral arm (IV) hectocotylized by papillary type**; trabeculae on distal one-third of arm modified as rounded flaps on ventral row; flaps reduced then absent distally on dorsal row. Fins rhomboidal and elongated posteriorly to small tail; fin length 38 to 46% and fin width 54 to 66% of mantle length; fin angle 45° to 55°. The cone flags of the gladius are narrow, with indistinct radial creases in anterior part; greatest width about 50% rachis width. Marginal rigidity ribs of rachis simple; axial rigidity rib of rachis round-rectangular in cross-section. Lateral plates of gladius adhere to dorsal surface of rachis proximally. Distal ends of lateral plates free, form 2 longitudinal lobes above rachis; stem short, anchor-like in cross-section, width greater than thickness. Cone narrow, laterally compressed. Rostrum small, dorsoventrally compressed, curved ventrally. Alveola thick, with ribbed surface. Spermatozoa with 1 flagellum.

Remarks: The genus is monotypic.

Martialia hyadesi Rochebrune and Mabille, 1889

Fig. 317

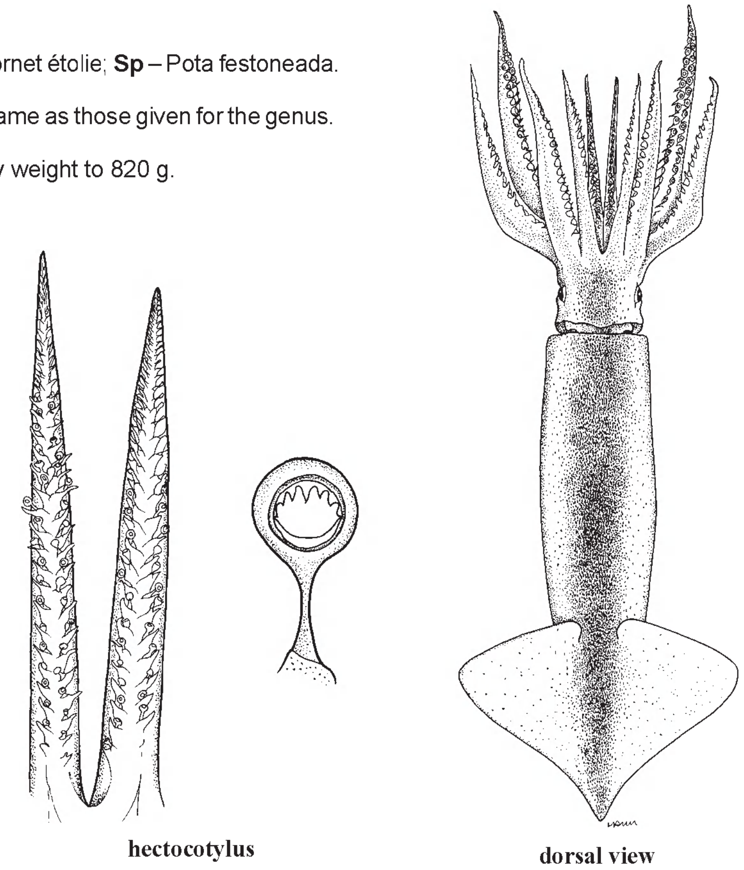
Martialia hyadesi Rochebrune and Mabille, 1889, *Mission Scientifique du Cap Horn, 1882–1883*, 6(2) (*Zoologie*): H1–H143. [H9]. [Type locality: Orange Bay (Isla Navarino), Chile, eastern South Pacific Ocean].

Frequent Synonyms: None.

FAO Names: En – Sevenstar flying squid; **Fr** – Encornet étolie; **Sp** – Pota festoneada.

Diagnostic Features: Specific characters are the same as those given for the genus.

Size: Maximum mantle length to 400 mm and body weight to 820 g.


hectocotylus

dorsal view

Fig. 317 *Martialia hyadesi*

Geographical Distribution: Circumglobal in cool temperate waters of the Southern Ocean; a nerito-oceanic slope species associated with high velocity cool waters of the Antarctic Circumpolar Current, especially along the Antarctic Polar Frontal Zone; southern Patagonian Shelf edge, Scotia Sea, New Zealand waters south of the subtropical convergence zone; sub- Antarctic islands (Fig. 318).

Habitat and Biology: Adults are oceanic-neritic in slope waters, seldom penetrating into waters where bottom depths are less than 200 m. ***Martialia hyadesi*** is classified as a Notalian-Antarctic species, endemic to the circumpolar zone bounded roughly by the subtropical southern boundary and the Antarctic Polar Front. Small juveniles, less than 10 mm mantle length, have been found in southern New Zealand waters south of the Subtropical Convergence, indicating spawning in the region of the Auckland Island Shelf. Paralarvae and juveniles occur in the Falklands Islands Shelf water mass in spring. The very distinctive tentacular club is evident on juveniles of 19 mm mantle length, while the distinctive arm trabeculae first appear at 40 to 50 mm mantle length. The size of ripe eggs is 0.7 to 2.4 mm and the potential fecundity of 20 000 to 2.5 million. Mature males of 233 to 260 mm have spermatophores 25 mm long with a fecundity of 500. Growth in ***M. hyadesi*** is characterized by slow juvenile growth (less than 100 mm mantle length), rapid growth in immature squids, and a sharp decrease in growth rate during maturation. The species matures later than other temperate ommastrephids (greater than 270 days), but final maturation is quite rapid, 2 to 3 months. Statolith analysis indicates an age of 12 to 13 months, but other life cycle data suggest a life span that approaches 2 years. In spite of its oceanic habitat, occasionally this species will undergo mass strandings, as occurred in the Falkland Islands in 1997, when more that 3 000 immature ***M. hyadesi*** (220 to 270 mm mantle length) forcibly drove ashore; 61% were females. Such strandings are believed to be related to temporal shifts in frontal zones that affect behaviour, range and environment of foraging squids. Parasites include a coccidian that occurs in 96.5% of the digestive tracts of the host specimens.

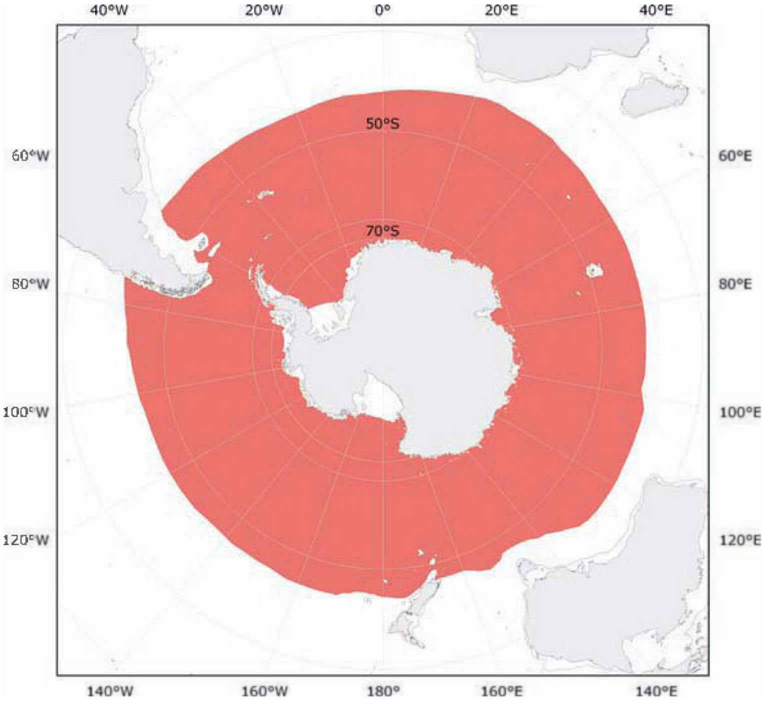


Fig. 318 ***Martialia hyadesi***

🟥 Known distribution

Martialia hyadesi is an active predator with a broad range of prey that includes the hyperiid amphopods, especially krill components (mainly *Euphausia superba*, occasionally *Thermisto gaudichaudi*), mesopelagic fishes (up to 90% myctophids, mainly lanternfishes (*Krefftichthys anderssoni* and *Electrona carlsbergi*) and squids, mainly cannibalism on small juveniles and immatures (20 to 102 mm mantle length). ***Martialia hyadesi*** is an extremely important prey species for many species of sub-Antarctic vertebrates; it is the most important single prey species for juvenile and adult southern elephant seals (*Mirounga leonina*) and it is preyed upon by the Antarctic fur seal (*Arctocephalus gazella*) and the sub-Antarctic fur seal (*Arctocephalus tropicalis*), the Patagonian toothfish (*Dissostichus eleginoides*) and the slender tuna (*Allothunnus fallai*). ***Martailia hyadesi*** is an important prey for the false killer whales (*Pseudorca crassidens*) and it is important to dominant (up to 89% biomass) in the diets of both adults and chicks of numerous oceanic birds (e.g. grey-headed albatross, black-browed albatross, light-mantled albatross, wandering albatross, white-chinned petrel) and the king penguins (*Aptenodytes patagonicus*).

Interest to Fisheries: While the dominant cephalopod fishery in the southwestern South Atlantic Ocean has been conducted on ***Illex argentinus***, for several decades, accumulated data on and assessment of the circumantarctic population of ***M. hyadesi*** indicate a very significant biomass of this species, with high potential for supporting a managed fishery. Commercial catches generally occur as by catch in the ***I. argentinus*** fishery in the southwestern South Atlantic Ocean, on the edge of the southern Patagonian Shelf, and catches vary significantly and do not reflect actual population abundance. This is demonstrated by the fact that the estimated annual consumption of this species by known predators in the Scotia Sea is higher than total catches values. An estimation of the instantaneous biomass of ***M. hyadesi*** is 1 to 3 million tonnes. Acoustical survey techniques offer potential for more accurately assessing stock abundance within proscribed areas. An assessment of stocks in the waters of South Georgia, south of the Antarctic Polar Front, in the austral winter, suggested a potential jig fishery on the stock of feeding ***M. hyadesi*** (1-year-old mature males, 220 mm to 350 mm mantle length, and the same aged, but immature, females, 212 mm to 370 mm mantle length). Exploratory fishing and predator catch analysis revealed the presence of significant stocks of cephalopods along the Antarctic Polar Frontal Zone in the Scotia Sea. The largest and most abundant species was ***M. hyadesi*** and mesoscale features suggest this is an area of foraging locations, thus accessible for fishery development. Variations in population structure, distribution and abundance correspond to variations in inter-annual oceanographic conditions in the West Wind Drift; such variations will affect the location, timing and productivity of fishing efforts.

Local Names: None available.

Remarks: An analysis of systematics and phylogenetic relationships of ommastrephid squids indicates that ***M. hyadesi*** is in the more primitive range of evolutionary development, more advanced than Illicinae and Todarodinae, but less advanced than the Ommastrephinae (Nigmatullin, 1992 [1991]). Genetic studies indicate considerable genetic differentiation across the circum-antarctic range of the species, suggesting the possibility that sibling or cryptic congeneric entities might exist (Brierley, *et al*., 1993).

Literature: Rodhouse (1992 [1991]), Nigmatullin (1992 [1991]), Brierley *et al.* (1993), Gonzalez *et al.* (1997b), Lipinski *et al.* (1998b), Wormuth (1998), Anderson and Rodhouse (2001), Nigmatullin (2002a), Nesis (2003), Okutani (2005).

Nototodarus Pfeffer, 1912

Nototodarus Pfeffer, 1912, *Ergebnisse der Plankton Expedition der Humboldt-Stiftung*, 2: 1–815 + Atlas. [434].

Type Species: *Nototodarus sloanii* (Gray, 1849)

Diagnostic Features: The **funnel groove has foveola, but it lacks side pockets**. **Photophores** are **absent** in all life stages. The **carpal-locking apparatus** is **absent** on the tentacular stalk. The dactylus of the tentacular club has 4 rows of small suckers. The largest medial suckers on the manus of the club has teeth of equal size, or 1 sharply pointed tooth larger than the other teeth (***N. hawaiiensis***). The protective membranes of the arms and tentacles are normally developed, without exposed trabeculae. **Both ventral arms are hectocotylized by the aberrant type**, with the **right arm modified completely** and **the left arm partially**; at the distal part of the right arm are papillae and in the proximal part of both arms is a very unusual sculptured structure of hyalineous integuments. The fins are rhomboidal, slightly attenuate posteriorly; fin length varies between 36 and 50% and fin width between 50 and 61% of mantle length; fin angle is 40° to 57°. The cone flags of the gladius are relatively narrow, with feeble radial creases in the anterior part. The greatest width of the cone flags ranges between 58 and 65% of that of the rachis. Marginal rigidity ribs of the rachis are simple; axial rigidity rib of the rachis is wide, rounded-rectangular in cross-section. Lateral plates of the gladius adhere to the dorsal surface of the rachis by their proximal parts. Distal parts of the lateral plates are free, forming 2 longitudinal flaps above the rachis. The stem is very short, anchor-like in cross-section. The width of the stem is approximately equal to or less than its thickness. The cone is short, narrow; it is flattened laterally. A rostrum is absent. The alveola is thin, smooth; it has broad wing-like longitudinal folds on the dorsal side. Spermatozoa with 1 flagellum.

Size: Medium-sized squid; maximum recorded mantle length about 420 mm.

Geographical Distribution: Distributed in tropical, subtropical and temperate waters of the Indian and Pacific oceans.

Habitat and Biology: ***Nototodarus*** species form a significant part of the diet of pygmy sperm whales (*Kogia breviceps*) stranded on New Zealand shores. Long-finned pilot whales in New Zealand feed exclusively on cephalopods, of which ***Nototodarus*** species are predominant. The diet of orange roughy (*Hoplostethus atlanticus*) has changed over time with a progressive decline in the occurrence of squid, principally ***Nototodarus*** species. ***Nototodarus*** species comprise major populations in the shelf-break zone where enriched food supplies are created by eastern and western boundary currents and their associated mesoscale and downwelling features, such as upwelling cells and eddies. Young of the species congregate seasonally over the continental shelf in large schools, feeding on the rich food supplies to foster growth and maturation.

Remarks: An analysis of morphological characters among ommastrephid species, in order to determine morphological evolution and phylogenetic relationships, indicated that ***Nototodarus*** (Todorodinae) is more advanced than the most primitive group, the Illicinae, but it is more primitive than the remaining genera in the Ommastrephinae (Nigmatullin, 1992 [1991]).

The number of specific and subspecific taxa had been in a confused state for decades, with several combinations of specific and subspecific entities in use. Finally Dunning and Förch (1998) concluded that the basic specific composition within ***Nototodarus*** is ***Nototodarus sloanii*** (Gray, 1849), ***N. gouldi*** (McCoy, 1888) and ***N. hawaiiensis*** (Berry, 1912) and reviewed the systematics, distribution and biology of the 3 species. Table XX provides a comparison of characters for these 3 species.

Recent mitochondrial DNA analyses indicate that ***Nototodarus gouldi*** and ***N. sloani*** are sister species and that they are more closely related to ***Todarodes pacificus*** than to ***Nototodarus hawaiiensis***. These results suggest that the form of the hectocotylus, currently a major morphological distinguishing character in ***Nototodarus***, may not be a reliable character (Wakabayashi *et al.* 2006).

Literature: Dunning and Förch (1998), Wakabayashi *et al.* (2006).

Table 13

Comparison of species characters in *Nototodarus* (see Roper, 1983, for explanation of indices) (from Dunning and Förch, 1998)

Character	*Nototodarus sloanii*[1/]	*Nototodarus gouldi*[1/]	*Nototodarus hawaiiensis*[2/]
Arms I sucker count	>60	28–50	19–28
Head-length index	<20	16–20	19–31
Head-width index	<24	18–22	21–30
Arms I sucker index	<1.5	<1.5	1.5–2.3
Tentacle-sucker index	<2.5	<3.0	2.8–3.7
Fin-length index	>42	>40	35–43
Arm and tentacular sucker teeth	~equal	~equal	1 tooth much larger
Teeth on largest medial manus sucker	12–15	12–15	14–18
Quadriserial rows of manus	12–13	12–13	10–11
Skin	smooth	smooth	smooth
Hectocotylus			
Proximal-sucker bases enlarged as cushions	~10 pairs	~5–6 pairs	~4–5 pairs
Normal sucker rows (right arm)	~5	~5	1–6
Ventral protective membrane (right arm)	present only on distal 1/5 of arm	wide, with attenuated supports to arm tip	wide, with attenuated supports to arm tip
Ventral-sucker bases (right arm)	rapidily diminish in height distally	rapidly diminish in height distally	modified as thin papillae
Dorsal-sucker bases modifications (right arm)	distally flattened papillae extend to arm tip	broad-based papillae exend to arm tip	broad-based papillae extend to arm tip, equal in length to ventral papillae

[1/] Syntheses of values from Kawakami and Okutani (1981) and Dunning (1988c).

[2/] Syntheses of values from Wormuth (1976) and Dunning (1988c).

Nototodarus sloanii (Gray, 1849)

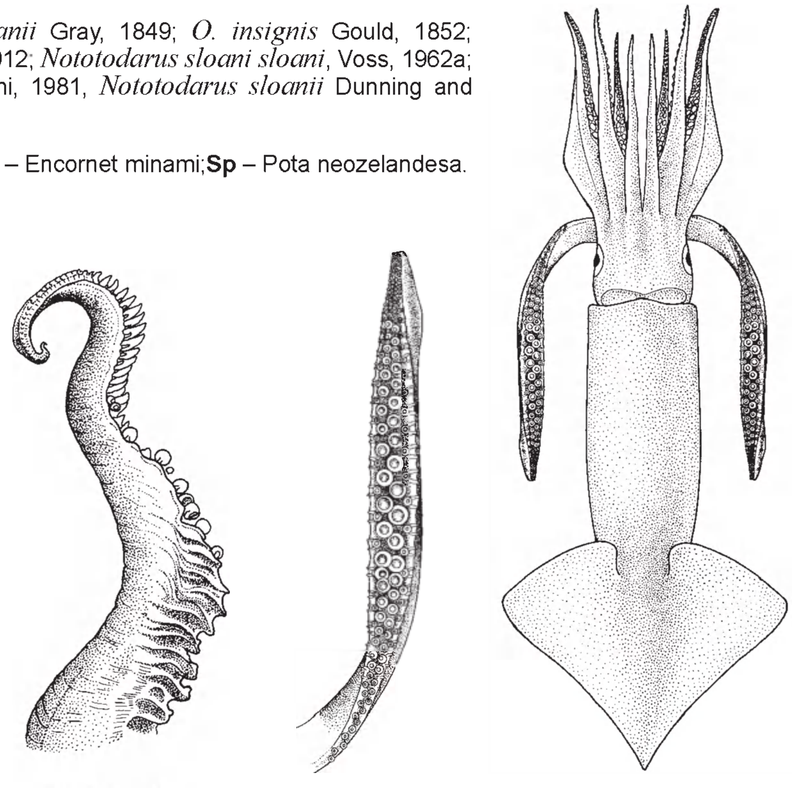
Fig. 319

Ommastrephes sloanii Gray, 1849, *Catalogue of the Mollusca in the British Museum, Part I. Cephalopoda artepedia.* 164 p. [61]. [Type locality: Waitemata Harbour, New Zealand, Tasman Sea, western South Pacific Ocean].

Frequent Synonyms: *Ommastrephes sloanii* Gray, 1849; *O. insignis* Gould, 1852; *Ommatostrephes sloanei sloanei*, Pfeffer, 1912; *Nototodarus sloani sloani*, Voss, 1962a; *Nototodarus sloani*, Kawakami and Okutani, 1981, *Nototodarus sloanii* Dunning and Förch, 1998.

FAO Names: En – Wellington flying squid; **Fr** – Encornet minami;**Sp** – Pota neozelandesa.

Diagnostic Features: Arms I have **more than 60 pairs of suckers**. Mantle muscular, tapers to pointed tail. Fins broad, sagittate; length 42 to 48% of mantle length; single fin angle 44° (40° to 50°). Funnel groove with foveola and 10 to 13 longitudinal ridges. **Tentacular club occupies much of tentacle length**; protective membranes very low, weak; largest sucker rings with 11 to 13 conical teeth around entire ring, interspersed with low truncate platelets; distal central tooth not enlarged. Arm sucker rings smooth proximally, grading to truncate teeth laterally, then to about 11 to 15 short, triangular teeth distally; the central tooth is enlarged. **Both arms IV in males hectocotylized basally** with modification of protective membranes and trabeculae into large, ridged, saw-tooth processes; **suckers absent**; **about 10 proximalmost pairs of suckers modified into large, swollen tubercles**. The hectocotylized right arm IV has a single row of slender, conical papillae distally; the ventral protective membrane has expanded supports only opposite to the extreme tip of the arm.



hectocotylus tentacular club dorsal view

Fig. 319 *Nototodarus sloanii*

Size: Maximum mantle length about 420 mm, maximum weight 1.8 kg in the western, South Island, New Zealand population, but 320 mm and 0.6 kg in the warmer waters of northeastern New Zealand.

Geographical Distribution: ***Nototodarus sloanii*** occurs in New Zealand continental shelf waters off and around South Island, southward from the northern boundary of the Subtropical Convergence Zone (about 41°S to the Auckland Islands, 51°S) and the Campbell Islands (53°S) at bottom depths that vary from 50 to 500 m; it extends eastward to the southeast of the Chatham Islands (175°40'W). It also occurs along the west coast of New Zealand's South Island from off Cook Strait southward along the narrow continental shelf to merge with the southeastern subpopulation south and east of South Island (Fig. 320).

Habitat and Biology: ***Nototodarus sloanii*** is a neritic-oceanic species that occurs from near the surface to about 500 m depth; occasionally it forms large aggregations down to 300 m. It is most abundant on the continental shelf in depths of less than 200 m. At the northern end of its range it overlaps with its congener, ***N. gouldi***, while in the southern part it co-occurs with ***Todarodes filippovae***, where the 2 species are caught together in the jig and trawl fisheries.

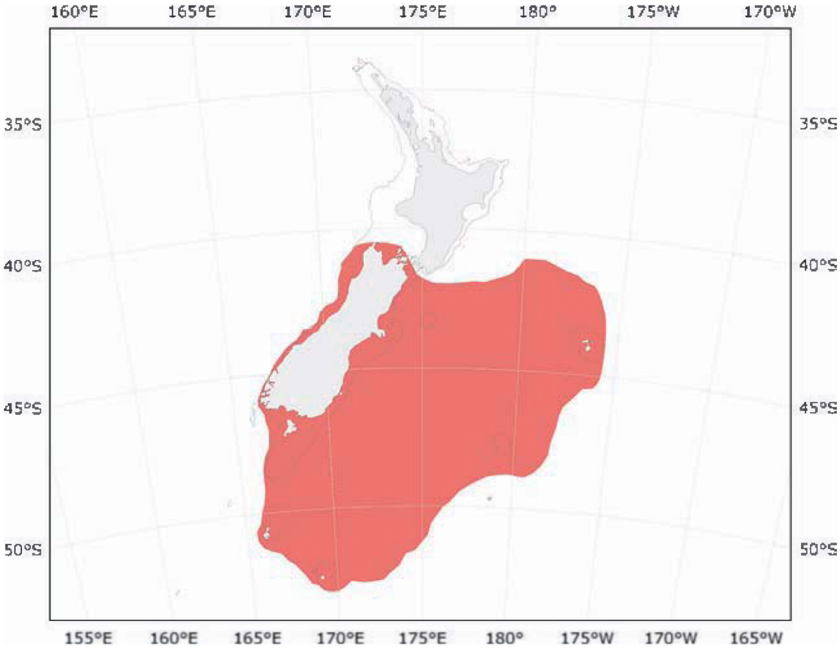


Fig. 320 ***Nototodarus sloanii***

🟥 Known distribution

The Antarctic Circumpolar Current that enriches New Zealand waters northward to about 41°S provides oceanic primary productivity that drives the flow of energy and material into the extensive ranges of secondary producers and predators, that, in turn, are preyed upon by ***N. sloanii***. Consequently, ***N. sloanii*** is an important member of the mid-to-outer continental shelf species assemblage. It occurs over a broad range of temperatures but seems to be either more abundant or more vulnerable to fisheries activities in colder waters.

Geographical subpopulations exist that vary in size and season of maturity and spawning. These groups are distinguished by minor morphometric features, biology and geography. Two major subpopulations exist, 1 north of the subtropical convergence zone and 1 within and south of the convergence. The northern group occurs in 2 "cohorts": 1 off eastern South Island, New Zealand, and through Cook Strait; the second cohort occurs in the upwelling region along the western coast of South Island over the narrow continental shelf; it grows to larger sizes than the eastern cohort. The second major subpopulation occurs south of the subtropical convergence and is associated with high velocity, cool waters of the Antarctic Circumpolar Current/sub-Antarctic Front. The interannual abundance of populations is correlated with environmental changes associated with the Southern Oscillation Index and the Trans-Polar Index. Small-scale environmental factors influence fluctuations in each seasonal cohort.

Spawning occurs throughout the year, mainly on the continental shelf throughout the adult life span. Each of the 2 northern populations has 2 peak spawning seasons: autumn (March and April) and spring (September to November) for the northwestern population, and July and December for the northeastern population. Eggs, paralarvae, sometimes juveniles, are transported by the current from the spawning grounds to the feeding grounds. Some inshore-offshore migration exists of older stages.

Testis somatic index (TSI) shows males begin to mature at 200 days and reach a maximum maturity at 270 days. Females start to mature when the maximum TSI in males is achieved. Development of the ovary, oviduct and nidamental glands occurs simultaneously, and copulation with spermatangia implantation around the buccal membranes occurs at this time, followed 2 months later by spawning, thus completing the 1-year life span.

Paralarvae of ***N. sloanii*** are distributed over the continental shelf and banks shallower than about 150 m; juveniles are distributed over the continental shelf along the east and south coasts of South Island, on the Auckland Islands shelf and around the Chatham Islands. Adult distribution patterns are very similar to those of the paralarvae and juveniles.

Hatching occurs principally in April to June, the austral autumn. Paralarvae are most abundant off eastern South Island, New Zealand, south of the subtropical convergence in sub-Antarctic waters. The size and age of the winter-spawned group is larger than the summer group at about 100 to 230 days, but the trend is reversed by about 250 days.

Nototodarus sloanii grows to a maximum mantle length of 420 mm but can be mature at 260 mm mantle length; fully mature females weigh 1.8 kg. Growth rates vary with size: smaller squid (180 to 240 mm mantle length) grow 25 to 40 mm per month, and larger squid (240 to 330 mm mantle length) grow 15 to 30 mm per month. Thus growth over the exploited size range from 7.5 to 11 months suggests a life span of 1 year. Parasites of ***N. sloanii*** include *Anasakis* nematodes that infest the visceral organs and membranes, rarely the muscular tissues. The prey of ***N. sloanii*** is varied and consists of crustaceans (euphausids, amphipods, crab zoea), fishes (myctophids, saury) and squids, including conspecific and congeneric forms. ***Nototodarus sloanii*** is preyed upon by seabirds such as the Southern Buller's albatross, fiordland crested penguin (*Eudyptes pachyrhynchus*), yellow-eyed penguin (*Megadyptes antipodes*) and little blue penguins, marine mammals, e.g. New Zealand fur seals (*Arctocephalus forsteri*), which prey predominantly on ***N. sloanii*** during summer and autumn, and Hooker's (or New Zealand) sealions (*Phocarctos hookeri*) around the Auckland Islands. Interestingly, neither ***N. sloanii*** nor ***N. gouldi*** appear to be prey of sperm whales (*Physeter catodon*), probably because they live in the shallower waters over the continental shelf, where sperm whales generally do not feed. However, ***N. sloanii*** formerly was abundant (18.5%) in the stomachs of sperm whales stranded on New Zealand coasts. In recent years, however, beaks of these species have been entirely absent. A second very large predator is the giant squid, ***Architeuthis***. The lengths of upper and lower rostra of the beaks taken from predators can predict both mantle length and wet weight of the squid consumed.

Interest to Fisheries: ***Nototodarus sloanii*** is fished in the sub-Antarctic waters south of the Subtropical Convergence Zone, about 44°S, over the continental shelf of South Island, New Zealand. It is the major squid fishery in New Zealand. The species may be represented by multiple cohorts, but insufficient biological data are available to confirm this; thus the entire stock is managed as a single cohort. The instantaneous biomass of both ***Nototodarus*** species is estimated to be 2 to 3 million tonnes of which 1 to 2 million tonnes are ***N. sloanii***, so the potential for a managed sustainable fishery is high. The fishery first developed in 1972 and landings continued to increase, with variability, including the exceptionally good landings in 2004 of a little over 108 000 tonnes. The catch recorded for 2007 was about 74 000 tonnes. The annual ***N. sloanii*** total landings accounts for about 2 to 4% of the total world cephalopod landings. Annual fishery statistics, catch per unit effort (CPUE), joint ventures and foreign vessel data are available in the Occasional Publication Data Series, Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington, New Zealand. Interannual variability in fishery catch demonstrates 2 peaks of abundance during good years, in mid-February and late March, and 1 peak during poor years, in mid-February. CPUE is higher when sea-surface temperature is greater than 16°C in mid-February; and higher in late March with temperatures less than 14°C. Peak catches occur in January-February, east of South Island within the 200 m isobath where surface temperature is 13° to 15°C. Catches are related to moon phase: full yields lower, new yields higher. This is typical for oceanic species that undergo diel vertical migration. The light intensity during full moon is sufficient to limit the extent of migration into shallower depths. Fishing at greater depths during full moon might increase otherwise reduced catches.

The fishery for ***N. sloanii*** in New Zealand's Economic Zone is dominated by foreign vessels that operate under government licenses, joint ventures and charter agreements. ***Nototodarus sloanii*** is taken by both jigging and trawling, with jigging often being more productive, as well as being more "resource friendly", because it does not produce unwanted, destructive incidental catches. Furthermore, jigging is selective on the size of squid it captures, produces a high-quality product that can be processed at a steady rate and it does not destructively interfere with benthic fauna and habitat. Japanese and South Korean jigging vessels, operating under joint-venture schemes with New Zealand, take about half the total catch, but they land only a fraction in New Zealand. This squid also is taken in trawling operations of foreign licensed vessels from the former USSR countries, Japan and the Republic of Korea. The fishery is regulated through a quota system. The vessels usually operate during a 90 to 120 day fishing season extending from December to April. The Total Allowable Catch is established annually, and this tonnage normally seems not to be achieved; TACs have ranged from 90 000 tonnes to 166 250 tonnes, but the combined total catch of both species, ***N. sloanii*** and ***N. gouldi***, seldom has exceeded 50 000 tonnes. Frozen and processed squids are exported to various countries. Domestically caught squid are marketed fresh or processed. The majority of the squid is processed for human consumption, but viscera also are used for other purposes. Biochemical analysis of proximate composition and fatty acid compositions of viscera shows the residual protein has high levels of essential amino acids that provide a good source of protein supplement for domestic animal feed.

The trawl fishery for ***N. sloanii*** inadvertently captures sea lions (*Phocarctos hookeri*), a threatened species. An annual catch limit is imposed on the squid fishery in order to stimulate healthy recovery of the sea lion.

Local Names: JAPAN: Minamisurumeika, Nyujirando-minamisurumeika, Nyujirandosurumeika; NEW ZEALAND: New Zealand arrow squid, Wellington flying squid.

Remarks: Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayshi *et al.*, 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodanae). However, within Todarodinae, ***Nototodarus*** appears to be paraphyletic under all analyses done: ***N. sloanii*** was shown to be a sister species of ***N. gouldi***, and these 2 species appear to be more closely related to ***Todarodes pacificus*** than to their congeneric entity, ***N. hawaiiensis***. Ultimately, this study was not able to resolve the phylogenetic relationships within the Ommastrephidae because of the significant genetic divergence among species. The identification of the sympatric species, ***N. sloanii*** and ***N. gouldi***, is difficult in areas of geographical overlap. The key distinguishing features are: the **number of suckers on right arm I** (greater than **60** versus **28** to **50**, respectively), the number of **proximal enlarged sucker bases/cushions** (**10** versus **5 or 6**, respectively) and the **morphology of the distal part of hectocotylized arm** (flattened papillae versus broad-based papillae, respectively) (Smith *et al.*, 1987).

Literature: Saito *et al.* (1974), Smith *et al.* (1981), Förch (1986), Smith *et al.* (1987), Nesis (1993a), Dunning and Förch (1998), Waluda *et al.* (2004a), Wakabayashi *et al.* (2006).

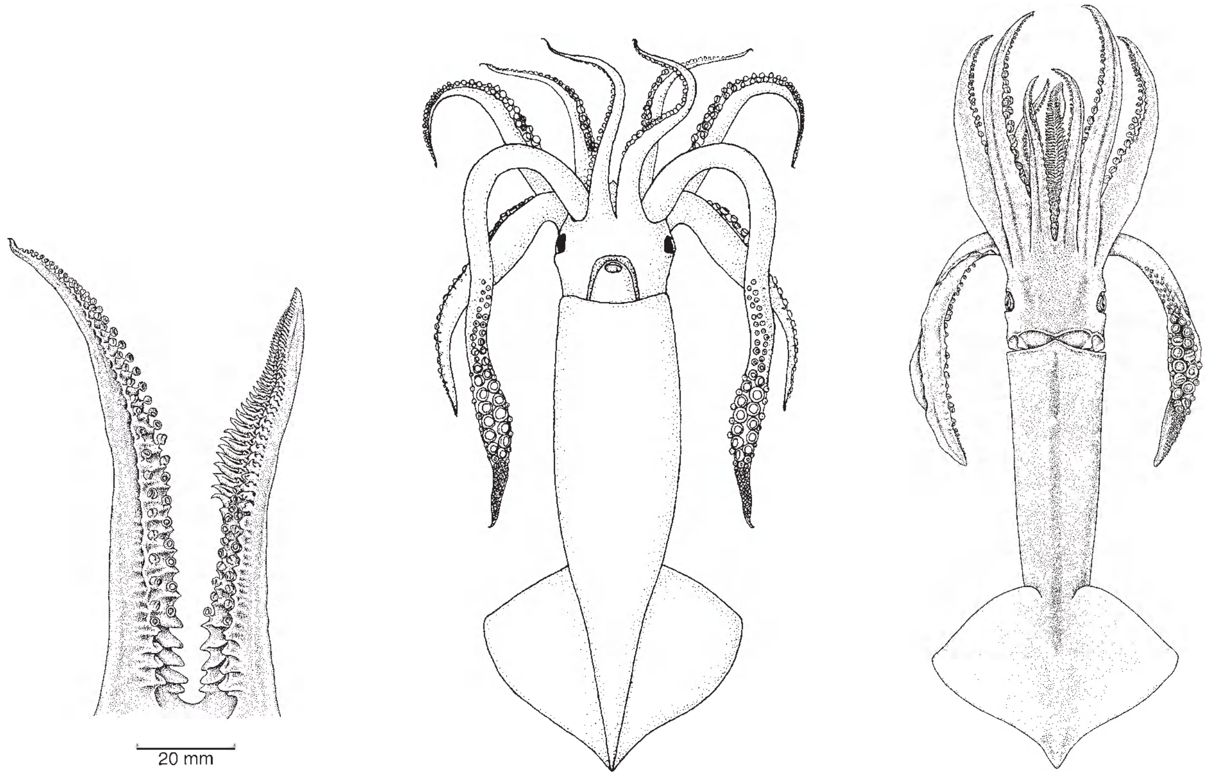
Nototodarus gouldi (McCoy, 1888)

Fig. 321

Ommastrephes gouldi McCoy, 1888, *Prodomous of the Zoology of Victoria, Decade*, 17: 255–257, 2 pls. [255, pl. 169]. [Type locality: Hobson's Bay, Victoria, southern Australia (fide Dunning and Förch, 1998: 397)].

Frequent Synonyms: *Nototodarus sloani gouldi* (McCoy, 1888); *Ommastrephes gouldi* McCoy, 1888; *Ommatostrephes sagittatus sloanei* Pfeffer, 1900; *O. sloanei sloanei* Pfeffer, 1912; *Nototodarus sloani gouldi* Voss, 1963a.

FAO Names: En – Gould's flying squid, Gould's arrow squid; **Fr** – Encornet éventail; **Sp** – Pota australiana.



hectocotylus **ventral view** **dorsal view**

Fig. 321 ***Nototodarus gouldi***

Diagnostic Features: Arms I have **28 to 50 pairs of suckers**. **Mantle robust, heavily muscled, tapers gradually then very acutely to a point posteriorly**. Fins strong, about 45% as long as mantle length; angle broad, 90° to 110° (45° to 55° single fin). Funnel groove with foveola and 6 to 8 low longitudinal ridges anteriorly. **Tentacular club long, 60 to 70% of tentacle length**; about 8 pairs of enlarged manal suckers in median rows, marginal suckers small, subequal; largest sucker rings toothed all around with 15 separated, stout, triangular, pointed teeth interspersed with low, side platelets. Arm sucker rings with 12 or 13 sharp, triangular teeth graded to a single large central tooth distally; proximal one-third smooth, without teeth or denticles; **both ventral arms (IV) in males hectocotylized**: the right arm with a heavily tuberculate basal region, a narrow sucker-bearing midpart, and a distal part with very broadly expanded, pectinate protective membrane; **the left ventral arm one-fourth longer than right IV, about 5 proximalmost pairs of suckers modified into large, swollen tubercles**.

Size: Maximum mantle length 420 mm in females, 350 mm in males; weight to about 1.2 kg in females.

Geographical Distribution: Temperate to subtropical areas off Australia: from south of 27°S off the east coast (Queensland), southward around Tasmania through the Bass Strait, westward along the south coast, then northward off Western Australia to about 25°S off Shark Bay; off the northern and central coasts of New Zealand, principally off North Island (Fig. 322).

Habitat and Biology: ***Nototodarus gouldi*** is sympatric with ***N. sloanii*** where the area of overlap occurs between 40° and 44°S and in the northern extreme of its range of eastern Australia it overlaps in slope waters with ***N. hawaiiensis***.

It is a neritic and oceanic, mostly epipelagic species, that occurs from the surface to about 500 m depth. Its abundance in surface waters is correlated with the lunar cycle; in full moon nights the squids tend to remain in deeper waters where they are less vulnerable to the fishing gear.

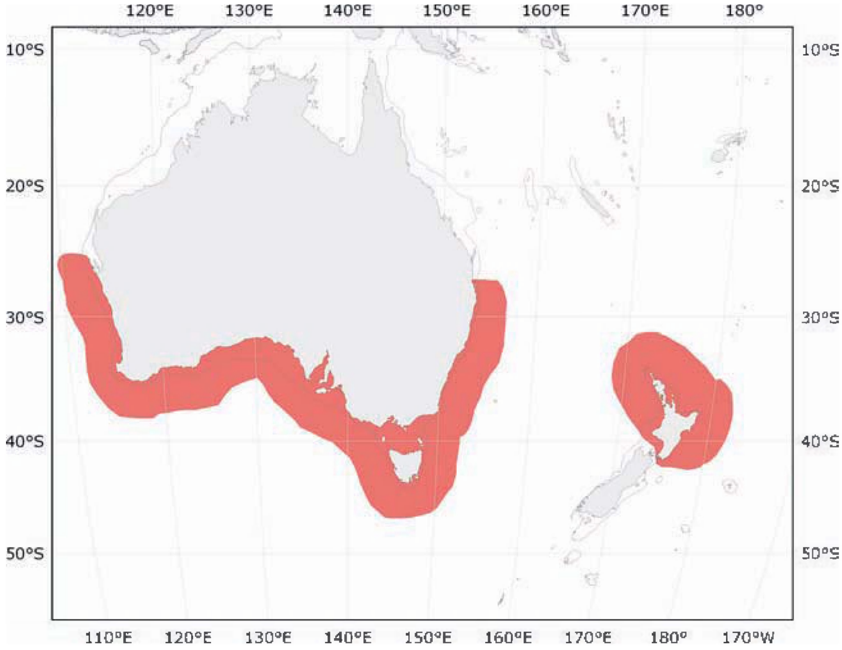


Fig. 322 ***Nototodarus gouldi***

🟥 Known distribution

The principal oceanographic feature that supports and sustains the ***N. gouldi*** populations is the productivity of the Antarctic Circumpolar Current through the distribution and dispersal of energy flow into the region of secondary producers and predators that form their prey.

Nototodarus gouldi is a dominant species in the mid to outer continental shelf species assemblage in New Zealand waters. While its greatest abundance is over shelf waters at 50 to 200 m (300 m), ***N. gouldi*** occasionally is abundant in shallow coastal waters in the summer in Australian waters. The distribution of paralarval and juvenile ***N. gouldi***, 20 to 40 mm mantle length, in New Zealand occurs principally in continental shelf waters off the east and west coasts of North Island and to the northwest of South Island. This distributional pattern is very similar to that of the adults, so the entire life cycle is spent in continental shelf waters.

Age at sexual maturation has been determined using statolith aging techniques. Males start to mature at about 200 days, and the testis somatic index (TSI) reaches its maximum at about 270 days. Females begin to mature as the TSI reaches its maximum in males. The rapid development of the ovary, oviducts and nidamental glands occurs simultaneously, and copulation takes place during this period, as well. Spawning occurs about 2 months after copulation, completing the slightly less than 1 year life cycle, based on statolith analysis.

Males exhibit no seasonal differences in growth rates, but females do: females hatched in summer have significantly higher growth rates than those hatched in winter, autumn or spring. During cool months females are larger, have slower lifetime growth, lower gonadic investment and better somatic condition than those caught in warm months, representing a trade-off between gonadic investment and somatic condition. Males have a tight coupling between gonadic investment and somatic condition throughout the seasons, with gonadic and somatic tissues growing concurrently. This strategy of "using" monthly variations in ambient conditions to govern egg production and spawning would have positive effects to maximize reproduction and survival. Studies over a broad range of southeastern Australian localities confirm complex variations in size, age, growth and maturation among sites, where life span is slightly less than 1 year. Considerable genetic mixing occurs across all sites, that allows a possibility of populational substructures and suggests the existence of more than 1 stock in Australian waters. However, an allozyme electrophoresis study of squid from the same geographical area revealed no evidence to support the existence of separate stocks.

Females grow larger than males, but males tend to be heavier at a given mantle length, until females surpass them at maturity. Across the range of the species in southeastern Australian waters considerable variation exists in size, growth rates and maturity between sites, seasons and years. The age of mature squid varies by over 100 days from youngest to oldest. Interannual variations in the Southern Oscillation Index (SOI) and the Trans Polar Index (TPI) affect the environment and abundance of ***N. gouldi***: juveniles are affected mainly by the SOI at lower latitudes, while the adults are affected by the TPI in higher latitudes. This mechanism influences recruitment and stock abundance. ***Nototodarus gouldi*** exhibits the multiple-spawning strategy whereby eggs are laid in discrete batches during the course of the spawning period. Mature ovaries contain oocytes with a range of sizes with discrete peaks. The life cycle generally is related to warm currents and eggs, paralarvae, occasionally juveniles, are transported by the current from the spawning grounds to the feeding grounds, where they become available to the fishery. Following mating and spawning, the muscular tissues of spent individuals begin to degrade and become weakened and flaccid. Probably the very rapid disposition of somatic protein into protein-rich yolk during vitellogenesis in the ovary, coupled with reduced or ceased feeding, leads to the somatic degradation after spawning, soon followed by death.

Nototodarus gouldi is an opportunistic predator that preys on planktonic/nektonic crustaceans, fishes and cephalopods. The incidence of crustaceans in the diet decreases with growth, while the incidence of cephalopods, including ***N. gouldi*** and other ommastrephids, increases. Feeding occurs mainly at night and at dawn and digestion is rapid. Fishes *Sardinops pilchardus* and *Leionura auntae* and the crustacean *Leptochela sydniensis* and *Cirolana*, and some isopods and amphipods are the most common prey. Ommastrephids made up most of the cephalopod component: frequently smaller ***N. gouldi*** and ***Todarodes filippovae***; other squids: occasionally ***Onychoteuthis*** sp., ***Brachioteuthis*** sp. and ***Sepioteuthis*** sp. The quantity of each main food group varies monthly, depending on the availabilty of preys. The digestive gland of ***N. gouldi*** acculULates high levels of trace metals (cadmium, copper, zinc, polonium–210).

The predators of ***N. gouldi*** vary widely and include seals, dolphins, tuna, as well as pelagic, benthic and bathypelagic fishes. This species is a significant prey of pygmy sperm whales in New Zealand waters. Larger ***N. gouldi*** are a dominant prey of swordfish (*Xiphias gladius*) off eastern Australia, as well as important in the diet of yellowfin tuna, school shark (*Galeorhinus australis*) and gummy shark (*Mustelus antarcticus*). Other species of sharks from eastern Australian waters preying on ***N. gouldi*** include the smooth hammerhead shark (*Sphyrna zygaena*), the scalloped hammerhead shark (*S. lewini*), the blue shark (*Prionace glauca*) and the shortfin mako (*Isurus oxyrinchus*). Examination of stomach contents revealed that the giant squid, ***Architeuthis***, preys on ***Nototodarus*** species; undoubtedly that would include ***N. gouldi***. Among marine mammals, ***N. gouldi*** is a dominant prey of Australian fur seals (*Arctocephalus pusillus*) which are attracted to squid jigging operations where they prey upon ***N. gouldi***. The Gould's squid is the most abundant cephalopod in the diet of the shy albatross on Albatross Island, Tasmania, of juvenile southern bluefin tuna in the waters off coastal southern Western Australia and of short-tailed shearwater in Tasmanian waters. This species also is the most frequent cephalopod prey of the little penguin (*Eudyptula minor*) at Phillip Island, Victoria, Australia. ***Nototodarus gouldi*** was a significant prey of sperm whales stranded in New Zealand in the 1960s, but these species have been entirely absent from stranded sperm whales in recent years.

Interest to Fisheries: Prior to the development of a directed fishery, the species was only taken as by catch in the Australian prawn fishery. Feasibility fishing started in the summer 1978/1979, with 19 Japanese jigger vessels operating in southeast Australian waters. In the light of promising catch rates, exploratory fishing was subsequently expanded. Chinese jigging vessels (from Taiwan Province of China) operate intermittently in the area. Catches are best in the waters around Tasmania and the western Bass Straits, particularly from December to March. In early years, the annual catch fluctuated between 4 000 and 5 000 tonnes. An active fishery then developed for ***N. gouldi***, principally around southern Australia and Tasmania in temperate waters, then in subtropical waters north to 27°S off the east coast, and to 25°S along the west coast.

A smaller stock of ***N. gouldi*** is fished in subtropical waters around North Island, New Zealand, north of the Subtropical Convergence Zone. There, the major fishing grounds are off southwestern North Island and off northwestern South Island over a broad area of the shelf in waters of the Westland/D'Urville Current system at temperatures greater than 18°C. Fishing is conducted by a New Zealand fleet, as well as by an international fleet, using a combination of gears: jigging machines on specialized jigging vessels, and bottom otter trawls and pelagic trawls on large stern trawlers.

The instantaneous biomass of ***Nototodarus*** species throughout their ranges has been estimated at 2 to 3 million tonnes of which 0.5 to 1 million tonnes are ***N. gouldi***.

The principal goal in management of a fishery on squid with an annual life cycle is to enable a sufficient number of spawning individuals to escape. In the case of ***N. gouldi***, regulation of effort is the best tool to manage the fishery, regardless of the fishing area. Clearly, knowledge of the timing of spawning, the ecology of hatchlings, the larval distribution and the growth dynamics of juveniles are critical to understand the location and life cycle of the adults in order to sustain a well-managed, consistent fishery.

Echo sounding and sonar surveys were conducted to determine the suitability of alternative fishing techniques for ***N. gouldi***. This species forms demersal aggregations during daylight hours. Around dusk, squid leave the bottom, and disperse into the water column to feed at night. This behaviour is conducive for bottom and midwater trawling. Purse seining was suggested as an alternative technique for capturing squid attracted by lights at night and clustered in demersal aggregations during daylight hours.

During the week of full moon, catch rates are about 25 to 50% lower than during darker weeks. Catch rates generally are greatest during the days following new moon. Commercial jigging operations are conducted both during the day and at night, but nighttime catches are greater, probably because the diel vertical migration pattern brings the squid off the bottom layer and closer to the surface at night. In the developing squid fishery off New South Wales, ***N. gouldi*** is the most abundantly caught species.

The fishery for ***N. gouldi*** at present is managed as one stock.

Local Name: AUSTRALIA: Gould's squid; NEW ZEALAND: Gould's arrow squid.

Remarks: Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayshi *et al.*, 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodanae). However, within Todarodinae, ***Nototodarus*** appears to be paraphyletic under all analyses done: ***N. sloanii*** was shown to be a sister species of ***N. gouldi***, and these 2 species appear to be more closely related to ***Todarodes pacificus*** than to their congeneric entity, ***N. hawaiiensis***. Ultimately, this study was not able to resolve the phylogenetic relationships within the Ommastrephidae because of the significant genetic divergence among species. ***Nototodarus gouldi*** and ***N. sloanii*** are closely-related, similar-looking species that are difficult to discriminate. The following distinguishing characters aid in specific identification: ***N. gouldi*** has **28 to 50 suckers** on arms I versus **60 suckers** on ***N. sloani***; ***N. gouldi*** has about **5 or 6 pairs** of proximal sucker bases enlarged as cushions on the hectocotylus, versus **10 pairs** on ***N. sloanii***; ***N. gouldi*** has dorsal sucker bases on right arm IV modified **as broad-based papillae** that extend to the tip of the arm, versus distally flattened papillae to the arm tip in ***N. sloanii*** (Smith *et al.*, 1987).

Literature: Thrower (1978), Roberts (1983), Hatanaka *et al.* (1985), Smith *et al.* (1987), Gibson (1995), Dunning and Förch (1998), McGrath and Jackson (2002), Stark (2006b), Wakabayashi *et al.*(2006).

Nototodarus hawaiiensis (Berry, 1912)

Fig. 323; Plate X, 59

Ommastrephes hawaiiensis Berry, 1912, *Proceedings of the Academy of Natural Sciences Philadelphia*, 64(2):434–437 [434]. [Type locality: off Oahu Island, Hawaiian Islands, North Pacific Ocean].

Frequent Synonyms: ?*Ommatostrephes sloanei sloanei* Pfeffer 1912; *Ommastrephes hawaiiensis* Berry, 1912; *Nototodarus sloani philippinensis* Voss, 1962c; *Nototodarus sloani hawaiiensis* Voss, 1962c; *Nototodarus nipponicus* Okutani and Uemura, 1973; *Nototodarus philippinensis* Roper *et al.* 1984; *Nototodarus sloanii philippinensis* Dunning, 1988c.

FAO Names: En – Hawaiian flying squid; **Fr** – Encornet bouquet; **Sp** – Pota hawaiana.

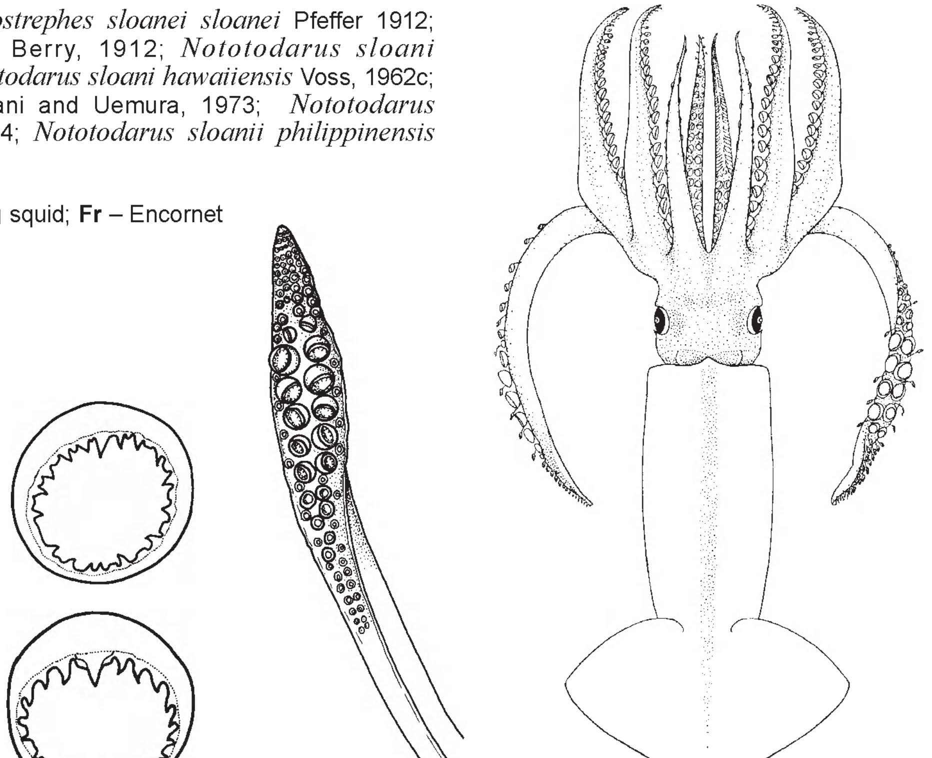


Fig. 323 *Nototodarus hawaiiensis*

Diagnostic Features: Mantle cylindrical, muscular; it tapers to a narrow, conical tip posteriorly. **Fins muscular, broad, short**; **fin length 35 to 43% of mantle length**; single fin angle (50° to 57°); a dark stripe of thickly set chromatophores occurs along dorsal midline of mantle and fins. Arms I have fewer than 30 pairs of suckers (18 to 28); head length index high (19 to 31). **Funnel groove with foveola, without side pockets**. Tentacular club with 4 rows of suckers on dactylus; **carpal area occupies most of tentacle length along stalk (about 70%)**; about 12 medial manus suckers are 3 to 4 times larger than the lateral suckers; largest medial manus sucker rings have 14 or 18 large conical, pointed teeth with low, truncated platelets between each tooth; distal, central tooth much enlarged. Arm sucker rings toothed all around with 19 to 21 small, conical (distally) to rounded (proximally) teeth; distal, central tooth much enlarged; small denticles between some distal teeth. **Both arms IV hectocotylized in males, right especially so**; it is longer and larger than the left and has a double row of slender, conical papillae and expanded protective membrane distally; **proximal one-quarter of each arm IV has 4 or 5 enlarged cushion-like trabeculae** and wide protective membranes (a saw-like or comb-like appearance) that have attenuated supports that extend to arm tip; dorsal and ventral distal right arm trabeculae, sucker stalks and suckers modified by enlargements, reductions, etc.

Size: Maximum mantle length varies according to locality: off southern Queensland, Australia, males 215 mm, females 248 mm; western Indian Ocean, males 290 mm; southeastern Pacific Ocean, 318 mm; Philippine waters, 180 mm; total weight 0.5 kg or more in large specimens.

Geographical Distribution: ***Nototodarus hawaiiensis*** has a very broad, disjunct distribution in tropical to subtropical waters of the Pacific and Indian Oceans: Hawaiian Islands to Midway Island, South China Sea, Japanese waters (south of 35°N), Hong Kong, Philippine and Vietnamese waters, northeastern Australia, Northwest Shelf of Western Australia, Andaman Sea, Bay of Bengal, Hawaiian Ridge, Sala y Gomez Ridge to Nazka Ridge, Saya de Malha Bank, off Somalia, Madagascar, Seychelle Islands, Mozambique, KwaZulu-Natal, Southern African waters. It also has been reliably reported from a seamount in the far southeastern South Pacific Ocean off Chile, 35°39'S, 85°31'W (Fig. 324).

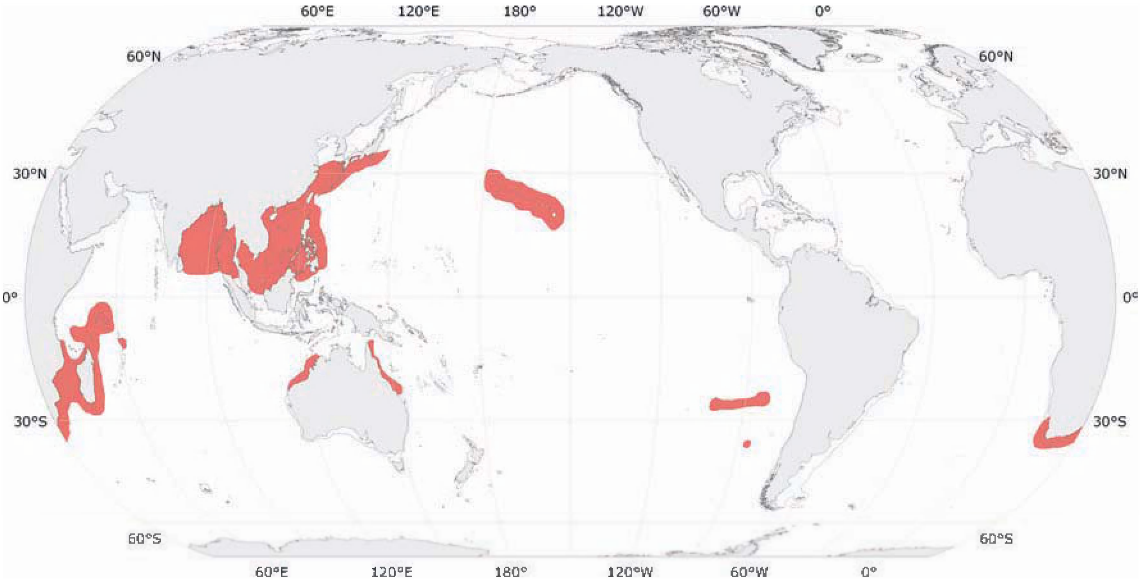


Fig. 324 ***Nototodarus hawaiiensis***

🟥 Known distribution

Habitat and Biology: ***Nototodarus hawaiiensis*** is a pan-tropical nerito-oceanic species associated with continental shelf and slope waters, oceanic seamounts, ridges and banks. Distributed down to depths of 650 m, it also occurs in shallower waters where it is an important food item in the diet of seabirds and fishes. This species occupies the mesopelagic-boundary region in Hawaiian waters where it is both epipelagic and demersal, as evidenced by *in-situ* observations from a submersible. During the daytime ***N. hawaiiensis*** "sits" on the bottom on its arm tips and posterior mantle tip, a common behaviour in ommastrephids, then it disperses into midwaters at night to forage. Paralarvae, juveniles and subadults inhabit midwaters in the epi- to upper mesopelagic zones over the tops of sea mounts, slopes and oceanic depths, and the adults spawn near or on the bottom. ***Nototodarus hawaiiensis*** occupies this niche in the Indian Ocean: Saya de Malha Bank; Pacific Ocean: Hawaiian Ridge; Sala y Gómez Ridge; transitional zone between Sala y Gómez and the Nazca Ridge. Adults of ***N. hawaiiensis*** do not occur in the open ocean, but they always remain near oceanic seamounts, ridges and banks, in spite of significant expatriation of young stages into the open ocean. The dispersal of paralarvae and juveniles by oceanic currents supports the very broad distribution of most species that spawn at or near the bottom; this occurs with ***N. hawaiiensis*** that is dispersed across the Indo-Pacific realm from Somalia and Mozambique to Hawaii and Sala y Gómez. Interestingly, in spite of the very extensive range of ***N. hawaiiensis*** throughout the Indo-Pacific region, it does not occur in the Gulf of Aden nor on the Nazca Ridge eastward of 85°W. ***Nototodarus hawaiiensis*** is considered a very rare epipelagic species in the Sea of Japan, where it occurs south of 35°N latitude and specimens are considered to be strays from other communities. Its biology is little known. A survey of egg size and fecundity in selected species in the Todarodinae revealed that ***N. hawaiiensis*** is characterized in the group that has ripe egg sizes on the order of 0.7 to 2.4 mm and low to medium fecundity of 20 000 to 2.5 million oocytes. The spermatophoric organ in mature males of about 150 mm mantle length contains around 2 700 developing spermatophores at an average length of 18 mm and a fecundity of 1 000 spermatophores. Paralarvae are caught at or near the surface year-round in the South China Seas, where they are spatially concentrated in a particular area in Vienamese waters. Paralarval distribution patterns of squid species in Hawaiian waters are divided into 2 assemblages: island-associated and oceanic. A large range in age at maturity exists in individuals of a similar size depending on locality and season. For example, off western Australia males of 98 mm and females of 100 mm are mature.

Interest to Fisheries: ***Nototodarus hawaiiensis*** is common in bottom trawls over the slope at 200 to 620 m off Mozamibique and KwaZulu-Natal, north of Durban, South Africa and it is the predominant cephalopod species caught as bycatch in the shrimp and prawn demersal trawl fishery on the Northwest Slope off Western Australia, principally in the Ramkin Bank area. Its abundance in these fisheries and the quality of its muscular tissues indicate a high potential as a fishery resource (Australia, Hawaii, Philippines, Mozambique, South Africa), even though its occurrence in relatively deep waters may limit access by common trawling techniques. An artisanal fishery exists off Hawaii (Big Island) out of the Port of Hilo. Exploratory fishing was conducted with jigs and gillnets and the species is believed to have sufficient potential for an expansion of the fishery. An estimate of the instantaneous biomass of ***N. hawaiiensis*** is 0.5 million tonnes.The species is used for human consumption and as bait.

Local Names: AUSTRALIA: Hawaiian arrow squid; FRANCE: Encornet fuiripin; INDO-PACIFIC: Hawaiian arrow squid; JAPAN: Fuiripinsurumeika; NEW ZEALAND: Hawaiian arrow squid; PHILIPPINES: Philippine flying squid; SPAIN: Pota Filipina.

Remarks: Recently, the phylogenetic relationships in the Ommastrephidae were analyzed with mitochondrial DNA sequencing (Wakabayshi *et al.*, 2006) and the monophyletic status of the 3 currently recognized subfamilies was supported (Illicinae, Ommastrephinae, Todarodanae). However, within Todarodinae, ***Nototodarus*** appears to be paraphyletic under all analyses done: ***N. sloanii*** was shown to be a sister species of ***N. gouldi***, and these 2 species appear to be more closely related to ***Todarodes pacificus*** than to their congeneric entity, ***N. hawaiiensis***. Ultimately, this study was not able to resolve the phylogenetic relationships within the Ommastrephidae because of the significant genetic divergence among species. ***Nototodarus nipponicus*** Okutani and Uemura, 1973 was described from Japanese waters off southern Honshu, but its differentiating characters were shown to merge within the range of variation with those of ***N. sloanii philippinensis*** Voss, 1962, so it was considered a junior synonym of this subspecies (Okutani and Kuroiwa, 1985). Subsequently, ***N. sloanii philippinensis*** Voss 1962 was demonstrated to be a junior synonym of ***N. hawaiiensis*** by Dunning (1988c), so continued use of the trivial name ***philippinensis*** is untenable.

Literature: Smith *et al.* (1987), Young (1995), Dunning and Förch (1998), Bower *et al.* (1999c), Nateewathana *et al.* (2000), Wakabayashi *et al.* (2006).

Todaropsis Girard, 1890

Todaropsis Girard, 1890. *Jornal de Sciencias Mathematicas, Physicas e Naturaes*, (series 2)1(3): 200–205. [204].

Type Species: *Todaropsis eblanae* (Ball, 1841).

Diagnostic Features: Dactylus of tentacular club with 4 rows of longitudinal suckers; medial manus sucker rings with 30 or more, evenly spaced, approximately equal, long, pointed teeth; **both arms IV hectocotylized in mature males**; cross-section A of gladius with 2 lateral lobes. Monotypic.

Todaropsis eblanae (Ball, 1841)

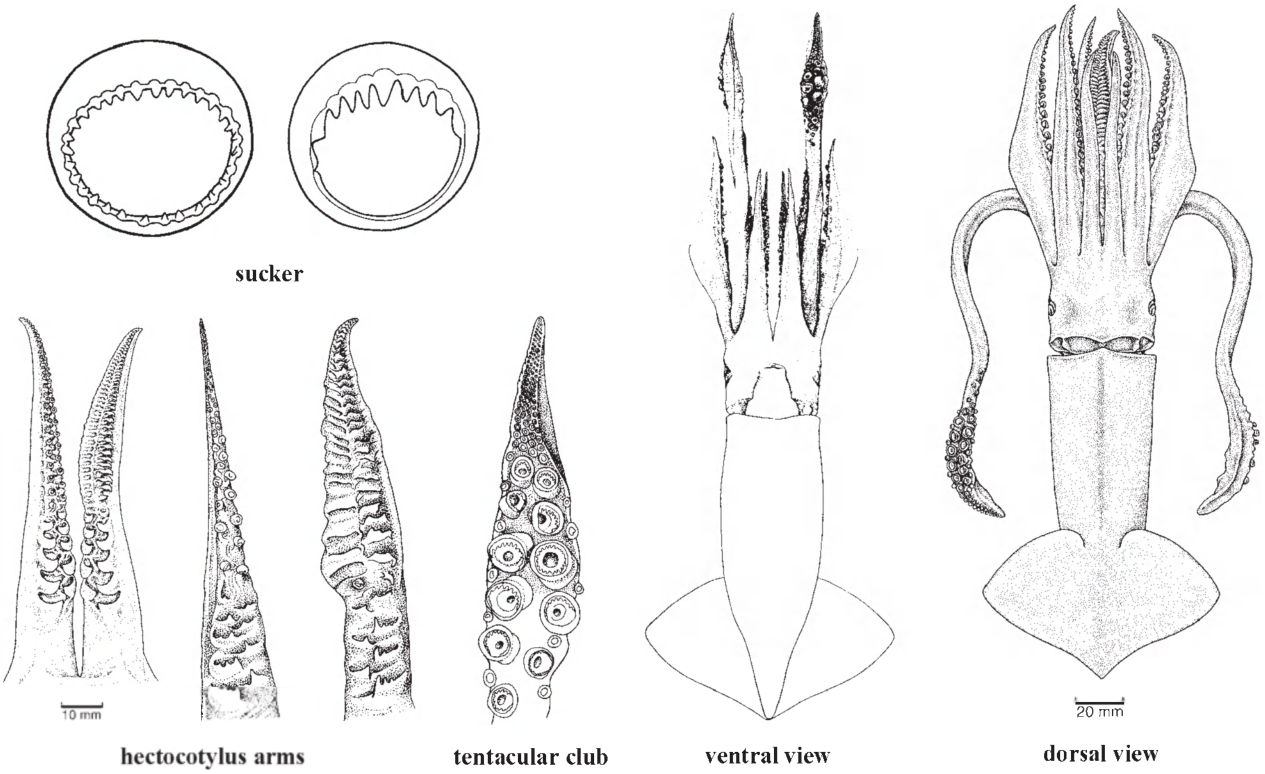
Fig. 325

Loligo eblanae Ball, 1841, *Proceedings of the Royal Irish Academy*, 1 (19): 362–364. [362]. [Type locality: Dublin Bay, Ireland, Irish Sea, North Atlantic Ocean].

Frequent Synonyms: *Loligo eblanae* Ball, 1841; *Loligo sagittata* Verany, 1851; *Todaropsis veranii* Nobre, 1936; *Todaropsis veranyi* Girard, 1890.

Misidentifications: None.

FAO Names: En – Lesser flying squid; **Fr** – Toutenon souffleur; **Sp** – Pota costera.



sucker

hectocotylus arms

tentacular club

ventral view

dorsal view

Fig. 325 ***Todaropsis eblanae***

Diagnostic Features: Mantle robust, stout; head large, broad, 4 nuchal folds on posterior of head (neck); funnel groove without foveola or side pockets. Fins broad, anterior border more convex than posterior border; fins length less than 50% of dorsal mantle length, combined fin width equal to 90% of dorsal mantle length. Dactylus of tentacular club with **4 longitudinal rows of small suckers**; **manus of club with 6 tranverse rows of 4 suckers, each with median pairs up to 4 times larger in diameter than lateral suckers**. Sucker rings of largest median club suckers with about 30 short, pointed teeth, occasionally alternating with minute teeth. Left and right ventral arms (IV) hectocotylized by modification of suckers into cirrated lappets and with transverse lamellae and expanded protective membrane; sucker rings of largest arm suckers with 1 large pointed median tooth and 3 or 4 smaller pointed teeth.

Size: Medium-sized species; maximum recorded size 290 mm mantle length for females and 220 mm mantle length for males (North Atlantic).

Geographical Distribution: This species exhibits a very disjunct distribution, as follows: Eastern Atlantic Ocean from 61°N (Shetland Islands) to 36 °S (Cape of Good Hope, Cape Town, South Africa [Adam, 1952]), including the British Isles and the entire Mediterranean Sea; western Indian Ocean (Saya de Malha and Nazareth Banks, Mascarene Ridges); western Pacific Ocean, South China Sea and Australian waters: the Timor Sea (northern Australian coast), along the western and eastern Australian coasts, to Tasmania on the eastern side (Fig. 326).

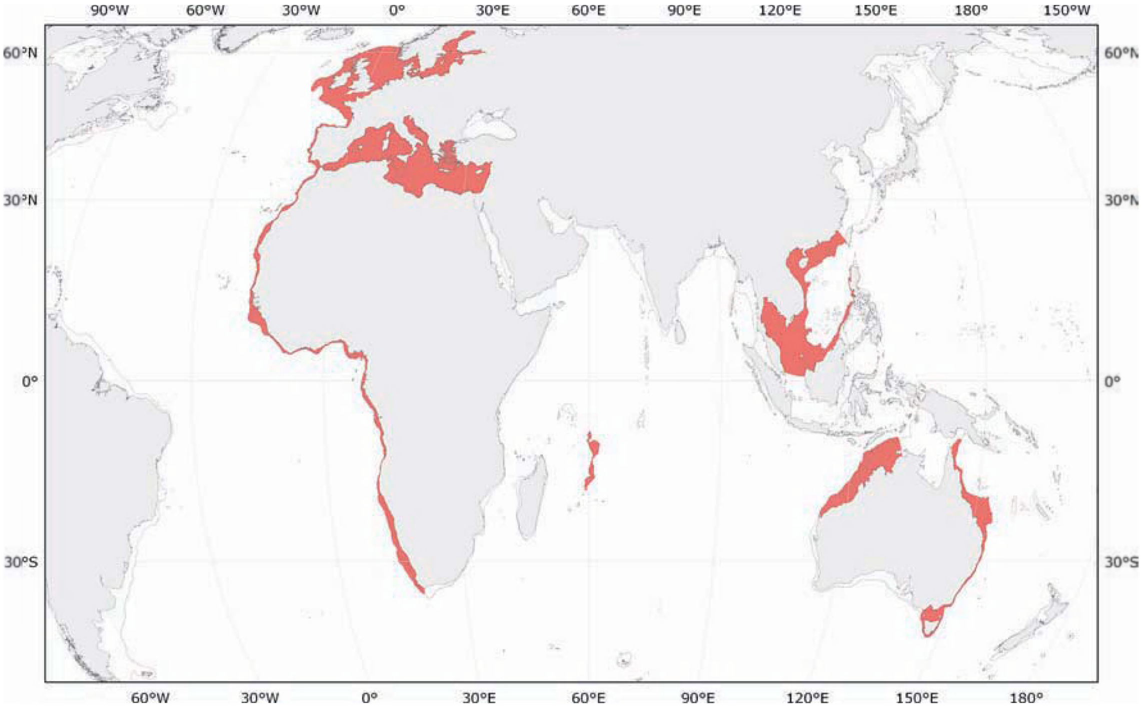


Fig. 326 ***Todaropsis eblanae***

🟥 Known distribution

Habitat and Biology: This demersal species usually is associated with sandy and muddy bottoms, within a temperature range from 9° to 18°C in depths between about 20 and 850 m, but it is confined to depths less than 200 m in the North Sea. Typically it is associated with the shelf break zone where boundary currents and associated mesoscale oceanographic events such as downwelling eddies and upwelling cells promote rich food supplies. No clear evidence exists of seasonal migrations or any other type of major migration. ***Todaropsis eblanae*** probably is the least mobile of the ommastrephid squids in terms of migratory habits, and it tends to behave like a neritic loliginid squid species. The sex ratio is usually 1:1 in all the populations studied to date, in contrast to the female dominated sex-ratio observed in the more oceanic ommastrephids; slight deviations to that condition usually are caused by ecological and/or fishery related constraints than to genetic differences in population structure. Females grow larger than males, but no other sexual dimorphism is evident. Smallest mature males from the central Mediterranean Sea measured 100 mm mantle length, while smallest mature females were 120 mm mantle length (Tyrrhenian Sea), similar to what occurs in Atlantic populations. The western Mediterranean and the Australian populations, however, begin to mature at a slightly larger size (males at 160 mm mantle length, and females at 120 to 150 mm mantle length). Generally, size at 50% maturity is estimated to be 120 to 130 mm mantle length for males and 160 to 170 mm mantle length for females. The spawning season probably extends year-round in both the Atlantic Ocean and the Mediterranean Sea, with seasonal spawning peaks that depend on geographic area. In eastern Australian waters spawning occurs from late summer until early winter. Fecundity varies greatly, depending on size of females and specific populations; total fecundity ranges between a few thousand to over 250 000 ova. Evidence suggests that the energy for egg production is taken directly from food, rather than from stored products. The number and the size of spermatophores increase with the size of the males; spermatophore length ranges between 11 and 30 mm, and their numbers range between 10 and 20 in excess of 250. The final maturation phase is rapid, and spawning constitutes the terminal phase of the life cycle. Intermittent terminal spawning is possible, but the degeneration process after the last spawning event must be rapid, since spent females are seldom found. Immature oocytes are pale yellow in colour, while mature oocytes are bright orange and measure from 0.8 to 2.5 mm in diameter. Eggs are laid in a large capsule secreted by the greatly enlarged nidamental glands. No *in situ* observations on egg deposition are available, although they probably are laid in floating masses, as observed for many other ommastrephids in the natural environment and in captivity. No information exists on the embryonic development nor on the newly hatched squids. Growth is rapid, especially in the initial phase, with females growing faster than males. Length-weight relationships differ between geographical regions; for example, males from the Spanish Atlantic waters are comparatively more robust than those from other areas. In both sexes growth is allometric, at least until maturity is reached. Observations from Italian waters show that growth in mature females is isometric, indicating a change in the growth performance once maturity is achieved. The duration of the life cycle determined by statolith analysis is about 1 year, a little shorter than that suggested by indirect observations on females of the western Mediterranean, for which a second year of life was hypothesized. ***Todaropsis eblanae*** preys on fishes, crustaceans and other cephalopods, in decreasing order of importance. Anatomical and behavioural changes occur in the diet, during ontogeny.

The lesser flying squid is a typical opportunistic predator that feeds on its principal available prey species depending on geographical area and other environmental factors. Analyses of stomach contents show a predominance of pelagic and nektobenthic species, such as myctophid, clupeid and gadoid fishes. The absence of sympatric benthic organisms in stomach contents indicates that ***T. eblanae*** feeds mainly in the water column. Cannibalism also occurs, but it is mainly an occasional phenomenon associated with anomalous concentrations of conspecific squid and/or scarcity of commonly available prey. No differences in the diets of males and females have been observed; however, mature females with food in their stomachs outnumbered feeding males, confirming that mature females continue feeding actively, i.e. that reproductive investment is mainly dependent on food intake and that spawning is protracted over an extended time period. ***Todaropsis eblanae*** is preyed upon by a variety of fishes and cetaceans, for some of which this squid constitutes an important component in the diet. Recent observations indicate that ***T. eblanae***, along with ***Illex coindetii*** and ***Todarodes sagittatus***, is the most important paratenic host for anisakid nematods. A better understanding of parasitic transfer and parasite-induced diseases throughout the food web will help in a better management of marine resources in general as well as of human consumption of raw marine food in particular.

Interest to Fisheries: ***Todaropsis eblanae*** is taken mainly as bycatch in otter trawl fisheries throughout its distributional range. In the Mediterranean and the eastern Atlantic, ***T. eblanae*** also is caught by artisanal fisheries. This species exhibits a highly irregular and discontinuous abundance in some areas of its distributional range, e.g. in the North Sea and in Spanish Atlantic waters. However, it is a constant and consistent component of the catches in other areas, where it is of significant commercial interest. These areas include the western Irish waters, the southern African Atlantic waters, and the Sicilian Channel (Central Mediterranean). Separate statistics are not reported for this species.

Local Names: AUSTRALIA: Golden arrow squid; ITALY: Totano tozzo.

Remarks: Roeleveld (1988) reviewed the importance of the characteristics of the funnel groove as a primary taxonomic character within the family Ommastrephidae and reassessed the placement of ***Todaropsis*** within the subfamily Illicinae. Consequently, she placed this species within the subfamily Todarodinae, in a monophyletic group with ***Nototodarus***. Nigmatullin (1992 [1991]), based on the analysis of variability of 18 morphological characters, distinguished directions and stages of morpho-functional evolution of ommastrephids. He presented the recognized taxa in phylogenetic order ranging from primitive to more advanced forms in terms of evolutionary development. In his interpretation, 5 subfamilies are considered, 3 basic, Illicinae, Todarodinae and Ommastrephinae and 2 intermediate ones, Todaropsinae, monotypic for ***Todaropsis***, and Ornithoteuthinae. He considered ***Todaropsis eblanae*** more closely related to the Todarodinae than to the Illicinae, without, however, belonging to either subfamily, a point of view repeatedly stressed (Laptikhovsky and Nigmatullin, 1999, Nigmatullin and Laptikhovsky, 1999, Nigmatullin *et al.*, 2003). This peculiar isolation of ***Todaropsis*** with respect to the other species of the family is supported to a degree by a genetic study carried out on 16 ommastrephids species by Yokawa (1994). Recent studies on ***T. eblanae*** from the Atlantic and the Mediterranean (Dillane *et al.*, 2005) indicate the existence of at least 3 genetically isolated populations in the eastern Atlantic. This finding, along with the broad and unusually disjunct geographical distribution of the species, supports the need for further detailed studies on its identity and systematic status throughout its world wide range.

Literature: Mangold-Wirz (1963), Clarke (1966), Lu (1982), Roper *et al.* (1984), Roeleveld (1988), Nigmatullin (1992 [1991]), Gonzalez *et al.* (1994), Hastie *et al.* (1994), Yokawa (1994), Lordan *et al.* (1998a), Wormuth (1998), Laptikhovsky and Nigmatullin (1999), Nigmatullin and Laptikhovsky (1999), Hernandez-Garcia (2002b), Robin *et al.* (2002), Nigmatullin *et al.* (2003), Dillane *et al.* (2005), Okutani (2005), Hastie *et al.* (2009).

2.23 Family ONYCHOTEUTHIDAE Gray, 1849

by Clyde F.E. Roper and Patrizia Jereb

Onychoteuthidae Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia*, 164 pp. [206].

Type Genus: *Onychoteuthis* Lichtenstein, 1818.

FAO Names: En – Clubhook squids; **Fr** – Cornets crochu; **Sp** – Lurias granchudas.

Diagnostic Features: Mantle densely muscular, or less muscular with softer, semigelatinous consistency, occasionally ammoniacal; tail moderately to prominently pointed (except ***Onykia***). **Fins with sharp lateral angles, rhomboidal, heart-shaped or transversely oval** (in ***Onykia***); buccal connectives (7) attach to ventral borders of ventral arms (IV); funnel-locking apparatus simple, groove and ridge straight; **tentacular clubs with 2 medial series of strong hooks, those of ventromedial series the largest**; 2 marginal series of small suckers on manus usually absent in subadults,or (rarely) marginal suckers rudimentary; small suckers on terminal pad; well-defined (by ridge or elevation) discoidal to oval locking apparatus on carpus with both suckers plus associated knobs; 8 muscular arms and 2 contractile tentacles around mouth; arms with 2 series of suckers with smooth, non-dentate rings, except in mature males of ***Walvisteuthis***. Neck region with nuchal (occipital) folds in ***Onychoteuthis***, ***Ancistroteuthis*** and ***Notonykia***. Lower jaw (beak) with a "step" proximal to jaw angle. Photophores on ventral surface of eyes only in ***Ancistroteuthis*** and ***Onychoteuthis***, which in addition has 2 discrete photophores on the ink sac/intestine. Hectocotylus absent in males of ***Onykia*** and ***Onychoteuthis***, but the spermatophoric sac ("penis") elongate; unusual sexual dimorphism in ***Walvisteuthis***; mature males in other genera unknown. Gladius with primary conus and with a rostrum, usually prominent. **Colour:** maroon to brick red, darker dorsally. ***Onykia*** dark blue to deep purple, especially on dorsal surface, with reflective sheen.

Size: Varies among species from 15 to 230 cm mantle length.

Interest to Fisheries: Several species from the 6 genera in this family currently are commercially exploited and have significant potential for fisheries.

Remarks: Six genera currently are recognized: ***Ancistroteuthis***, ***Kondakovia***, ***Notonykia***, ***Onychoteuthis***, ***Onykia*** and ***Walvisteuthis***. The generic boundaries, however, are not well defined nor understood, and the family is in need of revision, in spite of several systematic studies over the past 2 decades (e.g. Kubodera *et al.* 1998, Vecchione *et al.* 2007c). ***Onychoteuthis***, the most widely distributed genus, is cosmopolitan and occurs in open-ocean in all but the polar and subpolar seas; it is the only genus of the onychoteuthids to possess visceral photophores, but eye photophores are a shared character with ***Ancistroteuthis***. The genus ***Onykia*** contains numerous described species, including a number of poorly defined species in tropical and subtropical seas, several of which are new species in need of description. Current thought confirms that the formerly recognized genus ***Moroteuthis*** (which includes the giants of the family, with mantle lengths up to 2.3 m) is synonymous with ***Onykia*** (e.g. Wakabayashi *et al.*, 2007, Vecchione *et al.*, 2007c). This concept was first expressed by Tsuchiya and Okutani (1992 [1991]), but had not been universally accepted earlier (e.g. Nesis, 2000, 2002). Thus, confusion in the nomenclature persisted for some years.

In this catalogue, the generic name ***Onykia*** is used to refer to all those species formerly known as ***Moroteuthis*** species. However, we recognize that systematics within the family is unstable and we strongly encourage that further studies and research be carried out to advance and stabilize our knowledge. We also note that while this catalogue was in press, a major revision on the family had just been completed and a summary of that work was presented in Vigo (Spain), at the 2009 CIAC meeting (Bolstad, in press). We suggest the reader refer to that very important work, that significantly improves our knowledge on this family, for additional information.

Chaunoteuthis, long recognized as a distinct genus from all other onychoteuthid genera by its gelatinous consistency and autotomized tentacles in the adult stage, clearly and unequivocally is synonymous with ***Onychoteuthis banksii*** (Arkhipkin and Nigmatullin, 1997); this body form represents the post-maturation, post-spawning, senescent stage of females and the existence of a "***Chaunoteuthis***" stage for other ***Onychoteuthis*** species is probable.

Kondakovia is an Antarctic (circum-Antarctic) form that can attain a mantle length of 108 cm, but relatively little is known about its biology. ***Notonykia*** was newly described in 1998 from the southern Atlantic waters off southwestern and southeastern South Africa, and subsequent reports indicate that it is circumpolar in the sub-Antarctic belt.

Phylogenetic studies on the family (Bonnaud *et al.* 1998; Nesis, 2000) confirm its monophyletic status to the extent that specimens were available to these authors

Onychoteuthids are very abundant oceanic forms that frequently aggregate in schools. Some species, e.g. ***Onychoteuthis borealijaponica***, undergo seasonal migrations for feeding, then spawning.

Literature: Roper *et al.* (1984), Nesis (1982, 1987), Tsuchiya and Okutani (1992 [1991]), Arkhipkin and Nigmatullin (1997), Bonnaud *et al.* (1998), Kubodera *et al.* (1998), Nesis (2000), Sweeney and Young, 2003v), Vecchione *et al.* (2007c), Wakabayashi *et al.* (2007).

Key to the genera of Onychoteuthidae

1a. Presence of warts or wrinkles on the skin[1/] . . . . ***Onykia***
1b. Skin smooth . . . . ***→2***

2a. Mantle muscle soft, fleshy, ammoniacal . . . . ***→ 3***
2b. Mantle muscular, firm, dense, non-ammoniacal . . . . ***→ 4***

3a. Tentacular club with 2 marginal series of small suckers . . . . ***Kondakovia***
3b. Tentacular club with no marginal series of suckers . . . . ***Notonykia***

4a. Nuchal folds numerous . . . . ***→ 5***
4b. Nuchal folds few . . . . ***Walvisteuthis***

5a. Two small, round photophores (light organs) present on intestine . . . . ***Onychoteuthis***
5b. No photophores present on intestine . . . . ***Ancistroteuthis***

Table 14

Character states within genera of the Onychoteuthidae (from Vecchione *et al*., 2007c)

Genus	Many occipital folds	Visceral photophores	Gladius rostrum	Warts or wrinkles in skin	Club: marginal suckers	Fin shape
Ancistroteuthis	**Yes**	No	Thin, pointed	No	No	Sagittate
Kodakovia	No	No	Thick, pointed	No	**Yes**	Rhomboidal
Notonykia	**Yes**	No	Thin, pointed	No	No	Rhomboidal
Onychoteuthis	**Yes**	**Yes**	Thin, pointed[1/]	No	No/few	Rhomboidal/ sagittate
Onykia	No	No	Thick, pointed	Yes[2/]	No	Rhomboidal/ sagittate
Walvisteuthis	No	No	Thin, rounded	No	Few	Oval

[1/] Somewhat rounded in *O. meridiopacifica*.
[2/] Except in *"Onykia"knipovitchi*.

Onychoteuthis Lichtenstein, 1818

Plate IX, 60

Onychoteuthis Lichtenstein, 1818: *Isis, oder Encyclopädische Zeitung*, (9): 1591–1592 [1591].

Type Species: *Onychoteuthis banksii* (Leach, 1817).

Frequent Synonyms: *Onychoteuthis* Lichtenstein, 1818; *Teleoteuthis* Verrill, 1882a; *Chaunoteuthis* Appellof, 1891; *Teleonychoteuthis* Pfeffer, 1900.

Diagnostic Features: Mantle densely muscular, cylindrical, tapered posteriorly to pointed tail; **non-ammoniacal**. Skin smooth, without warts, wrinkles. **Gladius visible through integument along dorsal midline**; conus well developed, deep; rostrum thin, pointed, diagonally-directed dorsally, extends posterior to end of mantle musculature as characteristic spike. Fins rhomboidal, to slightly heart-shaped, sagittate, posteriorly attenuate. **Nuchal folds prominent, 8 to 10**. **Tentacular club with 2 medial series of large, strong hooks on manus (19 to 27)**; no marginal series of suckers in adult (occasionally a few present). Chitinous rings of suckers on arms smooth, without dentition. **Photophores present in mantle cavity**: 1 small, anteriorly on ink sac, near anus; 1 large, posteriorly on intestine; **a bilobed photophore present on the ventral surface of each eye**.

Size: Small- to medium-sized squids, maximum mantle length 350 mm.

Geographical Distribution: Mostly in tropical and subtropical waters throughout the world's oceans, although they are also common in high latitudes of the North Pacific.

Habitat and Biology: Species are epipelagic to mesopelagic, mostly strongly eurythermal.

Literature: Vechione *et al*. (2007b); for additional references see the family.

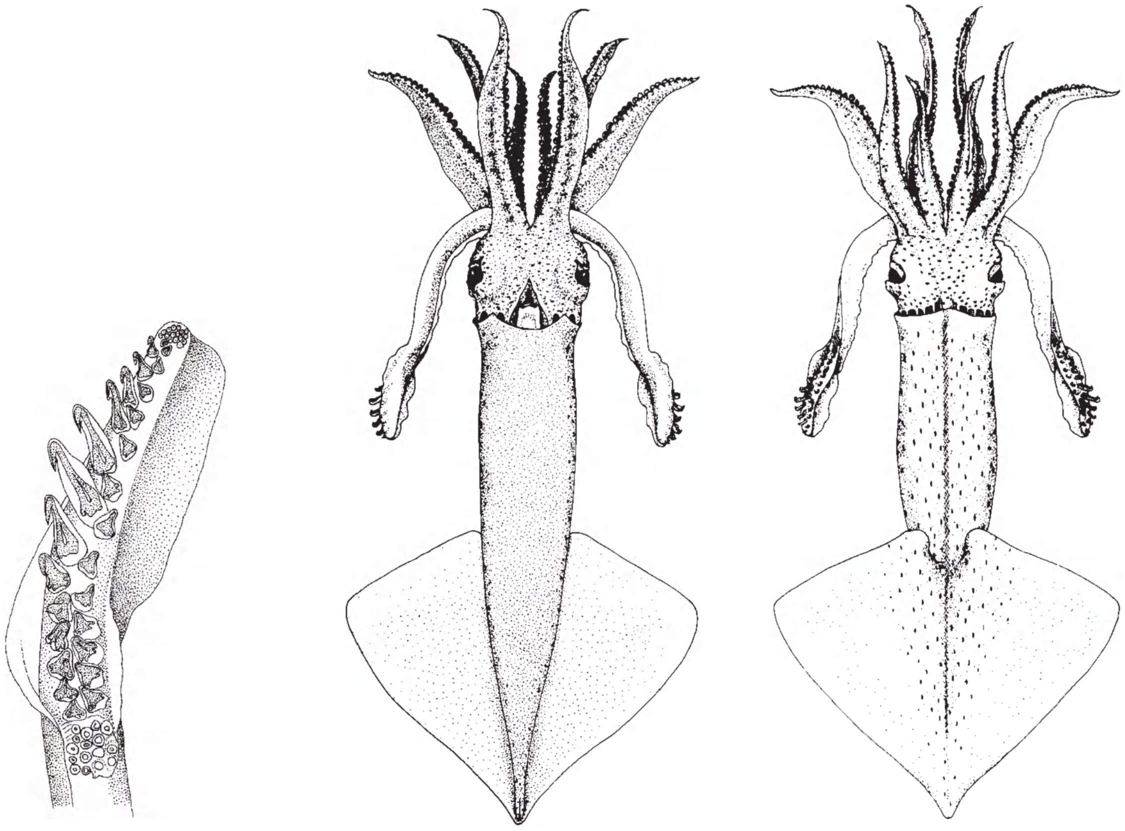
[1/] Except in "*Onykia*" *knipovitchi*, the atypical member of the genus *Onykia*.

Onychoteuthis banksii (Leach, 1817) **Fig. 327**

Loligo banksii Leach, 1817, *Zoological Miscellany; being Descriptions of New or Interesting Animals*, 3(30): 137–141 [141]. [Type locality: not designated].

Frequent Synonyms: *Loligo banksii* Leach, 1817; *Onychoteuthis bergii* Lichtenstein, 1818; *O. molinae* Lichtenstein, 1818; *Onykia angulatus* Lesueur, 1821; *Loligo bartlingi* Lesueur, 1821; *L. felina* Blainville, 1823; *L. uncinata* Quoy and Gaimard, 1825 *in* 1824-1826; *Onychoteuthis lessoni* Ferussac, 1830, *in* Lesson 1830–1831; *O. fleuryi* Reynaud, 1831; *O. lesueuri* d'Orbigny, 1835 *in* Ferussac and d'Orbigny 1834–1848; *O. krohni* Verany, 1847; ?*Loligo bianconi* Verany, 1847; *Onychoteuthis rutilus* Gould, 1852; *O. fusiformis* Gabb 1862; *O. aequimanus* Gabb, 1868; *O. lobipinnis* Dall, 1871; *O. raptor* Owen, 1881; *Chaunoteuthis mollis* Appellof, 1891; *Teleoteuthis caroli* Joubin, 1900.

FAO Names: En – Common clubhook squid; **Fr** – Cornet crochu; **Sp** – Luria ganchuda.



tentacular club **ventral view** **dorsal view**

Fig. 327 ***Onychoteuthis banksii***

Diagnostic Features: Mantle very robust, muscular; **numerous** (9 or 10 pairs) **elongate, flap-like nuchal folds around the dorsolateral surface of the neck**; a **large, elongate, patch-like photophore (light organ) on ventral surface of each eye**. **Fins muscular, rhomboidial, with sharp lateral angles (70° to 90°), tail pointed**; length of fins about 55 to 65% of mantle length. **Tentacular clubs slightly expanded with 20 to 22 large, claw-like hooks in 2 medial series**; no marginal series of suckers (occasionally a very few suckers); 13 to 15 small suckers in 4 series on dactylus; carpal-locking apparatus with 8 to 10 suckers plus accompanying 7 to 9 knobs; club length 35 to 45% mantle length. Gladius visible as a dark line through the skin along dorsal midline of mantle. **Two large, round, bulbous light organs** along ventral midline on intestinal tract/ink sac (anterior one-half diameter of posterior one).

Size: Medium-sized squid; mantle length up to 300 mm (370 mm only in the northern Pacific Ocean, Nesis 1982, 1987).

Geographical Distribution: This species occurs worldwide in tropical and temperate oceanic waters to 44°S, including the Mediterranean Sea; it is absent only from Arctic, northern boreal Atlantic, sub-Antarctic and Antarctic Oceans (Fig. 328).

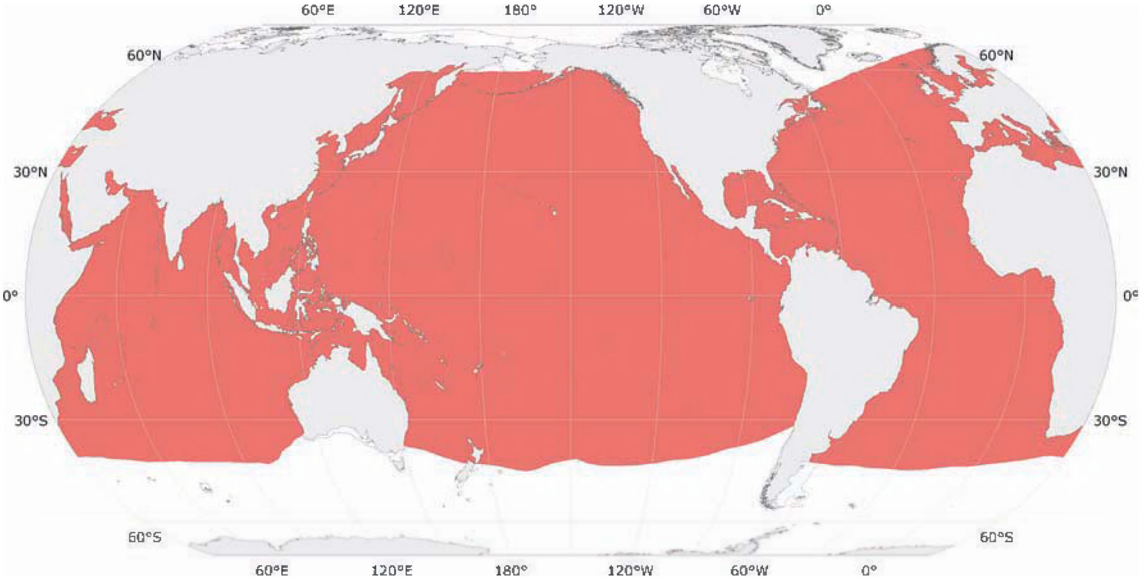


Fig. 328 ***Onychoteuthis banksii***

🟥 Known distribution

Habitat and Biology: ***Onychoteuthis banksii*** is an oceanic, eurythermal, meso- and epipelagic species that occurs from the surface to 150 m depth, but it may be found as deep as 4 000 m. This schooling species frequently is observed "flying" above the surface to escape predators in pursuit. Its biology is poorly known, but very dense muscular structure and high respiration rates confirm it is a fast-swimming, slow-growing species. Males mature earlier than females; eggs are small (0.2 to 0.5 mm), and oocyte development is synchronous with high fecundity (over 200 000 eggs). Paralarvae are abundant in the eastern Atlantic Ocean, particularly from January to March. Spent females have severely degenerated muscular tissue of head, mantle, fins, as well as missing tentacles, so that they appear almost gelatinous; this advanced senescent form was recognized as a distinct genus and species, ***Chaunoteuthis mollis*** Appellof, 1891, for many years, but it has been synonymized once the mystery was unraveled. Prey consists of fishes and squids. Predators include giant red shrimp, fishes, e.g. albacore, yellowfin tuna, lancetfish, swordfish, tiger shark, smooth hammerhead shark, spinner, Frasier's striped and Risso's dolphins, toothed whales and fur seals.

Interest to Fisheries: While this is a very firm-fleshed, meaty squid, surprisingly, it has few directed fisheries at this time. A fishery exists in the Kurile Islands-Hokkaido region off Japan, where the species can reach 370 mm mantle length. It frequently is lured by a bright light and dip-netted at night. Also it is found on decks of small underway vessels in the morning. The quality of the flesh as human food is judged to be good; occasionally it is dried and sold for human consumption. It is heavily preyed upon by pelagic fishes (tunas, swordfishes, etc.), blue sharks, fur seals, odontocete (toothed) whales; e.g. southern bottlenose whales, Risso's and spotted dolphins, etc.

Local Names: ITALY: Totano dalle unghie.

Remarks: It is believed that this taxon actually represents a complex of distinct species, perhaps 4 or 5 in the world's oceans (Young, 1972a, Young and Harman, 1987, Vecchione *et al.*, 2007b); in the type locality, for example, 2 species seem to coexist (Young, pers com. in Bolstad, 2007). This, however, has not yet been confirmed because of a lack of the entire growth series of specimens for each suspected "species". The bite of this squid appears to be toxic to humans and resembles a wasp sting in its effect. There has been some confusion on the spelling of the species name, "banksi" or "banksii". Following the International Code of Zoological Nomenclature, the original "ii" ending is considered correct (Kubodera *et al.*, 1998).

Literature: Sanchez and Moli (1985), Young (1995), Arkhipkin and Nigmatullin (1997), Kubodera *et al.* (1998), Nesis (2000, 2002), Bolstad (2007).

Onychoteuthis borealijaponica Okada, 1927

Fig. 329

Onychoteuthis borealijaponicus Okada, 1927b, *Bulletin de l'Institut Océanographique, Monaco*, 494: 1–7 [7]. [Type locality: Japan].

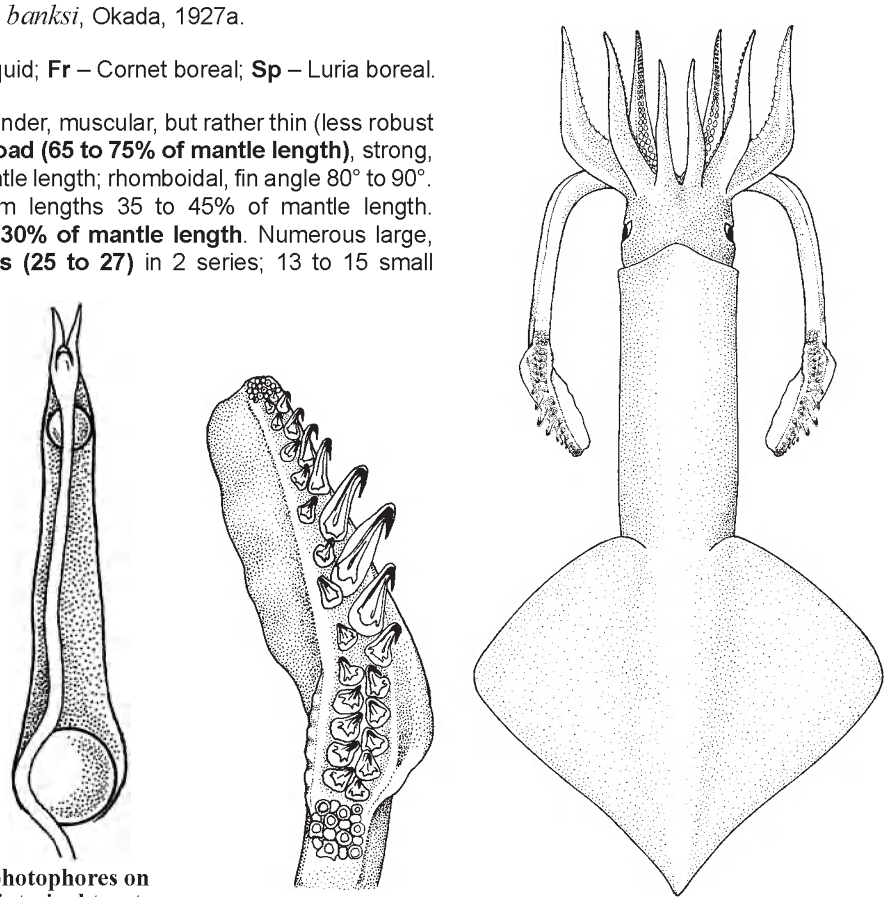
Frequent Synonyms: *Onychoteuthis banksi*, Okada, 1927a.

FAO Names: En – Boreal clubhook squid; **Fr** – Cornet boreal; **Sp** – Luria boreal.

Diagnostic Features: Mantle long, slender, muscular, but rather thin (less robust than ***Onychoteuthis banksii***). **Fins broad (65 to 75% of mantle length)**, strong, muscular, their length 55 to 60% of mantle length; rhomboidal, fin angle 80° to 90°. Eight or 9 pairs of nuchal folds. Arm lengths 35 to 45% of mantle length. **Tentacular club large, length 20 to 30% of mantle length**. Numerous large, **claw-like hooks on tentacular clubs (25 to 27)** in 2 series; 13 to 15 small suckers on dactylus; well-defined carpal apparatus with 8 to 10 suckers plus their accompanying 7 to 9 knobs. **Oval photophore patch on ventral periphery of each eye**; **2 ovoid light organs on ventral viscera** connected by a silver iridescent band: anterior organ is small on ink duct posterior to anal papilla; posterior organ is much larger, on ink sac.

Size: Medium-sized species; maximum mantle length 370 mm in females, 300 mm in males; maximum weight 1.1 kg.

Geographical Distribution: The species is distributed in the far North Pacific Ocean from the Japan seas to off northwestern United States and Canada (Fig. 330).



photophores on intesinal tract ventral view

tentacular club

dorsal view

Fig. 329 ***Onychoteuthis borealijaponicus***

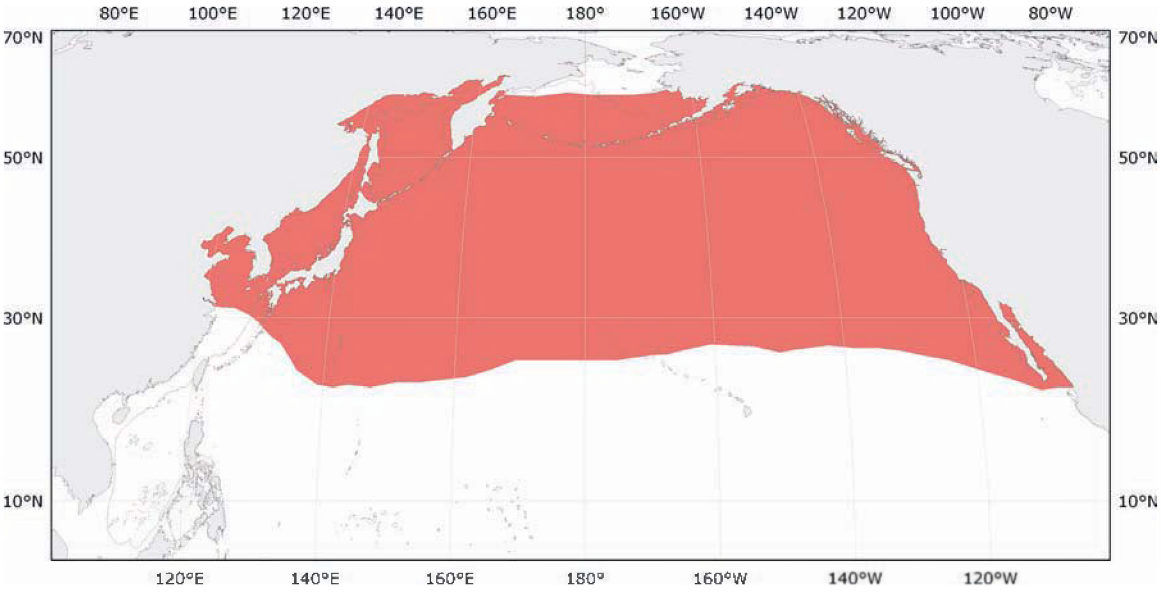


Fig. 330 ***Onychoteuthis borealijaponicus***

🟥 Known distribution

Habitat and Biology: ***Onychoteuthis borealijaponica*** is an oceanic, epipelagic to mesopelagic species that occurs from the surface down to undetermined upper mesopelagic depths. It is most abundant in the northwestern North Pacific Ocean in surface waters of 9° to 13°C. It replaces ***Onychoteuthis banksii*** in colder, northern Pacific waters and it migrates to sub-Arctic waters in summer to feed, then returns to subtropical oceanic waters in autumn and winter to mate and spawn. East of Hokkaido, Japan, adults concentrate along the 10°C isotherm. The population around the Japanese Islands appears to undergo seasonal north-south migrations. Juveniles are encountered exclusively in the warm-water area off southwestern Japan in the Kuroshio Current and the countercurrent area, while adults occur in the cold water zones off Hokkaido, further north. In June, subadults from the south arrive on these fishing grounds and remain there feeding until autumn. Then they migrate southwards to mate and spawn at medium depths from late autumn through the winter southwest of Japan. The life span of both sexes is approximately 1 year, but males mature at smaller sizes (i.e. about 250 mm), and younger ages than females, where mantle length at maturity varies between 300 and 350 mm. The species preys on small fishes, and cannibalism is common. Predators of this species include: epipelagic fishes, e.g. Pacific pomfret, swordfish, salmon shark; marine mammals, e.g. dolphins, sperm whales, Guadalupe fur seals and, most significantly in the central North Pacific Ocean, northern fur seals. ***Ommastrephes bartramii*** is a major predator in the transitional waters of the central North Pacific Ocean.

Interest to Fisheries: Following the decline in the yields of ***Todarodes pacificus***, ***O. borealijaponica*** increasingly is being fished commercially off northwestern Honshu, eastern Hokkaido, and in the northeastern Pacific off Washington State and British Columbia. It is taken primarily with jigs and drift gillnets. Jigging is particularly successful at night. The photophores make it appear as a dark shadow irradiating pale blue light near the surface. Sometimes it soars aboard moving vessels at night. It has been suggested that the species might support commercial fishing operations in the northwestern Pacific north of the sub-Arctic boundary, particularly during late summer and autumn.

Local Names: JAPAN: Tsumeika.

Remarks: ***Onychoteuthis borealijaponica*** is distinguished from ***O. banksii*** by its smaller clubs with a larger number of hooks, 2 oval visceral photophores connected by a silvery strand, of which the anterior is much smaller than the posterior; its size at maturity and maximum size are much larger than in ***O. banksii***; its distribution is restricted to the far northern Pacific where it prefers much cooler water than does ***O. banksii***.

Literature: Yamamoto and Okutani (1975), Kubodera *et al.* (1998), Nesis (2002), Watanabe *et al.* (2006b).

Ancistroteuthis Gray, 1849

Ancistroteuthis Gray, 1849, *Catalogue of the Mollusca in the Collection of the British Museum, I: Cephalopoda Artepedia*, 1–164 [55].

Type Species: *Ancistroteuthis lichtensteini* (Férussac, 1835).

Diagnostic Features: Mantle densely muscular, cylindrical, slender, tapered posteriorly, **non-ammoniacal**; **tail acutely pointed**, supported by long spine of gladius. **Fin heart-shaped, sagittate, attenuate into elongate tail**. Gladius not visible through dorsal mantle. **Nuchal folds prominent, 6 to 10**. Tentacular club with 2 medial series of large, strong hooks on manus, no marginal series of suckers. **Photophores absent on ink sac/intestine**; an oval, opaque zone with small posterior patch of photophoric tissue on ventral surface of eyes. Skin smooth on mantle, head.

Remarks: The genus currently is monotypic. However, 3 geographic forms occur in the Atlantic Ocean (type locality of ***Ancistroteuthis lichtensteini*** *sensu stricto* is in Mediterranean Sea) and 1 in the Pacific Ocean, so the species as currently designated actually represents a complex of closely related species, as yet not fully understood nor named. These currently are termed ***A. lichtensteini*** *senso stricto*, Mediterranean Sea, ***A. lichtensteini***, central Atlantic Ocean form, ***A. lichtensteini***, South Atlantic Ocean form, and ***A. lichtensteini***, Pacific Ocean form (see Kubodera *et al.*, 1998). According to Vecchione *et al.* (2008b), however, the South Atlantic and South Pacific forms, probably belong to ***Notonykia africanae*** (Nesis *et al.*, 1998b). Additional systematic study is needed to clarify the status of this species complex.

Ancistroteuthis lichtensteini (Férussac, 1835) **Fig. 331**

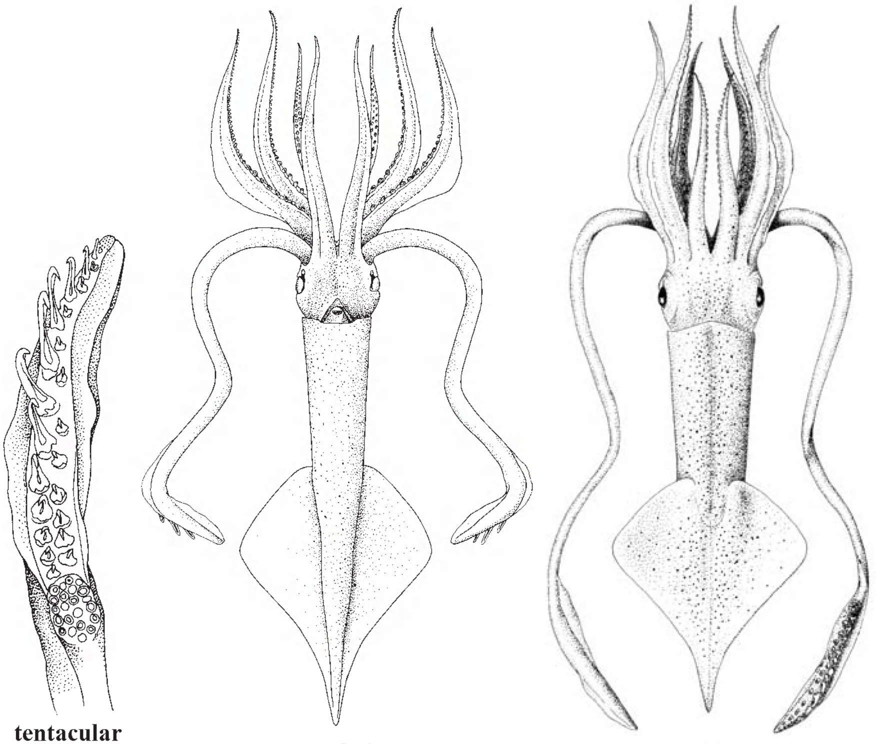
Onychoteuthis lichtensteini Férussac, 1835, *in* Férussac and d'Orbigny, 1834-1838, *Histoire Naturelle Générale et Particulière des Cèphalopodes Acètabulifères Vivants et Fossiles, Atlas*, *Onychoteuthis*, [pl.8]. [Type locality: Mediterranean Sea, near Nice, France).

Frequent Synonyms: *Onychoteuthis lichtensteini* d'Orbigny, 1839; *Onychoteuthis hamatus* Risso, 1854.

FAO Names: En – Angel squid; **Fr** – Cornet archangel; **Sp** – Luria paloma.

Diagnostic Features: Mantle slender, very muscular, posterior end acutely pointed and supported by long, thin, pointed spine of gladius. Occipital folds numerous. Skin smooth. **Fins strong, lanceolate, sagittate posteriorly; posterior margins concave**. Fin length 60% of mantle length, width 57% of mantle length. Tentacular clubs in adults slightly expanded, length 30% of mantle length, with **2 median series of hooks (20 to 21)**; **lateral series of suckers absent**; 16 or 17 small suckers on dactylus; carpal-fixing apparatus of club elliptical with 9 or 10 suckers plus 9 or 10 knobs; 8 or 9 pairs of flap-like nuchal folds in neck area. Arm formula IV>III=II>I, lengths 40 to 53% of mantle length. Rachis of gladius not visible along dorsal midline of mantle in subadults, visible anteriorly in adults; conus a minute spoon and long, thin, pointed rostrum. **Light organs absent on intestinal tract**; a small posterior patch of **bioluminescent tissue occurs on the ventral surface of each eye**.

Size: Maximum mantle length is 300 mm.



tentacular club

ventral view

dorsal view

Fig. 331 *Ancistroteuthis lichtensteini*

Geographical Distribution: Eastern Atlantic Ocean from northwestern Spain and the Straits of Gilbraltar to Angola, and throughout the Mediterranean Sea; the Gulf of Mexico, the central eastern Atlantic Ocean, and the South Atlantic Ocean; Melanesia and the southwestern Pacific (Fig. 332).

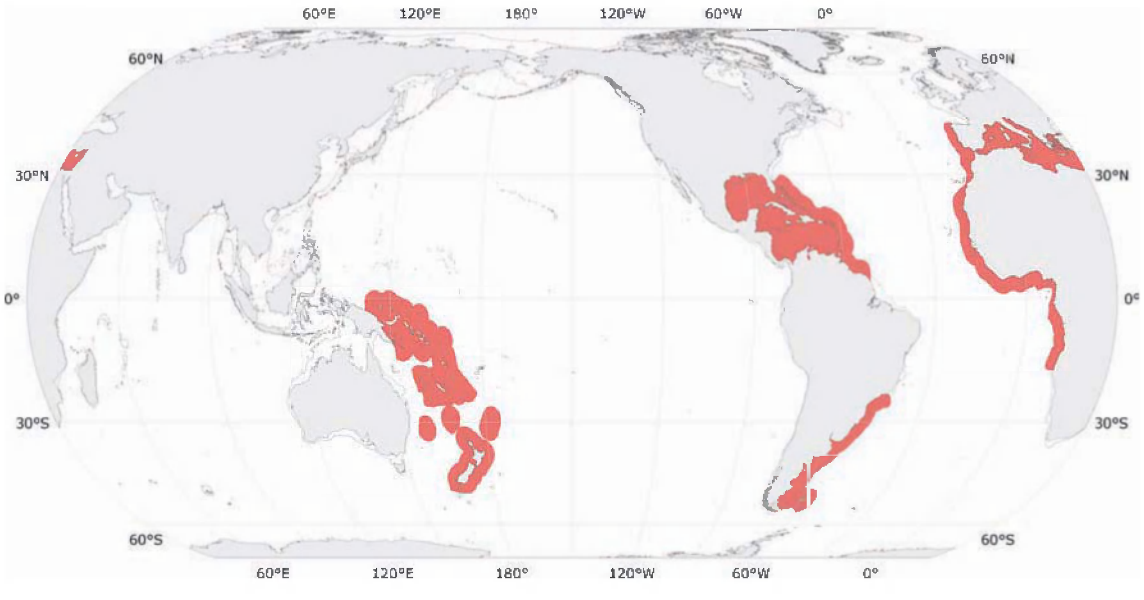


Fig. 332 *Ancistroteuthis lichtensteini*

🟥 Known distribution

Habitat and Biology: ***Ancistroteuthis lichtensteini*** is an epipelagic, mesopelagic to benthi-bathyal species that occurs in open warm-temperate waters from the surface to about 250 m depth; open net records to 1 270 m bottom depth. In the western Mediterranean it is associated with gravel bottoms during spring and summer. Males mature at around 200 mm mantle length; spawning occurs in the summer. It feeds on epipelagic and upper mesopelagic finfishes and crustaceans, and in turn is preyed upon by cetaceans, e.g. Risso's dolphin and striped dolphins, sperm whales, and pelagic fishes, e.g. swordfish, and by giant red shrimp in the Mediterranean.

Interest to Fisheries: Currently no directed fishery exists for this species; it is taken only as bycatch in pelagic and deep, open benthic trawls. However, the size and firm consistency of the flesh make it a potential target for a fishery.

Local Names: ITALY: Totano angelo; USA: Lichtenstein's angel squid.

Remarks: The geographical distribution of this species complex is incompletely known. The distribution appears very disjunct because so few specimens have been reported in the scientific literature.

Literature: Kubodera *et al.* (1998), Lefkaditou *et al.* (2003), Okutani (2005), Vecchione *et al.* (2008b).

Notonykia Nesis, Roeleveld and Nikitina, 1998

Notonykia Nesis, Roeleveld and Nikitina, 1998b, *Ruthenica*, 8(2): 153–168 [154].

Type Species: *Notonykia africanae* Nesis, Roeleveld and Nikitina, 1998.

Frequent Synonyms: None.

Diagnostic Features: Photophores absent. Dorsal **nuchal folds numerous, at least 4 or 5**. Conus of gladius short, chitinous; rostrum thin, pointed. Skin smooth, without wrinkles or warts. Marginal club suckers absent. Fins rhomboidal. See species characters for details.

Literature: Nesis *et al.* (1998b), Bolstad *et al.* (2007).

Notonykia africanae Nesis, Roeleveld and Nikitina, 1998

Notonykia africanae Nesis, Roeleveld and Nikitina, 1998b, *Ruthenica*, 8(2): 153–168 [154], 6 figs. [Type locality: 33°42'S, 17°21'E, off South-Western Cape, South Africa].

Frequent Synonyms: None.

FAO Names: En – African notalian clubhook squid; **Fr** – Cornet crochu africane; **Sp** – Luria ganchuda africana.

Diagnostic Features: Mantle densely muscular (non-ammoniacal), broad, cylindrical anteriorly, tapers to moderately pointed, conical tail. **Fins large**, muscular, rhomboidal; **length 58 to 66% of mantle length** (average 59%), width 66 to 84% of mantle length (average 72%). Anterior margins of fins slightly convex, posterior margins nearly straight, very slightly drawn out into a short tail. Skin smooth, not rugose or tubercular. **Nuchal folds present**, 4 or 5 per side. **Photophores absent**. **Tentacular club narrow, with 2 medial series of 14 to 20, usually 17 or 18, hooks**; fifth to sixth hooks in ventral row by far the largest; hooks on dorsal row small. No marginal series of suckers. Dactylus with 20 to 38 minute suckers; carpus well-defined, with 6 to 12 suckers plus their accompanying knobs. Buccal connectives attach dorsally to arms I and II, ventrally to III and IV (type DDVV). **Hectocotylus absent**. Gladius with strong longitudinal ridge, with short, terminal conus and short, thick, chitinous, cartilaginous rostrum.

Size: Small-sized species; maximum known mantle length 180 mm.

Fig. 333

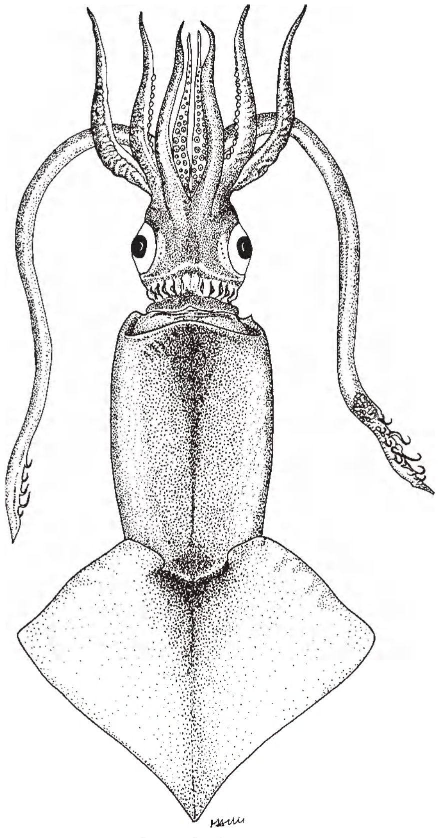


Fig. 333 ***Notonykia africanae***

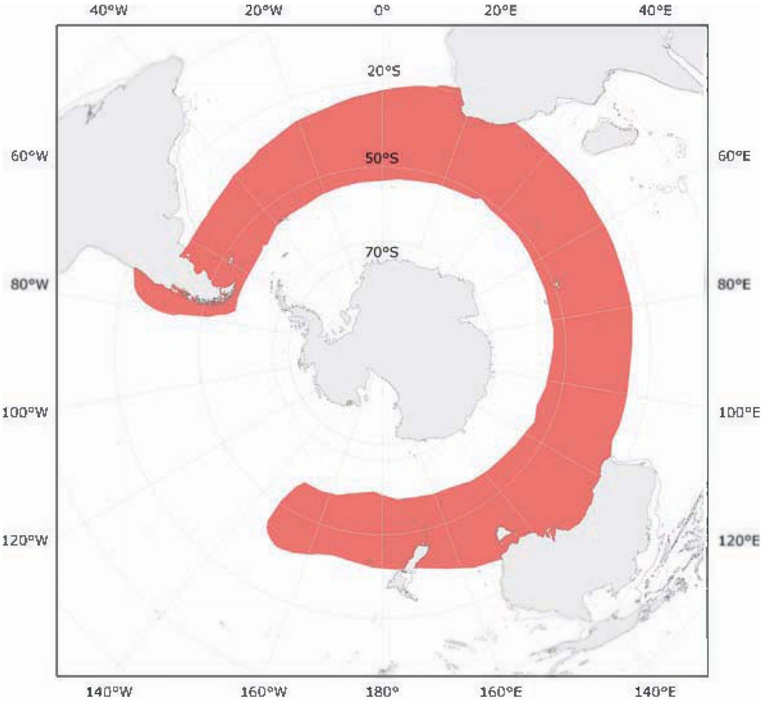


Fig. 334 ***Notonykia africanae***

🟥 Known distribution

Geographical Distribution: This species is circumpolar in a sub-Antarctic belt between 30°S (off Western Cape, South Africa) and 53°S (south of New Zealand): it occurs off South Africa, off southern Chile, off southern Australia, off eastern North Island, New Zealand to about 145ºW (Fig. 334).

Habitat and Biology: *Notonykia africanae* has a distribution range intermediate between a Southern Subtropical Convergence distributional pattern and the true notalian type of distribution. The species has a very broad vertical distributional range, also, as it occurs in epi-, meso- and bathypelagic layers, between 0 and 1 200 m, mostly 30 to 200 m, and ascends to the surface at night. Subadults and the earliest stages of maturity are broadly eurybathic, from approximately 0 to 1 000 m, but they are primarily mesopelagic with records from approximately 500 to 900 m. Maturation in males begins at 90 to 100 mm mantle length and in females at 100 to 130 mm mantle length. The size at full maturity for males seems to be greater than 130 mm and for females greater than 150 mm.

Interest to Fisheries: No interest in a fishery exists at the present time. But, because it is a member of the muscular, non-ammoniacal group of onychoteuthids, it seems possible that a fishery could develop in the future if large concentrations of this small squid are discovered.

Literature: Nesis *et al.* (1998b), Nesis (2000), Bolstad (2007).

Notonykia nesisi Bolstad, 2007

Notonykia nesisi Bolstad, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 305–335 [327]. [Type locality: 46°06’80”S, 171°52’00”E, New Zealand waters, over 1 333 m].

Frequent Synonyms: *Ancistroteuthis lichtensteini*, southern Pacific form (Kubodera *et al.* 1998: 282; non Ferussac 1835: 334, Pls. 8, 14); Nesis *et al.*, 1998: 164.

FAO Names: En – Nesis notalian clubhook squid; **Fr** – Cornet crochu de Nesis; **Sp** – Luria granchuda de Nesis.

Diagnostic Features: Neck (shaft) of largest ventral tentacular hooks straight; profile of hook forms an overall ‘J’-shape; carpus with 7 to 9 suckers; **dorsal tentacular hooks 1 and 2 noticeably larger than ventral tentacular hooks 1 and 2**.

Size: Small-sized species, up to 105 mm mantle length.

Geographical Distribution: Currently known only from the sub-Antarctic ocean, principally above and south of Chatham Rise, east of New Zealand, South Pacific Ocean.

Habitat and Biology: Occurs at depths of 0 to 950 m, mostly the upper 300 m.

Literature: Bolstad (2007), Bolstad *et al.* (2007).

Onykia Lesueur, 1821

Plate X, 61

Onykia Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101 [98].

Type Species: *Onykia carriboea* Lesueur, 1821.

Frequent Synonyms: *Onychia* Latreille, 1825; *Steenstrupiola* Pfeffer, 1884.

Diagnostic Features: Mantle muscular to moderately soft; **dermis of mantle with warty structures or soft wrinkles in adults** (***Onykia knipovitchi*** with smooth skin only). Gladius not visible through skin along dorsal mantle midline. **Three occipital folds present on lateral side of posterior head**; dorsalmost fold with occipital membrane curves dorsally and extends to or nearly to nuchal cartilage. **Tentacular club** in subadults and adults **with 2 medial series of hooks on manus, no suckers**; suckers occur only on carpal cluster (with alternating knobs), and minute suckers occur on the distal terminal pad. **Photophores are absent**. Funnel groove with inverted y-shaped ridge in animals longer than 100 mm mantle length (possibly absent in ***O. ingens*** and ***O. knipovitchi***); anterior margin of funnel groove rounded. Gladius with long, thick cartilaginous rostrum; long, lanceolate vanes extend to the conus field without a narrow posterior 'neck', as occurs in ***Onychoteuthis***, ***Ancistroteuthis*** and ***Notonykia***.

Size: Medium-sized (275 mm mantle length) to very large (1.6 to 2.3 m mantle length) squids.

Remarks: For many years a number of species now recognized as members of ***Onykia*** were placed in the genus ***Moroteuthis***. Tsuchiya and Okutani (1992 [1991]), demonstrated that specimens historically attributed to ***Onykia*** Lesueur, 1821, were the young stages of known species of ***Moroteuthis*** Verrill, 1881c, thus making the generic name ***Moroteuthis*** a junior synonym of ***Onykia***. Tsuchiya and Okutani (1992 [1991]) also demonstrated that "***Moroteuthis***" ***japonica*** Taki, 1964, and "***Moroteuthis***" ***pacifica*** Okutani, 1983a, were growth stages of ***Onykia robusta***. Kubodera *et al*. (1998) state that ***Onykia indica*** Okutani, 1981 probably is the young form of some known species of ***Onykia***. ***Onykia rancureli*** Okutani, 1981, has been widely recognized as being very different from other members of this genus and several authors have suggested that a new generic name is needed (e.g. Toll, 1982; Tsuchiya and Okutani, 1992 [1991]). Recent evidence suggests that this generic designation should be ***Walvisteuthis***, and consequently, the species is considered to be identical to ***Walvisteuthis virilis*** (see Remarks section under ***W. virilis***) by an authoritative fraction of the scientific community (Young *et al*., 2003). Molecular results of the genetic studies by Bonnaud *et al*. (1998) and Wakabayashi *et al*. (2007) indicate that the genus ***Onykia*** may not be monophyletic, since "***O. knipovitchi***" represents an atypical member of the genus. We strongly encourage that further research be carried out on this genus, in particular.

Literature: Tsuchiya and Okutani (1992 [1991]), Kubodera *et al*. (1998), Bonnaud *et al*. (1998), Nesis (2000), Vecchione *et al*. (2007c), Wakabayashi *et al*. (2007).

Onykia carriboea Lesueur, 1821

Fig. 335

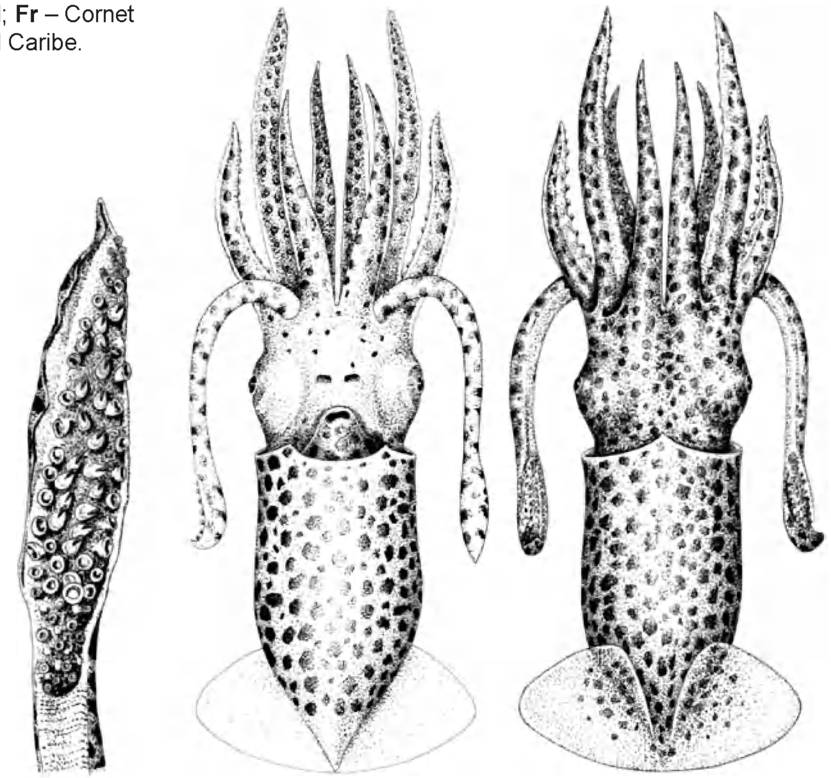
Onykia carriboea Lesueur, 1821, *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–107 [98]. [Type locality: Gulf of Mexico and Gulf Stream].

Frequent Synonyms: *Loligo cardioptera* Lesueur and Petit, 1807; *L. laticeps* Owen, 1836; *L. plagioptera* Souleyet, 1852 *in* 1841–1852; *Onychia binotata* Pfeffer, 1884; *Steenstrupiola atlantica* Pfeffer 1884; *Teleoteuthis carriboea* Verrill, 1885; *Teleoteuthis (Onychia) agilis* Verrill, 1885; *Teleoteuthis jattai* Joubin, 1900.

FAO Names: En – Caribbean clubhook squid; **Fr** – Cornet crochu de Caraïbes; **Sp** – Luria ganchuda del Caribe.

Diagnostic Features: Mantle muscular, cross-section nearly ellipsoidal in young, to cylindrical with growth. **Fins much wider than long**; **length nearly 50% of mantle length**; width 70 to 75% of mantle length; fins subrhombic, convex anterior and posterior margins, bluntly rounded lateral angles. **Tentacle club with 2 medial series of about 10 to 12 hooks each** (total 20 to 24 hooks), 2 marginal series of small suckers; well-developed **carpus with 8 or 9 suckers, plus their accompanying knobs**; dactylus with a few very small to minute suckers. Gladius with short, dorsally curved rostrum. Skin surface smooth with dense, purplish chromatophores and reflective, silvery sheen, even ventrally. Chromatophores of a vivid, deep purple colour, particularly densely packed on dorsal mantle and dorsal head.

Size: The maximum known mantle length is 100 mm.



tentacular club ventral view dorsal view

Fig. 335 *Onykia carriboea*

Geographical Distribution: This species is believed to have a cosmopolitan circumglobal distribution, throughout tropical and subtropical/warm temperate oceans. However, no definitive statement can be made before its specific status is clarified (see Remarks) (Fig. 336).

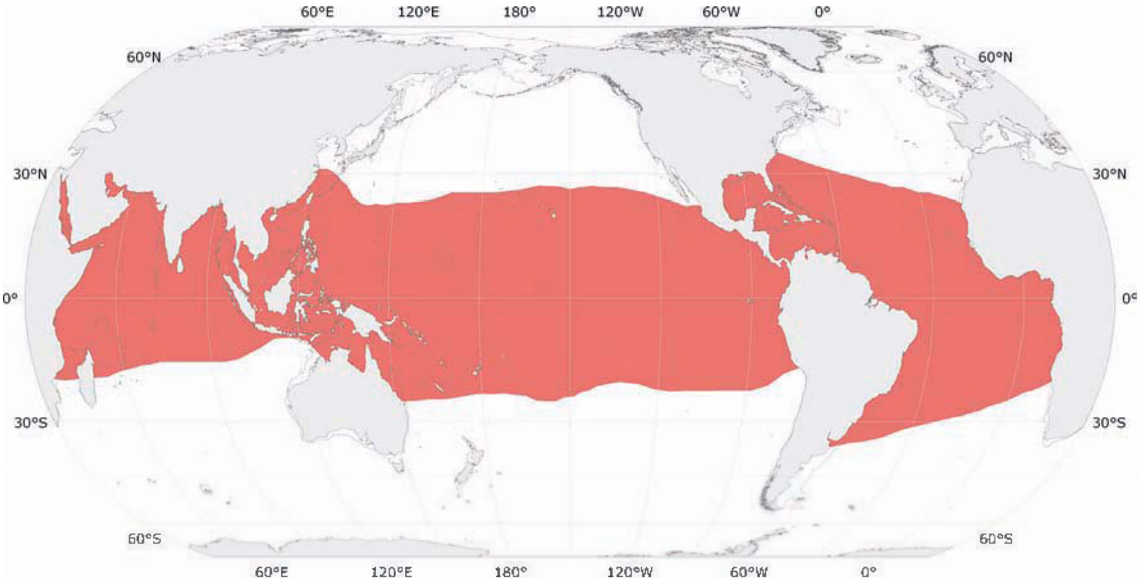


Fig. 336 ***Onykia carriboea***

🟥 Known distribution

Habitat and Biology: Paralarvae and juveniles of ***Onykia carriboea*** live near and at the surface, often in association with *Sargassum* weed. Biology, growth and maturity are very poorly known. This species is preyed upon by squid, ***Sthenoteuthis oualaniensis***, and by yellowfin and bigeye tunas, and undoubtedly by many other epipelagic fishes and pelagic birds.

Interest to Fisheries: Currently no interest exists for a fishery.

Remarks: ***Onykia carriboea*** is known, with certainty, only from small juveniles: no adult, mature specimen has been found/described. This suggests that the name could represent the immature growth stage of other onychoteuthid species (Kubodera *et al*., 1998, Bolstad, 2007). For example, as reported above, the type locality of the species is the Gulf of Mexico and the Gulf Stream; several subadult/adult specimens from the NMNH (Smithsonian Institution) from the Gulf of Mexico, originally labelled "***Ancistroteuthis***" were subsequently classified as ***Onykia robsoni*** (Kubodera *et al*., 1998). Therefore, ***O. carriboea*** from that geographic area could be ***O. robsoni***, in which case ***O. robsoni*** could ultimately prove to be a junior synonym of ***O. carriboea*** (see also Vecchione *et al*., 2003b). However, detailed comparisons of specimens from their respective type localities are needed before this problem can be resolved. This problem is further complicated by the fact that the holotype of ***O. carriboea*** no longer exits (Sweeney and Roper, 1998).

Local Names: None available.

Literature: Nesis (1982, 1987), Kubodera *et al*. (1998), Sweeney and Roper (1998), Vecchione *et al*. (2003b).

Onykia ingens (Smith, 1881)

Fig. 337

Onychoteuthis ingens Smith, 1881, *Proceedings of the Zoological Society of London*, 1881(1): 22–44 [25]. [Type locality: Port Riofrio, west coast of Patagonia, southeastern South Pacific Ocean].

Frequent Synonyms: *Onychoteuthis ingens* Smith, 1881; *Moroteuthis ingens* (Smith, 1881).

FAO Names: En – Greater clubhook squid; **Fr** – Cornet commun; **Sp** – Lurión comú.

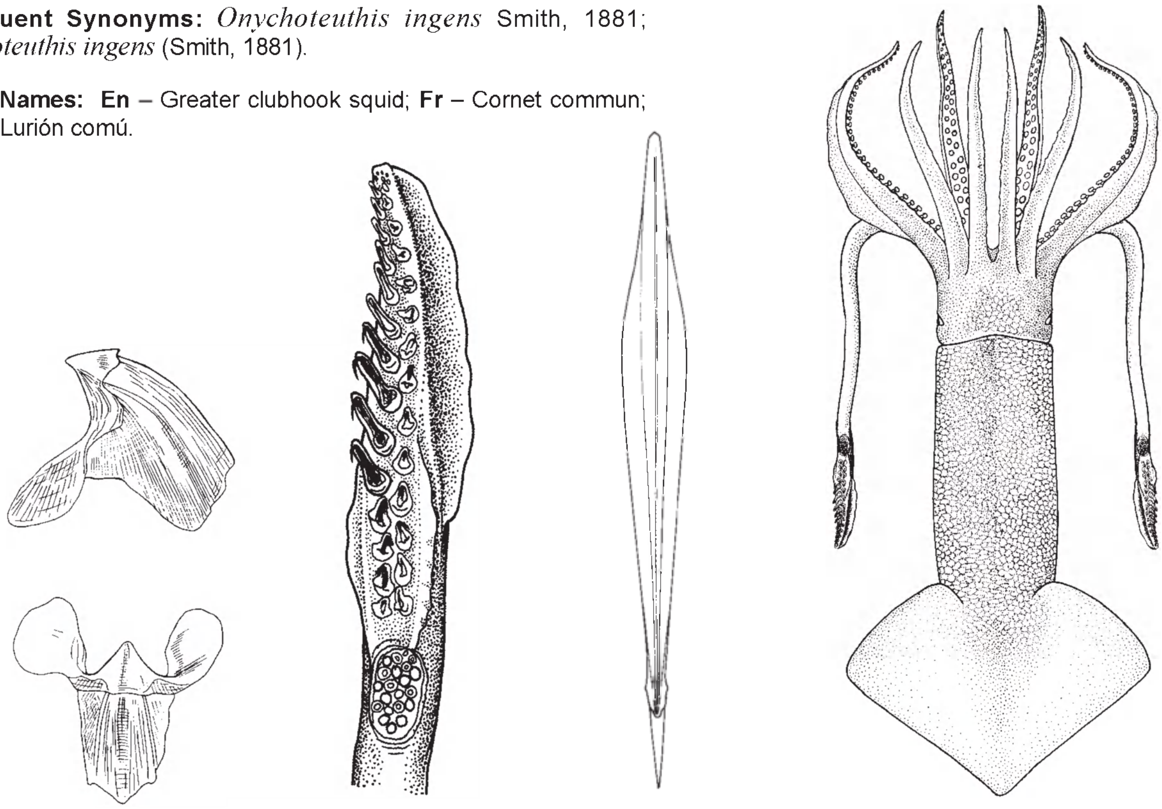


Fig. 337 *Onykia ingens*

Diagnostic Features: Mantle robust, broad, thick, heavily muscled, not drawn out into a sharp tail; **skin covered with fleshy warts**, as flat, elongate or curved tubercles, in a paving-stone pattern. **Fins large, broad, with broad fin angles** of 50° to 55° each; **fin length about 50%** (or slightly larger) **of mantle length**; **rhomboidal**, not attenuate into a tail. Rostrum of gladius triangular in cross-section, 10 to 12% of mantle length; endcone very short, shortest of all congeners. Tentacular clubs unexpanded, with 28 to 32 hooks in 2 medial series; hooks on ventral series much larger than on dorsal series, largest hooks positioned at sixth to eighth pair; carpus with 10 to 13 suckers plus their associated knobs; dactylus with 16 or 17 minute suckers. Longest arms (II and III) about 70% of mantle length.

Size: Large sized species; maximum mantle length 520 mm.

Geographical Distribution: *Onykia ingens* is a notalian circumpolar species in sub-Antarctic waters north of the Antarctic convergence, south of the Subtropical Convergence. It occurs on the Patagonian shelf, in southern Chile and the Prince Edward, Crozet, Kerguelen Islands and southern New Zealand islands (Antipodes, Campbell, etc.) as well as southern Australian and southern South Africa waters (Fig. 338).

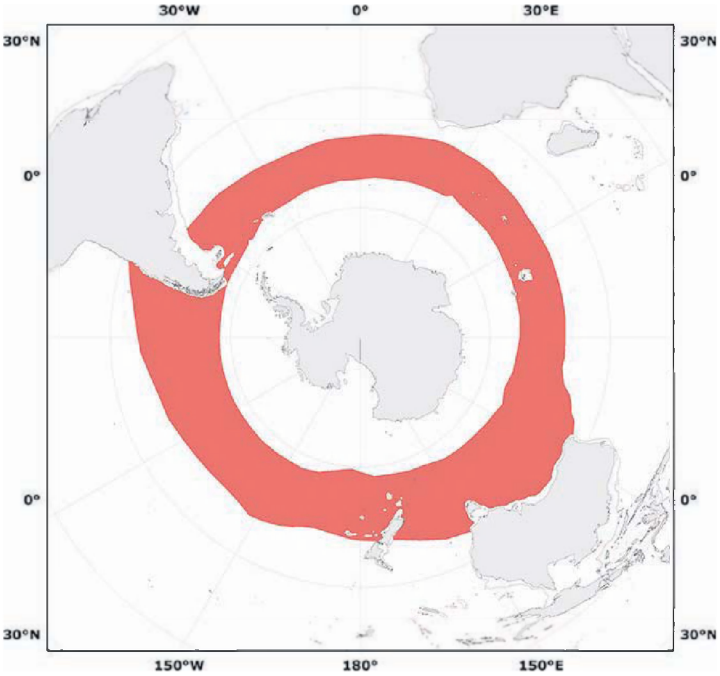


Fig. 338 *Onykia ingens*

🟥 Known distribution

Habitat and Biology: Adults of ***Onykia ingens*** apparently are primarily benthic/epibenthic in lower sublittoral and bathyal zones, having been caught in demersal trawls from 300 to 1 450 m in continental slope and bathyl waters. Juveniles and subadults are epi- to mesopelagic. This species is the prey of lancetfishes, slender and yellowfin tunas, southern opah, king penguin, wandering albatross. It also is a major food item of sperm whales, bottlenose whales and southern elephant seals. For example, the stomach of one stranded sperm whale in New Zealand, ***O. ingens*** represented the second most abundant species, 11.06%, and third most in weight by wet mass, 15.26%, following 2 specimens of ***Architeuthis***. Similar results for ***O. ingens*** were exhibited by sperm whales from the Tasman Sea. ***Onykia ingens*** preys on krill, deep water fishes, e.g. myctophids, viperfish, dragonfish, and on other species of squids. It exhibits strong sexual dimorphism: mature females weigh 5 times as much as mature males. This is an annual species and peak spawning and hatching occur in autumn and winter (June to August) near the bottom. Female reproduction is characterized by synchronous oocyte growth and ovulation; female fecundity approaches 400 000 oocytes and egg size is 1.8 to 2.7 mm. Females apparently undergo strong ontogenetic descent, but males do not exhibit such a behaviour. Mature and spent males and especially laying and spent females exhibit massive mantle tissue degradation, eventually into a complete, gelatinous consistency.

Interest to Fisheries: This extremely abundant species in sub-Antarctic waters is believed to have some fishery potential, but as a neutrally buoyant, ammoniacal species, this seems problematic currently. However, like so many other similarly endowed species, ***Onykia ingens*** could provide huge tonnage if the ammoniacal problem can be solved. In any case, it is an extremely important prey species for a number of commercially important fishes.

Local Names: None available.

Literature: Kubodera *et al.* (1998), Nesis (2002), Arkhipkin (2003b), Vecchione *et al.* (2003c), Bolstad (2007).

Onykia knipovitchi (Filippova, 1972)

Fig. 339

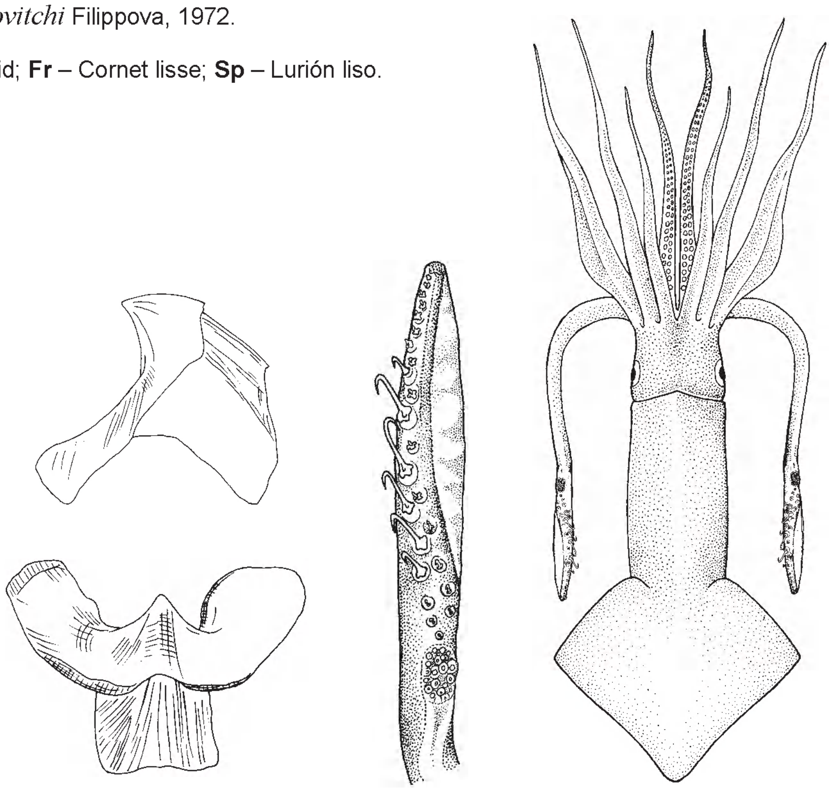
Moroteuthis knipovitchi Filippova, 1972, *Malacologia*, 11(2): 391–406 [392]. [Type locality: sub- Antarctic waters near South Georgia Island, South Atlantic Ocean].

Frequent Synonyms: *Moroteuthis knipovitchi* Filippova, 1972.

FAO Names: **En** – Smooth clubhook squid; **Fr** – Cornet lisse; **Sp** – Lurión liso.

Diagnostic Features: Mantle moderately broad, stout, not drawn out into prominent tail; ammoniacal; thin, smooth-textured skin surface. Fins large, broad, rhomboidal, not attenuate; fin angles 45° to 50° each; fin length 50 to 60% of mantle length. Gladius with cartilaginous conus, triangular in cross-section, 10 to 13% of mantle length. **Tentacular club manus long, slender, with 20 to 30 long, narrow hooks in 2 medial series**, those of ventral series larger than hooks on dorsal series; the second to fourth hooks on the dorsal series and sixth to eighth hooks on ventral series are the largest in respective series; 12 to 13 small suckers plus their accompanying knobs on carpus; 14 to 16 minute suckers on dactylus. Longest arms (II) 50 to 90% of mantle length.

Size: Large-sized species: maximum mantle length 450 mm.



mouth tentacular club dorsal view

Fig. 339 ***Onykia knipovitchi***

Geographical Distribution: This species is circum-Antarctic in distribution, south of the Antarctic Convergence. It occurs in the Scotia Sea, Argentine Basin, Drake Passage and around South Georgia, Kerguelen, Crozet, and Prince Edward Islands (Fig. 340).

Habitat and Biology: ***Onykia knipovitchi*** is an oceanic, mesopelagic, bathyal, ammoniacal species. The potential fecundity of females is 100 000 oocytes. Juveniles, young and adults occur near the surface in the austral winter where they are heavily preyed upon by king penguin, wandering, black-browned albatrosses and other pelagic birds. Larger and mature animals occur in deeper waters (at least to 550 m), where they are captured by fur seals, southern elephant seals (up to 31% of prey biomass), Ross seals and southern sea lions. Cetaceans also are major predators: southern bottlenose whales, sharp-toothed whales, other smaller odontocetes, and sperm whales, which take the large and mature animals as a major component of their diet. Circumglobal in the Southern Ocean.

Interest to Fisheries: Its abundance, size and consistency before spawning make this species a potential target for a significant fishery. However, as it is an ammoniacal species, ***Onykia knipovitchi*** is unsuitable for human consumption until a neutralizing process becomes available.

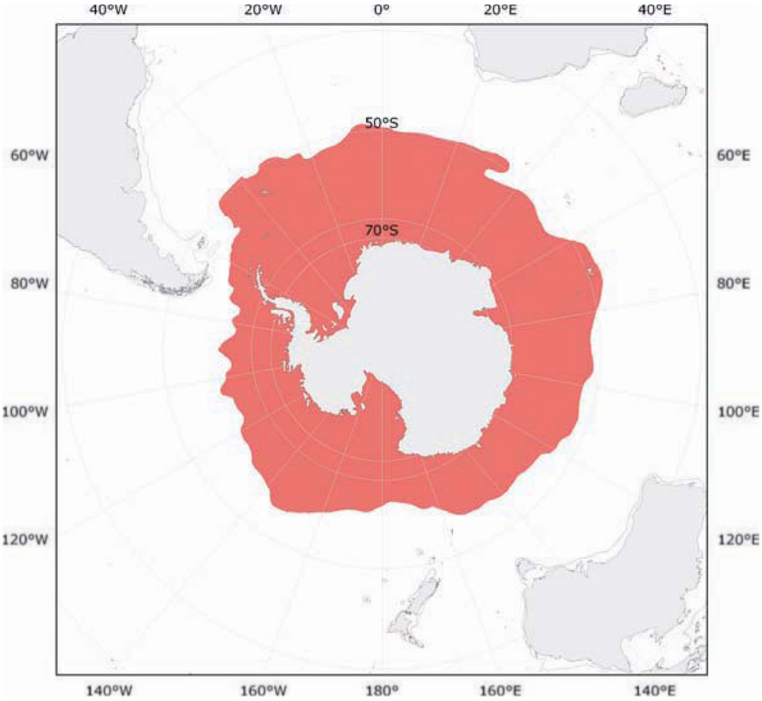


Fig. 340 ***Onykia knipovitchi***

🟥 Known distribution

Remarks: According to the molecular studies by Bonnaud *et al.* (1998) and Wakabayashi *et al.* (2007), this is the only species of the formerly recognized ***Moroteuthis*** genus that does not fit into the ***Onykia*** group, being more closely related to the genus ***Onychoteuthis*** than to the genus ***Onykia***. Therefore Wakabayashi *et al.* (2007) did not use the generic name ***Onykia*** for this species, referring to it as to "***Moroteuthis***" ***knipovitchi***. Additional research is needed to solve this problem; however, several morphological features (e.g. smooth skin, long, asymmetrical ventral club hooks), support the fact that "***Onykia knipovitchi***" is, indeed, an atypical member of the genus (see also Vecchione *et al.*, 2007c).

Local Names: None available.

Literature: Okutani (1980), Rodhouse (1989), Bonnaud *et al.* (1998), Kubodera *et al.* (1998), Vecchione *et al.* (2007c), Wakabayashi *et al.* (2007).

Onykia lönnbergi (Ishikawa and Wakiya, 1914)

Fig. 341

Moroteuthis lönnbergi Ishikawa and Wakiya, 1914, *Journal of the College of Agriculture, Imperial University of Tokyo*, 4(7): 445–460 [445]. [Type locality: Sagami Bay, Japan, northwestern North Pacific Ocean].

Frequent Synonyms: *Moroteuthis lönnbergi* Ishikawa and Wakiya, 1914.

FAO Names: En – Japanese clubhook squid; **Fr** – Cornet japonais; **Sp** – Lurión japonés.

Diagnostic Features: Mantle robust, muscular; **skin rugose**, with short, narrow, curved, fleshy ridges or pads that fuse with each other; **posterior tip drawn out into a moderately long, pointed tail**. Fins large, rhomboidal; fin length 50 to 60% of mantle length; fin width, broad, up to 50 to 55% of mantle length, roughly equal to fin length; fin angles about 35° to 40° each. Rostrum of gladius narrowly triangular in cross-section. **Tentacular club long, unexpanded, with about 25 (maximum 30) hooks in 2 median series on manus**; fourth to sixth hooks largest on dorsal series, sixth or seventh hook largest on ventral series; 7 or 8 small suckers plus associated knobs on carpus; 10 to 13 minute suckers on extreme tip of dactylus. Longest arms (IV) 60% of mantle length.

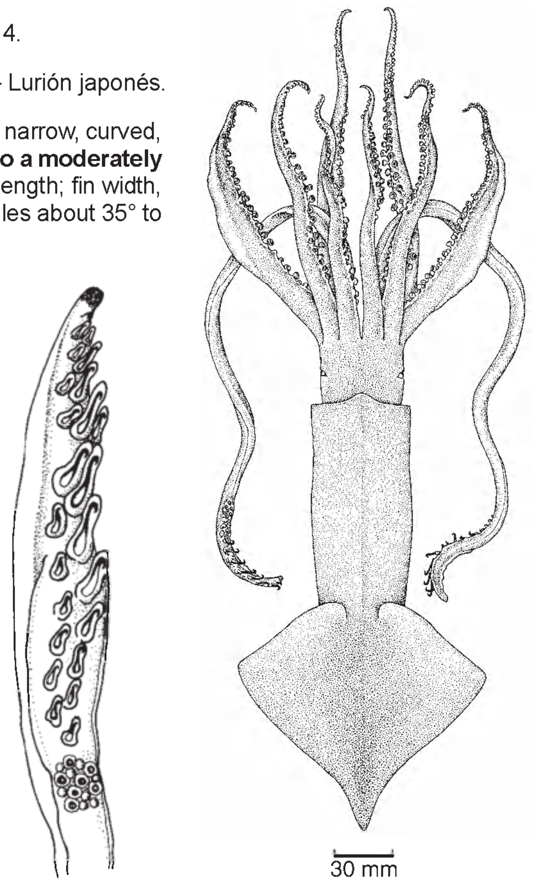
Size: Medium-large sized squid; maximum mantle length 350 mm.

Geographical Distribution: This species is distributed in the western North Pacific Ocean off eastern Honshu, Japan in the north, southward to Tsugaru Strait, the Kuroshiro Current, into the Indian Ocean (Saya-de-Malha Bank), and southward to the North West Shelf, Australia (Fig. 342).

Habitat and Biology: ***Onykia lönnbergi*** is an oceanic, ammoniacal, neutrally buoyant species (epipelagic, mesopelagic, bathyal) from temperate and subtropical waters. Its exact depth distribution is unknown, but it has been caught in open nets in depths between 730 and 920 m. However, it also occurs in depths of less than 200 m, because it is preyed upon by northern fur seals, as well as deeper-ranging sperm whales.

Interest to Fisheries: Undetermined, but currently unsuitable at full maturity because of its ammoniacal composition. It attains a size suitable for utilization.

Local names: None available.



tentacular club **dorsal view**

Fig. 341 ***Onykia lönnbergi***

Literature: Okutani *et al.* (1987), Nesis (1982, 1987), Kubodera *et al.* (1998), Nesis (2002), Vecchione *et al.* (2007c), Wakabayashi *et al.* (2007).

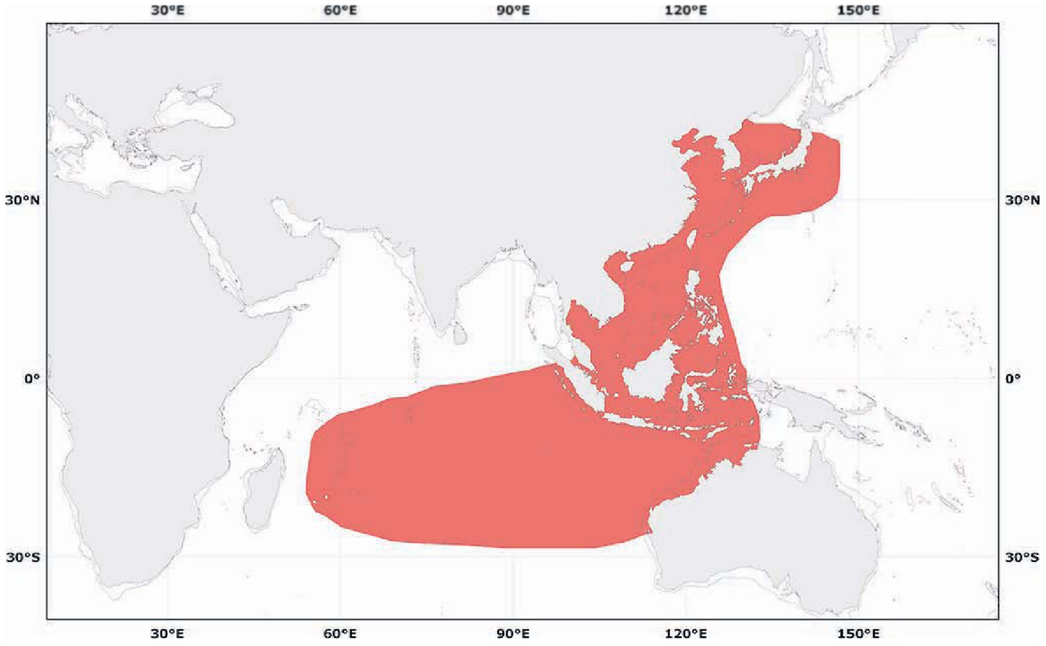


Fig. 342 ***Onykia lönnbergi***

🟥 Known distribution

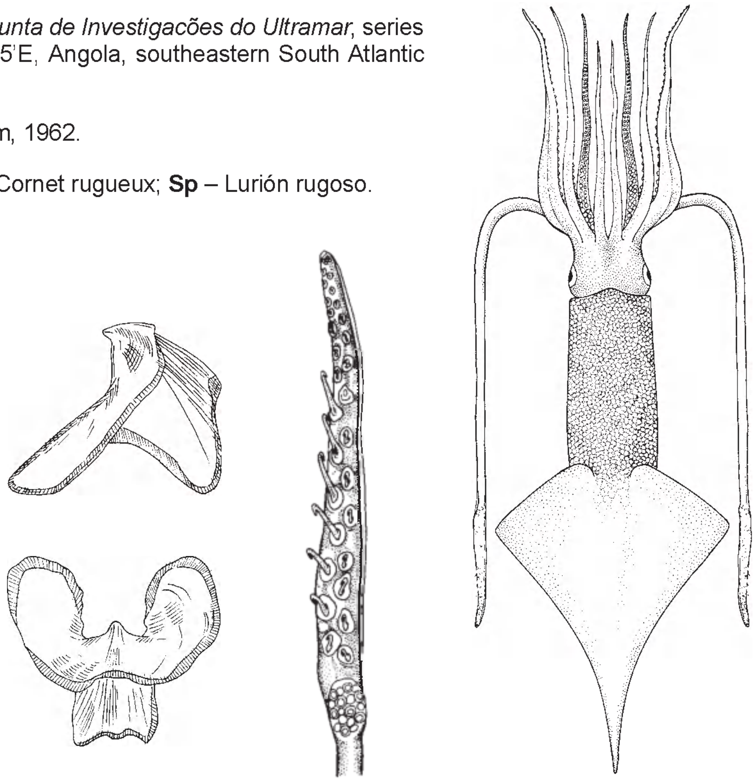
Onykia robsoni (Adam, 1962)

Fig. 343

Moroteuthis robsoni Adam, 1962, *Memórias da Junta de Investigacões do Ultramar*, series 2, 33: 9–64. [24]. [Type locality: 16°35.6'S, 11°19.5'E, Angola, southeastern South Atlantic Ocean].

Frequent Synonyms: *Moroteuthis robsoni* Adam, 1962.

FAO Names: En – Rugose clubhook squid; **Fr** – Cornet rugueux; **Sp** – Lurión rugoso.



beaks tentacular club dorsal view

Fig. 343 *Onykia robsoni*

Diagnostic Features: Mantle long, slender; skin rugose, covered with flat, fleshy, irregular tubercles, deep reddish coloration; **posterior tip drawn out into a very long, sharp tail. Fins heart-shaped, very long, attenuate** (not rhomboidal); **length 60 to 67% of mantle length**; together they form a very sharply pointed, lanceolate tail; relatively narrow, 45 to 50% of mantle length; fin angle 30° to 40° each. Rostrum of gladius triangular in cross-section, with ventral length of 23 to 36% of mantle length. **Tentacular club very narrow, unexpanded**; carpus with 10 to 12 small suckers plus their associated knobs; **manus with 26 to 32 hooks in 2 median series**; dactylus with 12 to 17 minute suckers. Arms attenuate, longest (IV) about 57 to 86% of mantle length.

Size: Large-sized species: maximum mantle length 750 mm.

Geographical Distribution: The distribution of ***Onykia robsoni*** is circumglobal in southern subtropical and notalian regions. The species occurs in the southern Atlantic to South Georgia, off southern and southwestern South Africa, as well as off southwestern Australia and southern New Zealand (Fig. 344).

Habitat and Biology: ***Onykia robsoni*** appears to be very similar to ***O. robusta***. It is an oceanic species, both pelagic and benthic. It is taken with open midwater trawls fished between 250 and 550 m depths (exact depth distribution unknown). Commonly it is bottom-trawled from deeper than 500 m. Analysis of sperm whale stomach contents indicates that ***O. robsoni*** spawns in the austral autumn off South Africa on the lower continental slope possibly to 2 500 m. Females are in maturing condition at 560 mm mantle length; life span approximately 2 years until single spawning occurs, followed by severe muscular degeneration and death. This species is heavily preyed upon by sperm whales and smaller odontocetes, including sharp-toothed and southern bottlenose whales. One New Zealand sperm whale stomach contained 1.25% by number and 5.35% by wet mass of this species. Fish predators include sharks, e.g. blue sharks and tiger sharks. ***Onykia robsoni*** preys on krill (*Euphausia superba*), fishes and other squids.

Interest to Fisheries: This species is caught by deep-set bottom trawls; it is believed to have some fishery potential on stages prior to full maturity. As it is an ammoniacal species, however, this is currently problematic, because maturation and spawning lead to severe muscular degeneration.

Remarks: ***Onykia aequatorialis*** (Thiele, 1920) was described from the eastern equatorial South Atlantic at 18°07'W. Kubodera, *et al*., 1998, examined a spent female of ***O. robsoni*** from Bermuda that was very similar to ***O. aequatorialis*** which caused them to question the validity of the latter. Since the holotype of ***O. aequatorialis*** has been lost and there are no distinguishing features in the type description, they designated ***O. aequatorialis*** a nomen dubium (Vecchione *et al*. 2003d).

Local Names: None available.

Literature: Nesis (1982, 1987), Kubodera *et al*. (1998), Nesis (2002), Bolstad (2007), Vecchione *et al*. (2003d, 2007c).

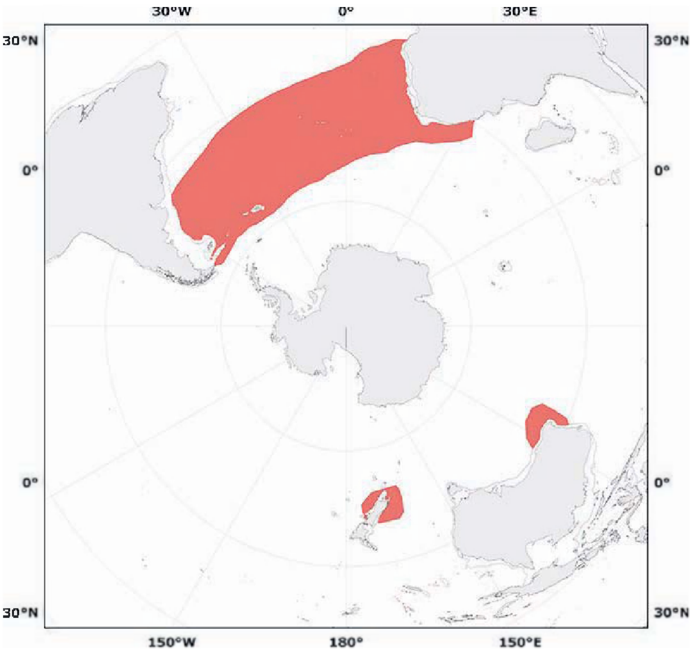


Fig. 344 *Onykia robsoni*

🟥 Known distribution

Onykia robusta (Verrill, 1876)

Fig. 345

Ommastrephes robusta Verrill, 1876, *American Journal of Science and Arts*, 12: 236–237 [237]. [Type locality: Aleutian Islands, North Pacific Ocean].

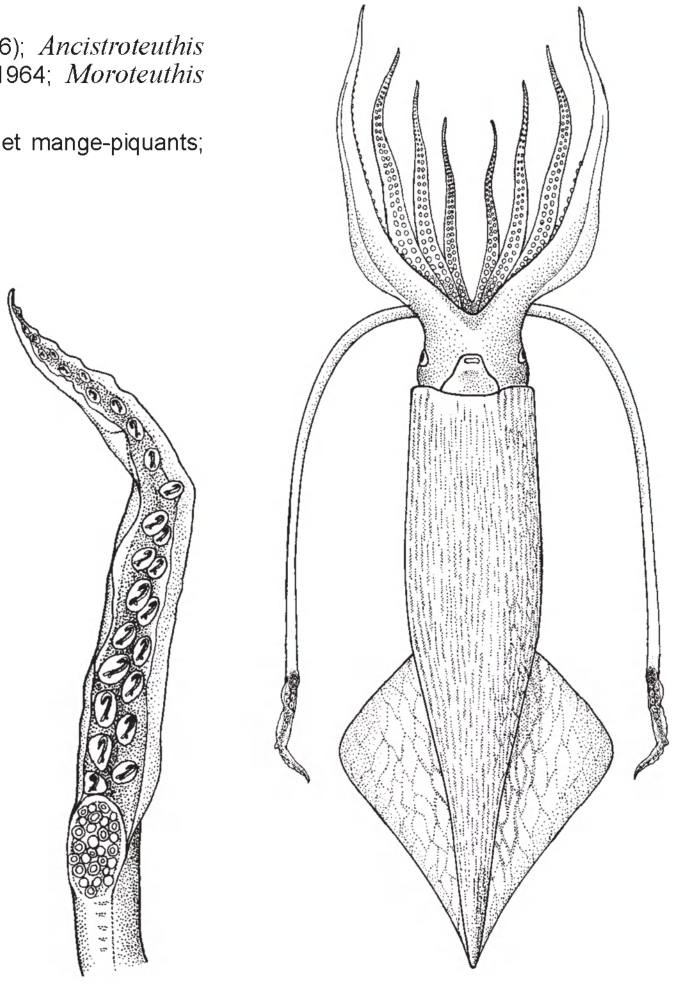
Frequent Synonyms: *Moroteuthis robusta* (Verrill, 1876); *Ancistroteuthis robusta* Steenstrup, 1882; *Onykia japonica* Taki, 1964; *Moroteuthis pacifica* Okutani, 1983a.

FAO Names: En – Robust clubhook squid; **Fr** – Cornet mange-piquants; **Sp** – Lurión maximo.

Diagnostic Features: Mantle robust, relatively broad; **skin surface covered with raised, fleshy, soft, relatively wide, longitudinal ridges**; posterior tip drawn out to a moderately long pointed tail. Fins large, saggitate, longer than broad; fin length 50 to 60% of mantle length; fin width narrower than mantle length, about 45% of mantle length or less. Rostrum of gladius large, round or oval in cross-section, length about 25 to 40% of mantle length (considered homolog of rostrum in extinct Belemnitida). **Tentacular club narrow, slender**; **manus with 32 to 36 hooks on 2 medial series,** third or fourth hook on ventral series the largest; 10 to 12 small suckers plus their associated knobs on carpus; 8 to 10 minute suckers on dactylus. Longest arms (IV) 90 to 100% of mantle length.

Size: Very large species; maximum mantle length reportedly up to 2.3 m, but this old record might be in error. The species commonly grows to 1.6 m mantle length and to 50 kg in weight.

Geographical Distribution: ***Onykia robusta*** is a panboreal species that spans the eastern and western far North Pacific Ocean in offshore waters from northeastern Japan throughout the Bering Sea, along the Aleutian Islands and into the Gulf of Alaska, and southward into deep southern California waters (Fig. 346).



tentacular club ventral view

Fig. 345 ***Onykia robusta***

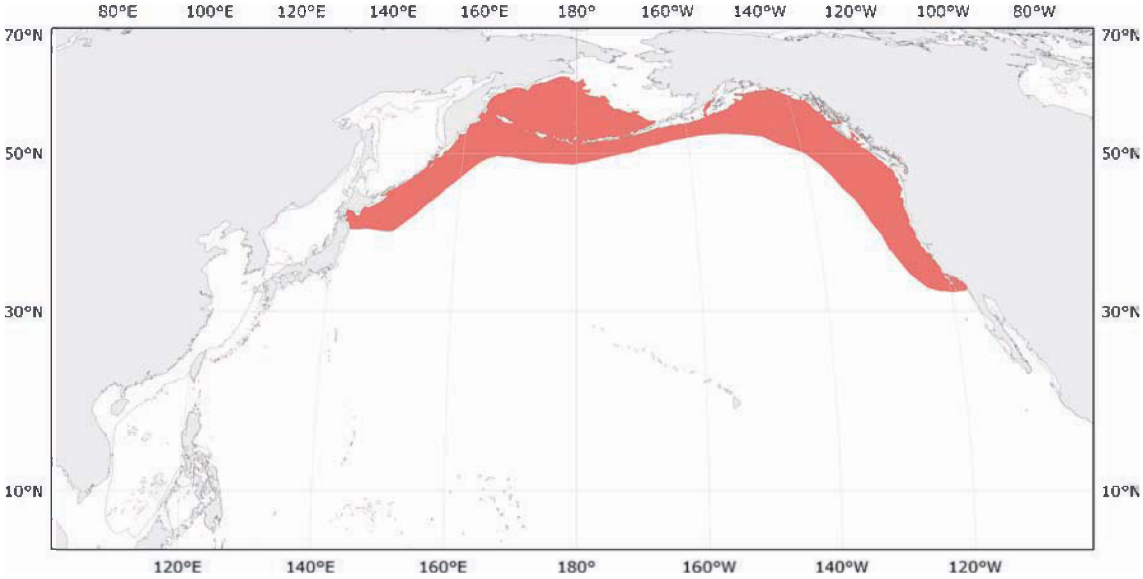


Fig. 346 ***Onykia robusta***

🟥 Known distribution

Habitat and Biology: An oceanic, boreal species, ***O. robusta*** occurs at or near the bottom, especially as adults, in lower sublittoral to upper bathyal waters, to at least 900 m. Juveniles and adolescent animals inhabit the midwater up to the surface, and the species has been identified as a component of the sound-scattering layer. This very abundant species attains a huge size, often leading to its being erroneously referred to as a "giant squid", but it bears no relationship to the true giant squid, ***Architeuthis*** spp. It is an ammoniacal species, so it is neutrally buoyant or nearly so. Adults feed on benthic fishes, e.g. blackcod, and have been reported to feed on benthic heart urchins such as *Brisaster townsendi*, as well as on epipelagic "jelly-fish" species such as *Velella velella*. ***Onykia robusta*** in turn is heavily preyed upon by sperm whales (e.g. to 72% numerically) and other marine mammals, e.g. northern elephant seals, pelagic fur seals.

Interest to Fisheries: This species is believed to have some fishery potential, even though attempts to prepare it for food in California have failed. The flesh is ammoniacal and fully mature adults become soft and semi-gelatinous as the mantle muscle degenerates during final maturation and spawning. Consequently, any fishery would have to target sub-mature animals, if the ammoniacal characteristic can be treated. Animals are taken as bycatch in the benthic blackcod long-line fishery; larger animals have been observed to attack and feed on hooked blackcod, often "riding" them to the surface. It is taken in large numbers in midwater/pelagic longline fisheries, as well.

Local Names: None available.

Literature: Okutani (1980), Nesis (1982, 1987), Kubodera *et al*. (1998), Vecchione *et al*. (2003e), Wakabayashi *et al*. (2007).

Kondakovia Filippova, 1972

Kondakovia Filippova, 1972, *Malacologia*, 11(2): 391–406 [395].

Type Species: *Kondakovia longimana* Filippova, 1972.

Frequent Synonyms: None.

Diagnostic Features: Currently the genus is monotypic, so the characters are included in the species description below.

Remarks: This is a large squid, perhaps second in size to the largest known onychoteuthid, ***Onykia robusta***.

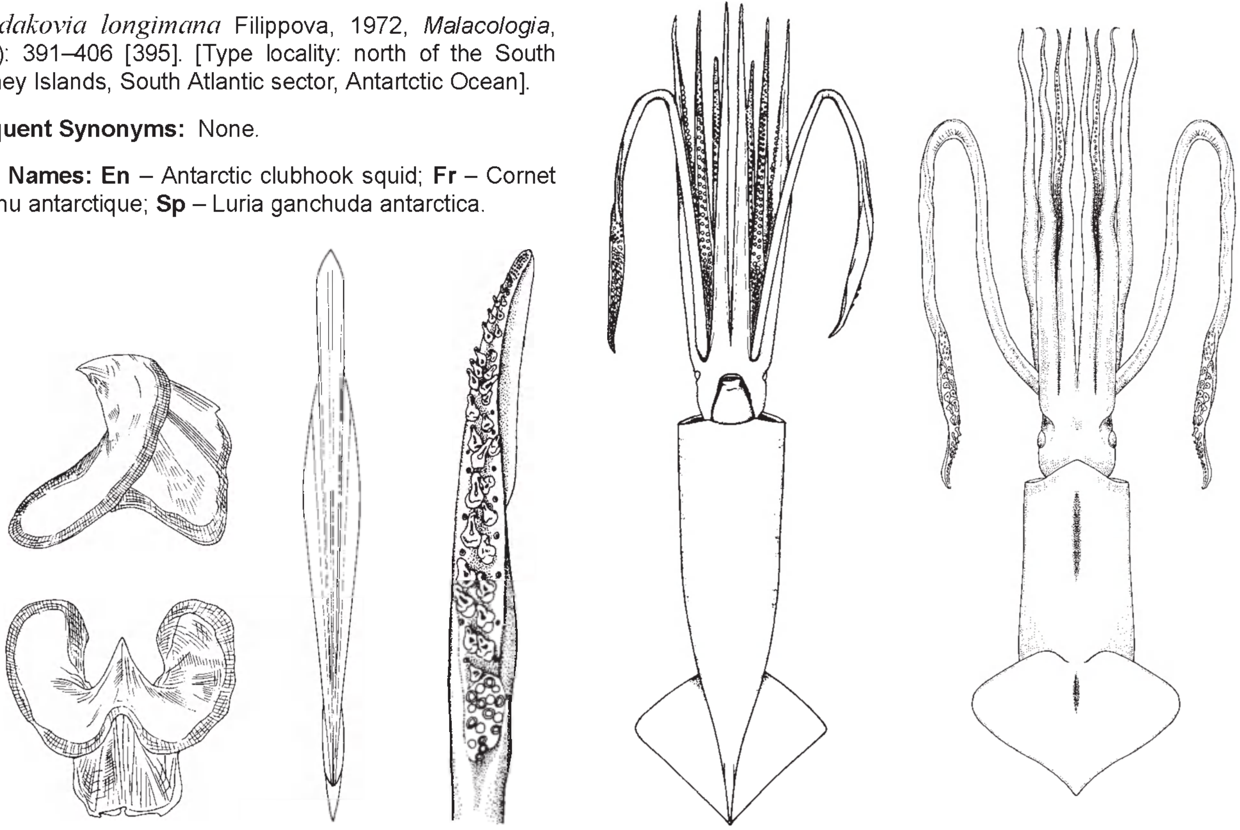
Kondakovia longimana Filippova, 1972

Kondakovia longimana Filippova, 1972, *Malacologia*, 11(2): 391–406 [395]. [Type locality: north of the South Orkney Islands, South Atlantic sector, Antartctic Ocean].

Frequent Synonyms: None.

FAO Names: En – Antarctic clubhook squid; **Fr** – Cornet crochu antarctique; **Sp** – Luria ganchuda antarctica.

Fig. 347



beaks **gladius** **tentacular club** **ventral view** **dorsal view**

Fig. 347 ***Kondakovia longimana***

Diagnostic Features: Mantle soft, fleshy, ammoniacal, broadly cylindrical, slightly tapered posteriorly; **numerous soft longitudinal ridges in outer integument external to thick, soft muscle layer**, especially in young stages. Skin thick, rugose, tuberculate in young. **Fins rhomboidal, but weak, short, broadly heart-shaped**, length about 42% of mantle length, width about 60% of mantle length. Gladius thin, fragile, with narrow, longitudinal thickenings; ventral length of thick, pointed cartilaginous rostrum 5 to 12% of mantle length. **Tentacular club elongate, with 2 medial series of a total of 27 to 38 hooks, and always 2 marginal series of small suckers** on manus throughout development to adulthood; carpus well-developed with 9 to 13 small suckers plus their associated knobs; dactylus with 17 to 40 minute, closely-set suckers. Nuchal folds absent. Photophores absent. Head and arms more massive than in ***Onykia ("Moroteuthis") Moroteuthis***, and together they are longer than the mantle; arms become very attenuate at the tips.

Size: Large-sized species; maximum reported mantle length of 108 cm and a total length of 225 cm.

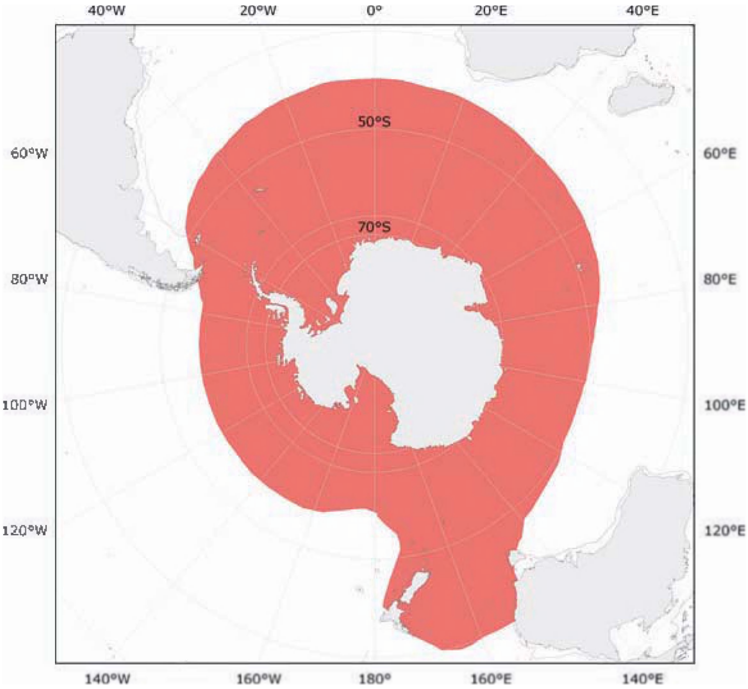


Fig. 348 ***Kondakovia longimana***

🟥 Known distribution

Geographical Distribution: This species is circumglobal in the Antarctic Ocean. It occurs in the Tasman Sea, and around South Georgia, Falkland, South Orkney (Scotia Sea), Prince Edward, Marion, Gough, Auckland, Antipodes, and Macquarie islands, as well as off Chile (Fig. 348).

Habitat and Biology: ***Kondakovia longimana*** is a large, very broadly distributed, abundant epipelagic to mesopelagic and benthic-bathyal species. It occurs from the surface to considerable depths, judging from their presence in predators' stomachs: Patagonian toothfish, sleeper sharks, wandering grey-headed and black-browed albatrosses, king penguins, southern elephant seals, southern bottle-nosed whales, sperm whales, hake; southern giant petrels, cape petrels, and brown skuas that were observed to scavenge on floating specimens. A principal prey item is the krill, *Euphausia superba.* Because it is an ammoniacal species, it is considered to be neutrally buoyant and to exhibit a rather passive life mode, feeding on massive, almost stationary, shoals of krill. It appears to mate and spawn in the austral winter around Crozet Island, and presumably around the other sub-Antarctic Islands listed above. Apparently this species is most abundant near the Antarctic Polar Front.

Interest to Fisheries: Because this large species is a soft-bodied, ammoniacal squid, its potential as a fishery target for human consumption currently seems questionable. However, its value as a major food source for a broad cross-section of predators is massive.

Literature: Filippova (1972), Bonnaud *et al.* (1998), Kubodera *et al.* (1998), Nesis (2002).

Walvisteuthis Nesis and Nikitina, 1986

Walvisteuthis Nesis and Nikitina, 1986a, *Zoologicheskij Zhurnal*, 65(1): 47–54 [47].

Type Species: *Walvisteuthis virilis* Nesis and Nikitina, 1986.

Frequent Synonyms: None.

Diagnostic Features: The tissues of mantle, fins, head, appendages are watery, semigelatinous. No warts, ridges, wrinkles on surface of mantle. Mantle broadly conical, bluntly rounded posteriorly, not drawn out into a tail. Fins very short (about one-third of mantle length), broad, transversely oval, width about 90% of mantle length; posterior lobes meet in midline, not separate. Head short, broad, narrower than mantle width. Eyes large, sinus present; olfactory papilla tongue-shaped. Nuchal folds absent. Funnel wide and long, reaches level of mideye; funnel-locking cartilage a simple, straight groove, slightly broader distally; mantle component a long, narrow, straight ridge. Buccal membrane with 7 lappets; connectives DDVV, i.e. arm IV connectives attach to ventral edge. Arms short, about half the mantle length; formula 4.3=2.1; arms I without keels, arms II with low keel the entire length, arms III with large, broad keel in distal portion; arms IV with well-developed keel, unusually broad along proximal portion. Arm suckers biserial, large, short-stalked, flattened, no hooks; especially significant are the 3 or 4 pairs of greatly enlarged suckers on the midportion of arms III, globe-shaped and twice as large as the normal suckers. Tentacles very thin, weak, non-muscular, short; length only approximates arm length; club occupies more than half the tentacle length; carpus with well-developed, dispersed, locking apparatus, 8 or 9 suckers, less than half the diameter of the normal arm suckers; 5 or 6 pairs of minute, widely spaced, medial suckers in 2 series on long stalks on manus; a few marginal suckers may occur. No visceral photophores. Needham's sac and penis extremely well-developed, at least half the mantle length, reach mantle opening; hectocotylus absent. Gladius with short, thin, blunt rounded rostrum oriented perpendicular to the gladius.

Geographical Distribution: The genus appears to be a southern subtropical to notalian bathypelagic form; it has been found in the topical Indian Ocean, in the temperate and tropical South Atlantic and in the tropical North and South Pacific.

Remarks: The genus currently is monotypic, comprised of the sole species ***Walvisteuthis virilis***. However, the very broad distribution of this species, unusual for an onychoteuthid, suggests that ***"Walvisteuthis virilis"*** probably represents a species complex. However, squid in present collections are insufficient to define possible species differences (Young *et al*., 2003).

Walvisteuthis virilis Nesis and Nikitina, 1986

Fig. 349

Walvisteuthis virilis Nesis and Nikitina, 1986a, *Zoologicheskij Zhurnal*, 65(1): 47–54. [47]. [Type locality: 33° 06'S, 02°7'E, Walvis Ridge, eastern South Atlantic Ocean, bottom trawl at 960 to 1080 m].

Frequent Synonyms: None.

FAO Names: En – Whale squid; **Fr** – Encornet baleine; **Sp** – Luria ballena.

Diagnostic Features: See generic section.

Size: Small-sized species; maximum mantle length to 103 mm.

Geographical Distribution: Worldwide in tropical to temperate seas (Fig. 350).

Habitat and Biology: ***Walwisteuthis virilis*** is an epipelagic to upper mesopelagic species. Paralarvae are known as small as 1.9 mm mantle length. The smallest paralarvae are extremely slender with a mantle width about 25% of the mantle length. Between this size and about 4 to 5 mm mantle length they are easily recognized by their slender appearance and a distinctive elongate patch of large chromatophores along the dorsal midline. The eyes are dorsoventrally elongate and strongly bulge from the head. Club suckers are in 2 series, large (about the same size as the arm suckers) and prominent. At roughly 4 to 5 mm mantle length the paralarvae undergo a strong morphological change. They become relatively broad, the eyes become hemispherical and the fins become much more prominent. At 7 mm mantle length the squid is very broad for its length. Chromatophores are small and scattered but larger on the dorsal surfaces than on the ventral surfaces. On the

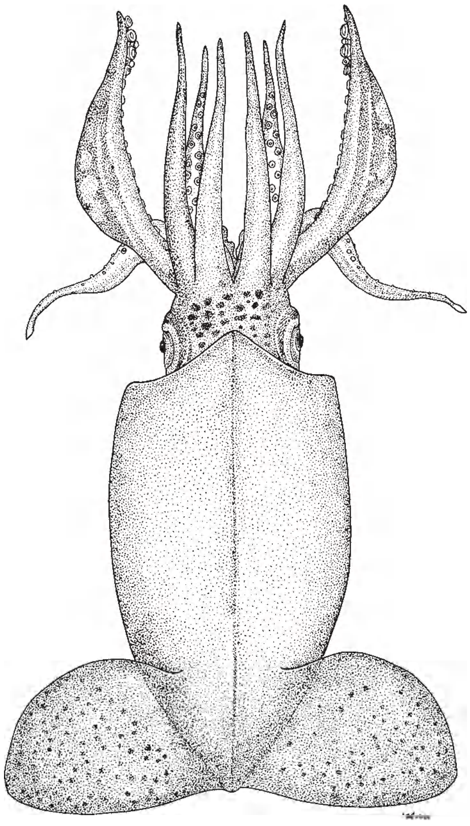

dorsal view

Fig. 349 ***Walvisteuthis virilis***

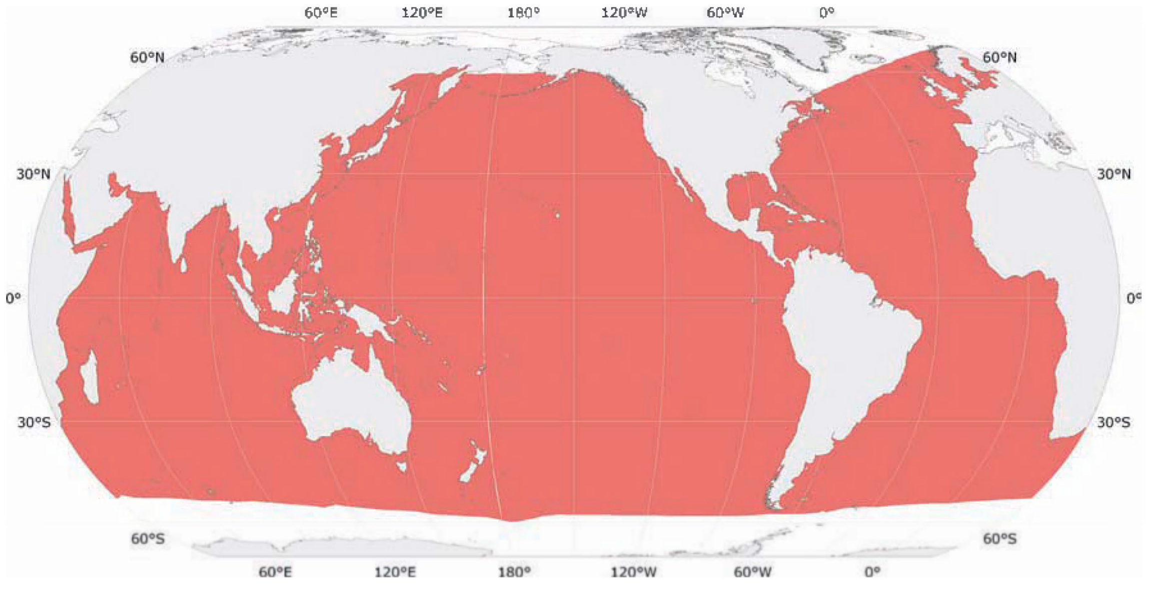


Fig. 350 ***Walvisteuthis virilis***

🟥 Known distribution

ventral surface of the head the chromatophores lie deep within the tissue and are not readily visible in preserved specimens. By 12 mm mantle length the V-shaped funnel groove and the distinctive rostrum are present and hooks begin to form in the medial-ventral series on the club.

Interest to Fisheries: None.

Remarks: Nesis and Nikitina (1986) described the new family of squids, Walvisteuthidae, based on a mature male which they named ***W. virilis***. The squid was somewhat similar to onychoteuthids but it had a number of very peculiar features that caused the authors to erect the new family. The status of this family recently has been reviewed by Tsuchiya (in preparation) who concluded that ***W. virilis*** is a synonym of the onychoteuthid ***Onykia rancureli***. The peculiar features noted by Nesis and Nikitina (1986) appear to be modifications that arise at sexual maturity. In fact, ***Onykia rancureli*** had been widely recognized as being very different from other members of the genus and several authors have suggested that a new generic name is needed (e.g. Toll, 1982; Tsuchiya and Okutani, 1992 [1991]). This generic name is considered to be ***Walvisteuthis*** and the new combination ***Walvisteuthis rancureli*** currently is used by an authoritative fraction of the scientific community (e.g. Young *et al*., 2003).

Literature: Rancurel (1970), Okutani (1981, 1995), Nesis and Nikitina (1986a), Young *et al*. (2003).

SPECIES OF NO CURRENT INTEREST TO FISHERIES,OR RARE SPECIES FOR WHICH ONLY FEW RECORDS EXIST

Onychoteuthis compacta (Berry, 1913)

Teleoteuthis compacta Berry, 1913b, *Proceedings of the United States National Museum*, 45(1996): 563–566 [565]. [Type locality: Hawaii, Central North Pacific Ocean].

Size: A small-sized species; maximum observed length 127 mm (mature male).

Geographical Distribution: Eastern Central Pacific Ocean, approximately 150°W to 180°W, 15°N to 30°N; Hawaiian waters.

Habitat and Biology: The species descends between 50 and 150 m depth during the day, and goes back to surface waters (i.e. 0–25 m) at night.

Literature: Bower *et al.* (1999c), Vecchione *et al*. (2003a), Okutani (2005).

Onychoteuthis meridiopacifica Rancurel and Okutani, 1990

Onychoteuthis meridiopacifica Rancurel and Okutani, 1990, *Venus*, 49(1): 25–30 [25]. [Type locality: 21°15’S, 155°11.5’E, Western South Pacific Ocean].

Size: Small-sized species; maximum recorded mantle length 90 mm.

Geographical Distribution: Southwestern Pacific Ocean, between 16°37’S to 23°56’S and 162°00’E to 133°15’W.

Habitat and Biology: The species is abundant in the central water mass of the South Pacific Ocean. Epipelagic (possibly to mesopelagic), it is preyed upon by lancetfish, *Alepisaurus ferox*, and tunas.

Remarks: This may be the smallest species in the genus. The short, broad fins and the presence of a few marginal suckers on the tentacular clubs of adults are diagnostic of this species.

Literature: Rancurel and Okutani (1990), Okuntani (2005), Vecchione *et al*. (2008d).

DOUBTFUL SPECIES, CONSIDERED TO BELONG TO THE GENUS *WALVISTEUTHIS* BY AN AUTHORITATIVE FRACTION OF THE SCIENTIFIC COMMUNITY

Onykia rancureli Okutani, 1981

Onykia rancureli Okutani, 1981, *Bulletin of the National Science Museum, Tokyo*, series A (Zoology), 7(4): 155-163 [155]. [Type locality: from the stomach of a lancetfish, *Alepisauris ferox*, 07°51'S, 88°02.5'E, tropical central Indian Ocean].

DOUBTFUL AND QUESTIONABLE SPECIES FOR WHICH ADDITIONAL MATERIAL, NEW DATA AND FURTHER RESEARCH ARE NECESSARY BEFORE THEY CAN BE ACCEPTED AS VALID

Onykia appellöfi (Pfeffer, 1900)

Teleoteuthis appellöfi Pfeffer, 1900, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2): 147–198 [158]. [Type locality: Atlantic Ocean].

Onykia intermedia (Pfeffer, 1912)

Teleoteuthis intermedia Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2F(a): 1–815 [68]. [Type locality: 38°S, 54°W, southwestern South Atlantic Ocean].

Onykia platyptera (d'Orbigny, 1834 [1834-1847])

Onychoteuthis platyptera d'Orbigny, 1834 (1834-1847), *Voyage dans l'Amérique Méridiaonale*, 5(3):1–758 [41]. [Type locality: 40°S and 85°W of Paris, off the coast of Chile, Southeastern South Pacific Ocean].

Onykia verrilli (Pfeffer, 1900)

Teleoteuthis verrilli Pfeffer, 1900, *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2): 147–198 [157]. [Type locality: 46°S, 147°E, southwestern South Pacific Ocean].

2.24 Family PHOLIDOTEUTHIDAE Voss, 1956

by Clyde F.E. Roper and Patrizia Jereb

Pholidoteuthidae Voss, 1956, *Bulletin of Marine Science of the Gulf and Caribbean*, 6(2): 85–178. [132].

Type Genus: *Pholidoteuthis* Adam, 1950.

FAO Names: En – Scaled squids; **Fr** – Loutène commune; **Sp** – Luria escamuda.

Diagnostic Features: Mantle cylindrical, elongate, thick, spongy, moderately to almost completely weakly-muscled, tapers posteriorly to a moderately to sharply pointed tail. Mantle of young and adults **covered with numerous, tightly-packed, rounded to polygonal, dermal cushions or papillose tubercles; dermal cushions terminate abruptly on ventral mantle at about midpoint of fins**. Fins with distinct anterior lobes, posterior borders extend to tip of tail, rhomboidal to heart-shaped, elongate; fins devoid of dermal cushions or tubercles; fin length variable between species, 35 to 75%. Tentacles long, slender; **tentacular clubs very long, only slightly expanded**; manus length about 2 times longer than dactylus; carpal locking mechanism absent. **Club suckers tetraserial, laterally compressed in late juveniles and adults** (> 20 to 25 mm mantle length), **with slit-like apertures and accute, peg-like teeth on inner ring**; small flaps with short membranes occur along lateral edges of club adjacent to stalks of lateral rows of suckers, not attached to protective membranes. Arms robust, subequal in length, maximum length 30 to 60% of mantle length in adults; suckers biserial, toothed (about 18 teeth); hooks absent. Buccal membrane with 7 lappets; connectives to arms IV attach to ventral margins. Funnel-locking cartilage a straight, simple groove. Gladius long, slender with narrow vane, constricted in posterior one-third, with a short to long conus. Photophores absent. Hectocotylus absent. Colour a dull mauve or purple, or lighter pinkish tone.

Size: Large-sized squids; maximum mantle length up to 800 mm.

Geographical Distribution: Oceanic, cosmopolitan in tropical and temperate seas.

Habitat and Biology: Formerly ***Pholidoteuthis*** species were considered relatively rare squids. However, considerable research on predator species, as well as trawl surveys in appropriate regions and depths, indicate that the 2 recognized species are geographically widespread and numerous. Among their predators are sperm whales, pilot whales, dolphins, tunas, deep-sea sharks, lancet fish, scabbard fish, swordfish and deep-sea rays. The vertical distribution is difficult to assess, but net captures indicate that paralarvae and juveniles occur in the upper 500 m, while adults occur in daytime bottom trawls to at least 1 500 m. Adults probably leave the bottom at night and disperse into the bathy-mesopelagic zone. ***Pholidoteuthis adami*** has been observed from a submersible in the slope waters at 592 m in the Bahama Islands; the squid was well off the bottom and was hovering in the "J-posture" (hanging vertically with head down, arms curved dorsally over the head and mantle), swimming with slowly flapping fins. Other specimens were observed off Cape Hatteras, North Carolina, aggregated in slope water off the bottom (Vecchione and Roper, pers. obs). ***Pholidoteuthis*** species are considered to be nerito-oceanic species that migrate to or over slopes as they mature, then spawn on or near the bottom. The paralarvae and juveniles are very widely dispersed by currents, even circumglobally in the case of ***P. massyae*** in the Southern Hemisphere.

Interest to Fisheries: Although the 2 species are large and at least regionally abundant, the weakly-muscled, spongy consistency of the mantle precludes an interest in a directed fishery.

Remarks: Two genera have been placed in this family: ***Tetronychoteuthis*** and ***Pholidoteuthis.*** Current thought, however, recognizes the sole genus ***Pholidoteuthis*** as valid (see details in the genus **Remarks** section). The family, therefore is monotypic.

Literature: Roper and Young (1975), Clarke (1980), Nesis and Nikitina (1990), Roper and Lu (1990), Vecchione and Roper (1991 [1992]), Nesis (1999b), Sweeney and Young (2003w),O'Shea *et al.* (2007), Vecchione and Young (2007f).

Pholidoteuthis Adam, 1950

Pholidoteuthis Adam, 1950b, *Koninklijke Nederlandse Academie van Wetenschappen*, 53(10): 1592–1598 [1592].

Type Species: *Pholidoteuthis massyae* (Pfeffer, 1912).

Frequent Synonyms: None.

Diagnostic Features: Only 1 genus currently is included in the Pholidoteuthidae, so the characters of the genus are the same as those given for the family.

Remarks: Pfeffer erected the genus ***Tetronychoteuthis*** in 1900 based on a damaged specimen he incorrectly thought to be ***Onychoteuthis dussumieri*** d'Orbigny, 1839, but was actually a specimen of ***Tetronychoteuthis massyae***, a species he described in 1912 (Vecchione and Young, 2007d). Pfeffer designated ***Onychoteuthis dussumieri*** d'Orbigny, 1839 the type species of his new genus. The specimen's illustrations show both onychoteuthid and non-onychoteuthid characters, such as numerous occipital folds and dermal scales; a confusing combination (see O'Shea *et al*. 2007, for further details). Additional confusion arises because ***Onychoteuthis dussumieri*** d'Orbigny, 1839, is considered a species dubium by some authors (i.e. Nesis and Nikitina, 1990). Adam (1950) erected ***Pholidoteuthis*** for his new species, ***P. boschmai***, without realizing that it shared all character states with ***T. massyae*** Pfeffer 1912. The type specimens of ***O. dussumieri*** d'Orbigny, ***T. massyae*** and the specimen referred to ***T. dussumieri*** by Pfeffer are no longer extant (Lu *et al*., 1995, Sweeney and Roper, 1998). Consequently, resolution of the nomenclatural problem based solely on the confused and often contradictory literature is not possible. Recently O'Shea *et al*. (2007), based on additional specimens from the South Pacific, designated ***P. boschmai*** as the junior synonym of ***T. massyae***. Consequently, ***Tetronychoteuthis*** becomes a junior synonym of ***Onychoteuthis***. Since the first available generic name for Pfeffer's "***Tetronychoteuthis***" ***massyae*** is ***Pholidoteuthis***, the authors referred to Pfeffer's species, i.e. the type species of the genus, as ***Pholidoteuthis massyae***, new combination (O'Shea *et al*., 2007). Leta (1987b) described ***P. uruguayensis*** from off Uruguay, but Nesis and Nikitina (1990) synonymized this species with ***P. adami***. The 2 recognized species, ***P. massyae*** (Pfeffer, 1912) and ***P. adami*** Voss, 1956, are considered to be closely related, as indicated by the nearly identical, unique, tentacular clubs. But, in general aspect, they look quite distinct. In particular, ***P. massyae*** has dermal structures that are solid papillose tubercles, while those of ***P. adami*** are vacuolate dermal cushions. The fins of ***P. massyae*** are short (35 to 45% of the mantle length), diamond-shaped or rhomboidal, not drawn out into a tail, while the fins of ***P. adami*** are much longer (65 to 75% of the mantle length), heart-shaped with rounded, less angular borders that extend posteriorly into a relatively elongate tail.

Key to the species of *Pholidoteuthis*

1a. Dermal structures solid, roundly stellate, minute (0.3 mm diameter), thightly-packed, roughly mushroom-shaped (cross section) papillose tubercles; fins short, rhomboidal, no prominent tail; arms short, subequal length; gladius with short primary conus . . . . ***Pholidoteuthis massyae***

1b. Dermal structures soft, rounded to roughly pentagonal, small (0.5 mm diameter), closely-set, vacuolate dermal cushions; fins long, heart-shaped, form a prominent tail; arms long, unequal length; gladius with both primary and secondary conus . . . . ***Pholidoteuthis adami***

Pholidoteuthis massyae (Pfeffer, 1912)

Fig. 351

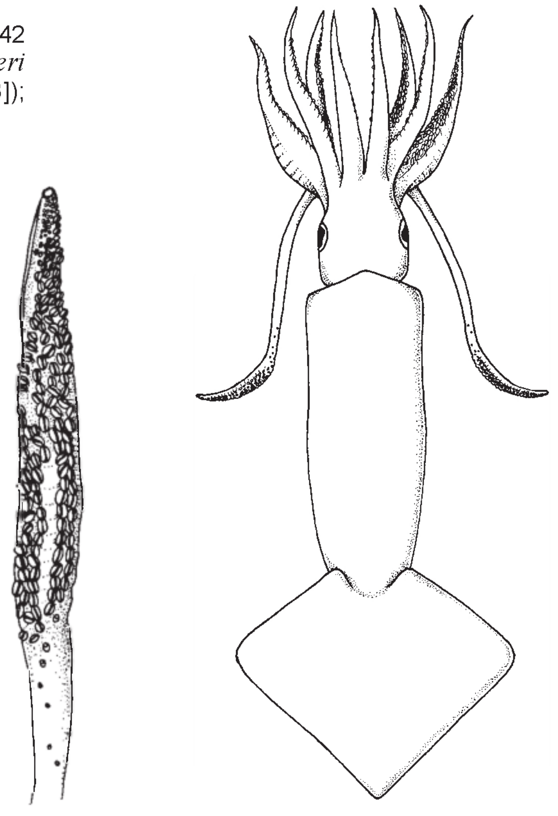
Tetronychoteuthis massyae (Pfeffer, 1912) *Ergebnisse der Plankton-Expedition der Humboldt-stiftung*, 2:1–815, 48 pls. [102, pl. 14, figs 15–19]. [Type locality: 48°N, 15°W, eastern North Atlantic Ocean].

Frequent Synonyms: *Onychoteuthis dussumieri* d'Orbigny, 1839–1842 (*in* Ferussac and d'Orbigny, 1834–1848); *Tetronychoteuthis dussumieri* (d'Orbigny, 1839–1842 [*in* Ferussac and d'Orbigny, 1834–1848]); *Tetronychoteuthis massyae* Pfeffer, 1912.

FAO Names: En – Coffee bean scaled squid; **Fr** – Loutène battoir; **Sp** – Luria escamuda cafetal.

Diagnostic Features: Mantle elongate, thick-walled, spongy in consistency, tapers to moderate point posteriorly. Beginning at about 20 to 25 mm mantle length, the mantle is **covered with dermal structures (papillose tubercules)** that consist of solid, densely packed material, histologically reminiscent of elastic cartilage, evenly distributed throughout the dense connective tissue matrix; these tubercules are roughly mushroom-shaped in cross section, with a slightly concave central disc and a thick base; the periphery of the tubercle contains 7 to 10 conical papillae, each with 2 to 4 prongs. **Fins short with distinct, small anterior lobes**, rhomboidal in outline, do not form elongate tail, fin length 35 to 45% of mantle length, fin width 50 to 70% of mantle length. The **arms are relatively short**, 30 to 60% of mantle length, robust, subequal in length; suckers biserial, no hooks. The gladius has a narrow lateral vane constricted in the posterior third, and a short needle-like rostrum on the tip of the conus. **Tentacles long, clubs virtually unexpanded, long**; club suckers tetraserial (no hooks), compressed in late juveniles and adults into ovoid, elongate structures with slit-like opening; the long sides of inner rings lined with acute teeth.

Size: Maximum recorded mantle length 720 mm.



tentacular club

dorsal view

Fig. 351 ***Pholiditeuthis massyae***

Geographical Distribution: A widely distributed, cosmopolitan species in southern subtropical, southern temperate and sub-Antarctic waters of the Atlantic, Pacific and Indian oceans (Fig. 352).

Habitat and Biology: The vertical distribution of adults encompasses mesopelagic to bathypelagic, bathybenthic zones. Paralarvae can occur in upper 200 m, while adults are mesopelagic to bathypelagic, concentrated in the 600 to 800 m zone; descent to bathyal bottom depths coincides with maturation. Spawning apparently occurs on or near the bottom, to at least 1 500 m. The species is heavily preyed upon by sperm whales, pilot whales, dolphins, tuna, swordfish, lancet fish, scabbard fish, deep-sea sharks and rays.

Interest to Fisheries: Currently this species is of no interest to fisheries because of its inaccessability in deep water and its spongy consistency and ammoniacal tissue. When a processing technique is developed, this species should be considered a potential resource because of its size, abundance and broad distribution.

Local Names: None available.

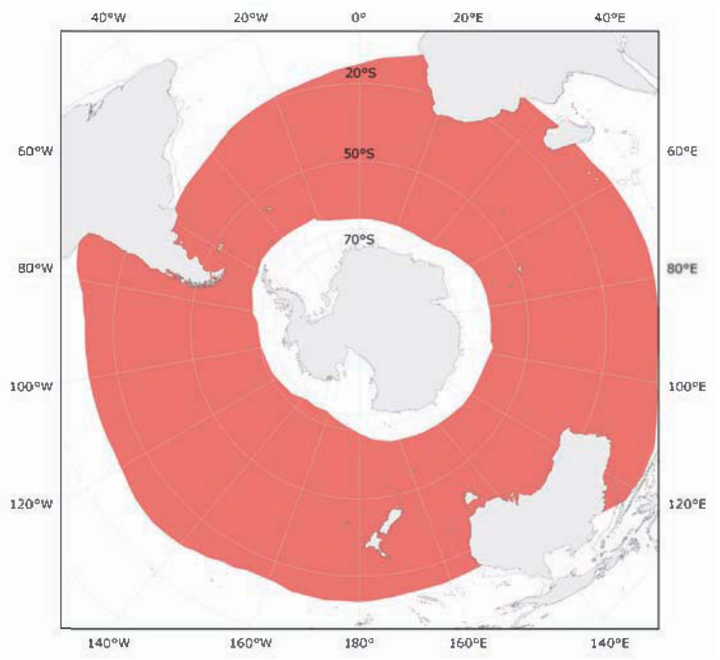


Fig. 352 ***Pholiditeuthis massyae***

🟥 Known distribution

Remarks: The papillose tubercules on ***P. massyae*** are believed to function to reduce hydrodynamic drag over the surface of the mantle, thus increasing the swimming efficiency. For details concerning the tubercles see Roper and Lu, 1990.

Literature: Nesis (1982, 1987), Nesis and Nikitina (1990), Roper and Lu (1990), Vecchione and Roper (1992 [1991]), O'Shea *et al.* (2007), Vecchione and Young (2008d).

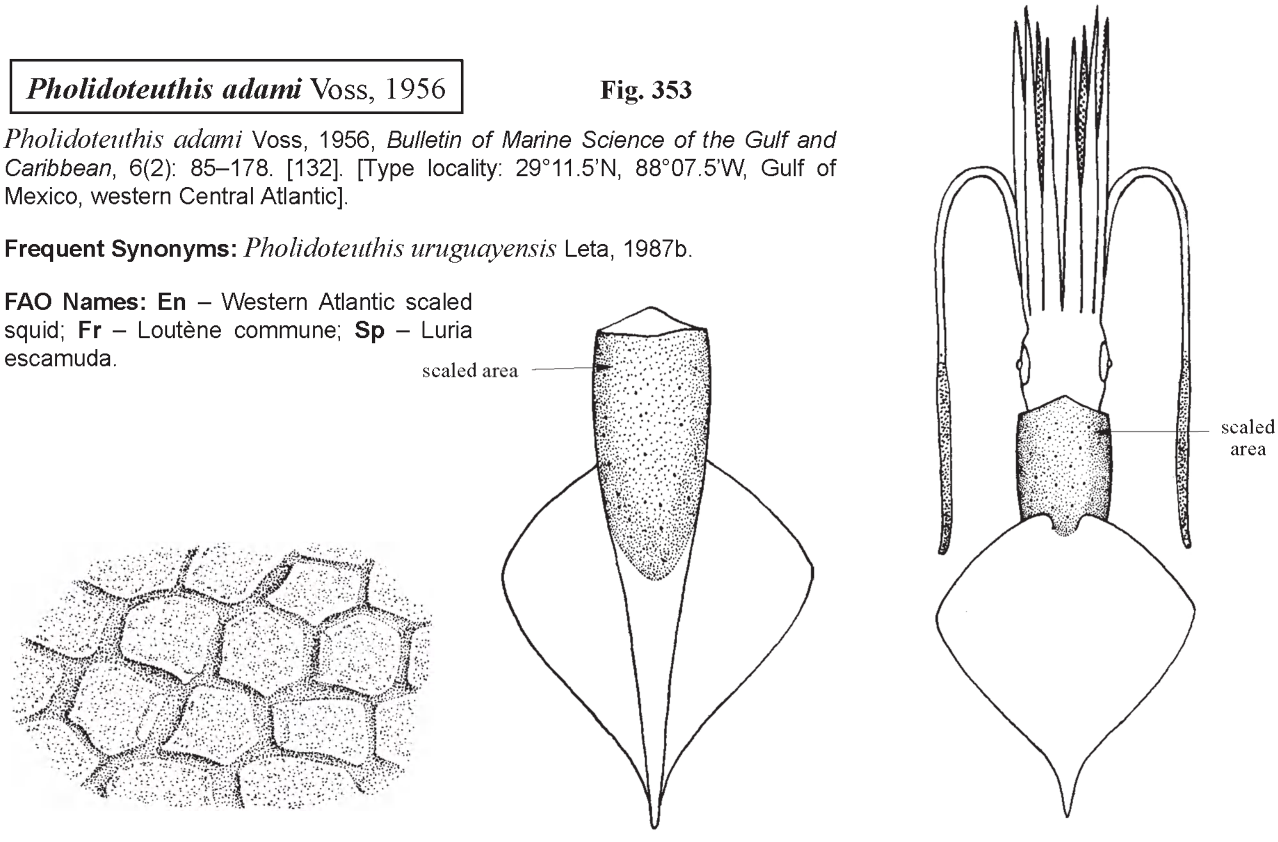
Pholidoteuthis adami Voss, 1956

Fig. 353

Pholidoteuthis adami Voss, 1956, *Bulletin of Marine Science of the Gulf and Caribbean*, 6(2): 85–178. [132]. [Type locality: 29°11.5'N, 88°07.5'W, Gulf of Mexico, western Central Atlantic].

Frequent Synonyms: *Pholidoteuthis uruguayensis* Leta, 1987b.

FAO Names: En – Western Atlantic scaled squid; **Fr** – Loutène commune; **Sp** – Luria escamuda.



cartilaginous scales **ventral view of mantle and fins** **dorsal view**

Fig. 353 ***Pholidoteuthis adami***

Diagnostic Features: Mantle thick, moderately muscled, yet spongy; **it tapers significantly from about the midpoint of the fins into a very long, thin, pointed tail**; mantle length to 800 mm. Beginning with juvenile stage, the **mantle surface is covered with a layer of very closely set, small, soft dermal structures, called dermal cushions, that are irregularly rounded to crudely pentagonal in outline**; these dermal cushions do not overlap and are about 0.5 mm in diameter and 0.3 mm in height (300 mm mantle length specimen); internally the cushions are almost entirely vacuolate, with thin-walled, irregularly shaped chambers (see Remarks); the ventral mantle is devoid of dermal cushions posteriorly from about the anterior third of the fins. **Fins very long in adults, length 70 to 75% of mantle length, width 60 to 70% of mantle length**, extend to tip of long tail, ventral margins concave, heart shaped; in juveniles the fins are 65 to 70% of mantle length, strongly heart-shaped, drawn out along the spike-like tail; anterior lobes strongly developed. Arms relatively long (65 to 75% of mantle length), slender, drawn out into long, sharply pointed tips; arms II and III the longest; suckers biserial, hooks absent. Basal suckers on arms with pointed teeth on distal half of inner ring; midarm suckers with teeth around entire margin, larger distally. The gladius is long, narrow, with a slightly widened vane and a secondary conus. Tentacles long; **clubs very long, only slightly expanded,** protective membranes low; suckers tetraserial, hooks absent, carpal knobs absent; club suckers compressed (folded) laterally, apertures elongate, slit-like.

Size: Maximum recorded mantle length attains 780 mm.

Geographical Distribution: The species is distributed in the western North Atlantic Ocean from off New England southward, where it is very abundant in the Gulf of Mexico; also, it is common throughout the Caribbean Sea to off Uruguay (Fig. 354).

Habitat and Biology: This species inhabits temperate to tropical zones in deep water. Adults are bathyl, captured in deep-set bottom trawls at least to 1 500 m (records to 2 000 m). One specimen has been observed from a submersible just above the bottom (about 850 m) on the continental slope off Cape Hatteras, North Carolina, eastern USA. A number of daytime captures occurred in the Gulf of Mexico at 360 to 925 m (predominately 625 to 750 m). No nighttime captures are recorded from deep benthic trawls, so this species probably disperses up off the bottom waters and into the water column to feed at night. In fact, huge “schools” of ***Pholidoteuthis adami*** have been observed at night at the surface in the Gulf of Mexico.

Interest to Fisheries: To date no interest exists for this species as a fishery product, even though extremely large concentrations have been reported in the Gulf of Mexico. The relatively soft ammoniacal mantle tissue currently precludes ***P. adami*** from interest for human consumption. When a processing technique is developed, this species should be considered a potential resource because of its size and broad distribution.

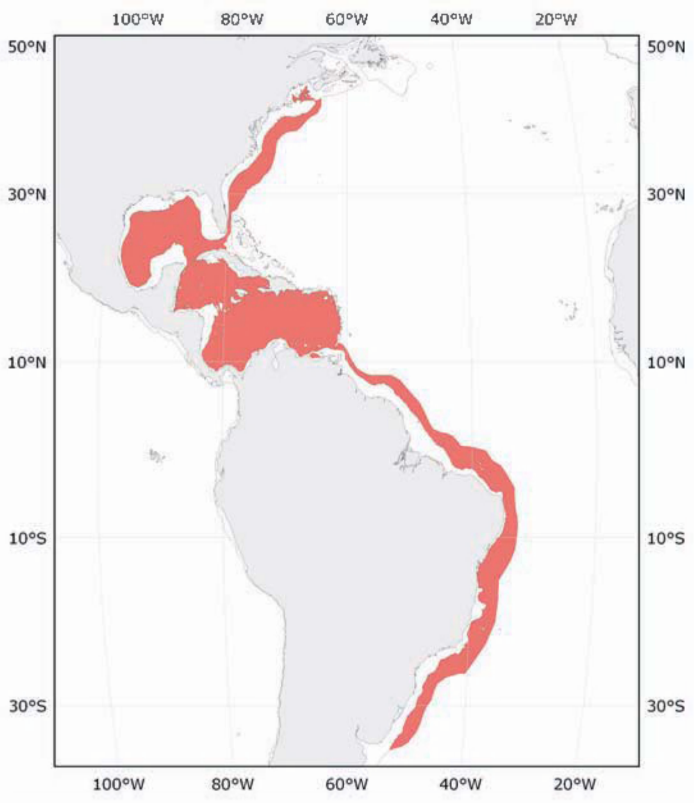


Fig. 354 ***Pholidoteuthis adami***

🟥 Known distribution

Remarks: The dermal cusions of ***P. adami*** are hypothesized to contain ammonium chloride solution that provides a buoyancy mechanism for these squids. The morphology and histology of the cushions are detailed in Roper and Lu, 1990.

Literature: Roper *et al.* (1969b), Nesis (1982, 1987), Roper and Lu (1990), Nesis (1993a); Vecchione and Young (2007f), O’Shea *et al.* (2007).

2.25 Family PROMACHOTEUTHIDAE Naef, 1912

by Clyde F. E. Roper and Patrizia Jereb

Promachoteuthidae Naef, 1912a, *Zoologischer Anzeiger*, 39(7): 241–244 [244].

Type Genus: *Promachoteuthis* Hoyle, 1885

FAO Names: En – Warrior squids; **Fr** – Encornets guerrier; **Sp** – Lurias guerreas.

Diagnostic Features: Squids of very small to medium-size. **Mantle short, broad, weakly muscled**; largest recorded (but not described) is 184 mm mantle length; all other described specimens are less than 50 mm mantle length. **Fins large to very large, round, usually with posterior lobes that extend beyond pointed tip of mantle**. **Eyes small to very small, embedded in gelatinous tissue**, reduced eye openings; eyes connected to eye openings via narrow channel; a semi-translucent section of eyelid may partially cover eye (“pseudocornea”). **Head often fused to mantle in dorsal nuchal region**. Funnel-locking component a simple, ovoid depression. **Arms with 2 to 6 series of suckers** (variable among species). **Tentacles thick, much larger in diameter than arm width** (except in 1 species); clubs not expanded; club suckers minute, numerous, in irregular transverse series across the oral surface. **Photophores absent**. **Ink sac absent**. **Anal flaps absent**. **Gladius reduced in size**, considerably shorter than the mantle, highly variable in shape among species.

Size: Squids of very small- to medium-size; largest recorded (but not described) is 184 mm mantle length; all other described specimens are less than 50 mm mantle length.

Geographical Distribution: As a family, species have been recorded from discrete localities in the northwestern North Pacific Ocean, northeastern North Atlantic Ocean, South Pacific Ocean, South Atlantic Ocean and southeastern South Atlantic Ocean.

Habitat and Biology: All species are truly bathypelagic to abyssopelagic, and the species appear to be geographically isolated, an unusual circumstance for such deep sea forms. Some depths of capture (open nets) are: 1 550 m, 1 830 m, 1 900 m, 2 440 m, 2 650 m, 2 972 m and 3 431 m.p

Interest to Fisheries: The extreme rarity, extreme depth range and very small size preclude any fishery potential.

Remarks: The Promachoteuthidae is monogeneric. This is an uniquely unusual family. Since the first specimen was described by Hoyle from the Challenger Expedition as ***Promachoteuthis megaptera*** Hoyle, 1885, only 12 additional specimens have been recorded, until recently. Remarkably, these specimens have been recognized as belonging to 5 different species; two of these have not been named yet (i.e. ***Promachoteuthis* sp. B** and **D**, Young *et al*., 2007), but are being formerly described currently by Young and Vecchione (pers. comm.).

Table 15

Species characters[1/]

Species	Mantle fused to head	Tentacle wider than arm III	No. sucker series on arms	Unique tentacle character	Fin length	Habitat
Promachoteuthis megaptera	No	Yes	2	Pigment band	75% of ML	NW Pacific
Promachoteuthis sloanii	No	Yes	2–6	Papillae	70% of ML	NE Atlantic
Promachoteuthis sulcus	Yes	Yes	2–3 (mostly 3)	Sunken club base; Aboral groove	35% of ML	South Atlantic
***Promachoteuthis* sp. B**	Yes	Yes	2	Reduced club diam. (?)	40% of ML	South Pacific, NE Atlantic
***Promachoteuthis* sp. D**	Yes	No	2–3 (mostly 2)	?	45% of GL	SE Atlantic

[1/] from Young and Vecchione (2003b). The undescribed species are being formerly described by R. Young and M. Vecchione.

Literature: Hoyle (1885a), Sweeney and Young (2003y), Young and Vecchione (2003a,b,c,d), Young *et al*. (2006a, 2007).

Promachoteuthis Hoyle, 1885

Promachoteuthis Hoyle, 1885a, *Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–76, Narrative*, 1(1): 269–274 [273].

Type Species: *Promachoteuthis megaptera* Hoyle, 1885.

Diagnostic Features: Characteristics are the same as given for the monogeneric family, but the following diagnosis should be adequate to delineate the genus. **Eyes small to very small with reduced opening to exterior**. Funnel-locking apparatus with oval depression. **Arms with 2 or 3 or more sucker series**. Tentacular stalks generally thick; stalk width greater than width of arm III in most species. **Tentacular club not expanded**; **club without keel, locking apparatus or terminal pad**; **club with suckers in numerous irregular series**. **Anal flaps absent**. **Ink sac absent**. **Photophores absent**. **Gladius reduced and variable in shape among species**.

Promachoteuthis megaptera Hoyle, 1885

Promachoteuthis megaptera Hoyle, 1885a, *Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–76, Narrative*, 1(1): 269–274 [273]. [Type locality: 31°00'N, 147°00'E, 2 750 m depth, eastern North Pacific Ocean].

FAO Names: En – Bigfin warrior squid; **Fr** – Encornet guerrier ailé; **Sp** – Luria guerrera alada.

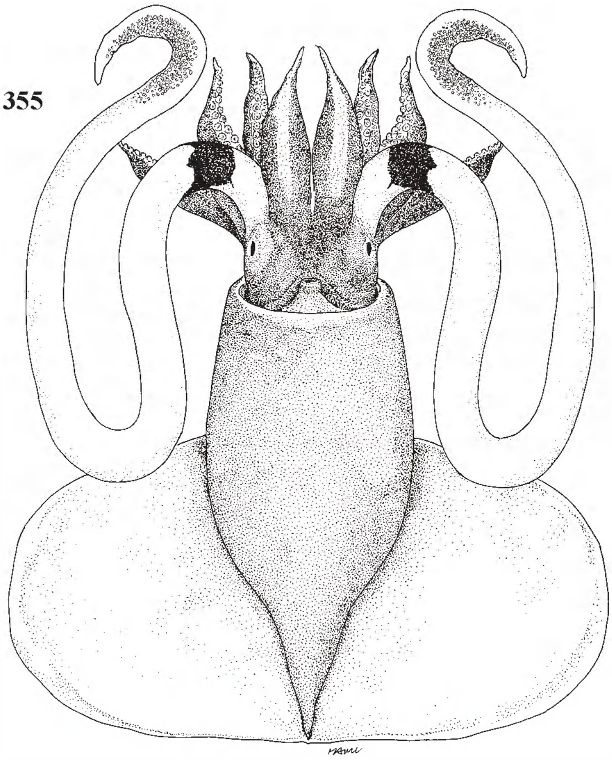
Size: The mantle length reaches 52 mm.

Geographical Distribution: Off Japan in the western North Pacific Ocean: 34°37'N, 140°32'E, 0 to 3 690 m (Fig. 356).

Remarks: Only two specimens are known, both from off Japan.

Literature: Roper and Young (1968), Young and Vecchione (2003b) [See family literature listing].

Fig. 355



ventral view

Fig. 355 *Promachoteuthis megaptera*

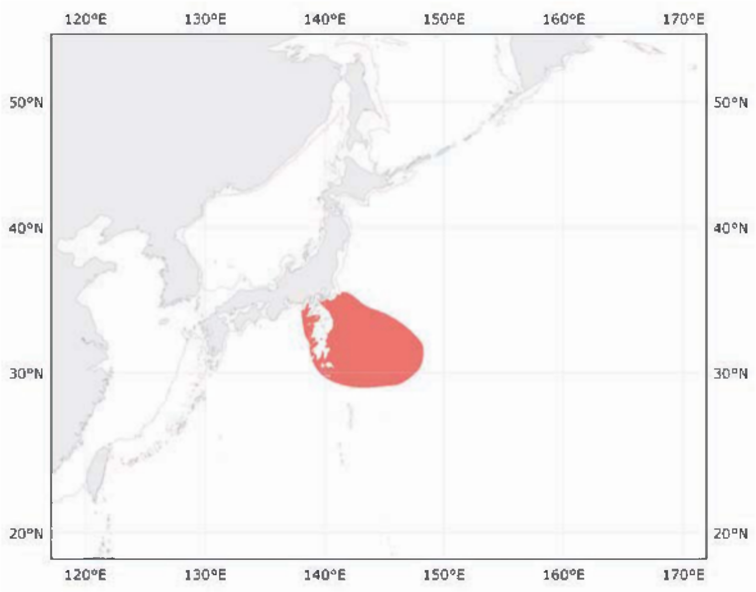


Fig. 356 *Promachoteuthis megaptera*

🟥 Known distribution

Promachoteuthis sloani Young, Vecchione and Piatkowski 2006

Promachoteuthis sloani Young, Vecchione and Piatkowski 2006a. *Proceedings of the Biological Society of Washington*, 119(2): 287–292 [289 figs 1–3]. [Type locality: 53°05'N, 36°46'W, 0 to 2 792 m, North Atlantic Ocean].

Size: The mantle length of the holotype is 58 mm and of the paratype 104 mm.

Geographical Distribution: Only 2 specimens of this species are known from the North Atlantic Ocean. The holotype was captured at 53°05'N, 36°46'W, 0 to 2 792 m, and the paratype was taken at 46°00'N, 15°49'W, 0 to 2 650 m.

Remarks: Only 2 specimens of this species are known.

Literature: Young and Vecchione (2006c), Young *et al.* (2006a).

Promachoteuthis sulcus Young, Vecchione and Roper, 2007

Promachoteuthis sulcus Young, Vecchione and Roper, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 353–365 [359, figs 15–22]. [Type locality: 36°49'S, 12°17'W at 1 750 to 2 000 m depth, off Tristan da Cunha, South Atlantic Ocean].

Size: The mantle length of the lone specimen is 25 mm.

Geographical Distribution: The single specimen was captured in the South Atlantic Ocean off Tristan da Cunha, at 36°49'S, 12°17'W at a depth of 1 750 to 2 000 m in an open net.

Remarks: Only one specimen was caught, in an open net.

Literature: Young *et al*. (2007).

***Promachoteuthis* sp. B** Young, Vecchione and Roper, 2007

Promachoteuthis sp. B Young, Vecchione and Roper, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 353–365 [362]. [Type locality: 33°18'S, 72°27'W (0–1800 m) and 56°06'S, 79°04'W (0–1400 m), eastern South Pacific Ocean].

Size: The known mantle length reaches 50 mm.

Geographical Distribution: Three specimens are known from the eastern South Pacific Ocean (10.5 to 17 mm mantle length) and one from the western South Pacific Ocean. One specimen of unconfirmed identification was captured in the western North Atlantic Ocean. Depths of capture are recorded from 1 400 to 2 972 m in open nets.

Literature: Young and Vecchione (2003c), Young *et al*. (2007).

***Promachoteuthis* sp. D** Young, Vecchione and Roper, 2007

Promachoteuthis sp. D Young, Vecchione and Roper, 2007, *Reviews in Fish Biology and Fisheries*, 17(2–3): 353–365 [362]. [Type locality: 16°35'E, 34°15'S in the south Atlantic Ocean. Captured from the WALTHER HERWIG R/V, at 1550 m depth].

Size: Mantle length as currently known is 16 mm. Original mantle length at capture was 42 mm.

Geographical Distribution: This species is known from only a single specimen that was taken at 34°15'S, 16°35'E in the South Atlantic Ocean, at 1 550 m, in an open net.

Literature: Young and Vecchione (2003d), Young *et al*. (2007).

2.26 Family PSYCHROTEUTHIDAE Thiele, 1920

by Clyde F.E. Roper and Patrizia Jereb

Psychroteuthidae Thiele, 1920, *Deutsche Südpolar Expediton, 1901 to 1903, Zoologie*, 16(8):433–465 [440]. [note: published in 1920, not 1921].

Type Genus: *Psychroteuthis* Thiele, 1920.

FAO Names: En – Glacial squids; **Fr** – Encornets glaciaire; **Sp** – Lurias glaciales.

Diagnostic Features: Mantle elongate, muscular, tapers to pointed tail. **Fins sagittate, rhomboidal, muscular, length 55 to 60%** of mantle length; anterior fin lobes distinct; posterior margins join mantle to form pointed tail. Eyes proportionally very large. Buccal connectives attach to dorsal borders of arms IV (formula DDVD). Funnel-locking cartilage a very slightly curved, narrow, simple groove. Arms muscular, subequal in length; arm suckers biserial; sucker rings smooth except on distalmost suckers. Tentacles long, muscular; **tentacular clubs expanded**; **carpal locking region extends proximally along ventral edge of tentacular stalk with a row of alternating knobs and suckers (some may be biserial) and dorsally along distal portion**; **manus with suckers quadriserial proximally**, the ventromedian series with greatly enlarged suckers, those of the dorsomedian series somewhat enlarged; distal manus and dactylus with 4 to 7 series of suckers. Gladius long, slender, with short rachis and very long vane that is widest anteriorly, then tapers evenly to the narrow, cup-like terminus. **A large, composite photophore occurs on the tips of arms III in mature females** (males?), consisting of transverse light-producing plates arranged in a zig-zag pattern and covered with black-pigmented shields. Photophores on mantle and head absent. Mantle length to 440 mm. Lower beak with an obtuse jaw angle not obscured from the side by a low wing fold; a long, curved jaw edge almost as long as the wing; wings broad; rostrum moderately narrow; hood stands high above unthickened crest and has a shallow notch; a thick fin or ridge runs to the middle of the posterior edge of the lateral wall.

Size: Medium-sides squid; maximum mantle length up to 440 mm.

Geographical Distribution: Southern Ocean.

Remarks: This monotypic family is based on ***Psychroteuthis glacialis***, originally described from incomplete specimens from the stomachs of penguins and seals. Two other species have been suggested (Roper *et al*., 1969b, Nesis, 1982), but they never have been described nor named. Specimens of ***P. glacialis*** now are very abundant in research collections as a result of several decades of intensive research and collections in Antarctic waters, as well as on Antarctic marine and terrestrial predators. The sole species, ***Psychroteuthis glacialis***, has been shown to be the most abundant species of muscular squid in the Weddell Sea, as well as the only pelagic cephalopod that occurs in considerable abundance in the Antarctic Sea Ice Zone (Piatkowski, 1999). It is the predominant squid in the Southern Ocean in waters close to the Antarctic continent.

Literature: Roper *et al*. (1969b), Nesis (1982, 1987), Roper *et al*. (1985), Sweeney and Young (2003x), Piatkowski (2008).

Psychroteuthis Thiele, 1920

Psychroteuthis Thiele, 1920, *Deutsche Südpolar-Expediton, 1901 to 1903, Zoologie*, 16(8): 433–465 [440].

Type Species: *Psychroteuthis glacialis* Thiele, 1920.

Diagnostic Features: The distinguishing features are the same as those of the monotypic family.

Psychroteuthis glacialis Thiele, 1920

Psychroteuthis glacialis Thiele, 1920, *Deutsche Südpolar-Expediton, 1901 to 1903, Zoologie*, 16(8): 433–465 [440]. [Type locality: 66°S, 89°E, southern Ocean].

Frequent Synonyms: None.

FAO Names: En – Glacial squid; **Fr** – Encornet glacial; **Sp** – Luria glacial.

Fig. 357

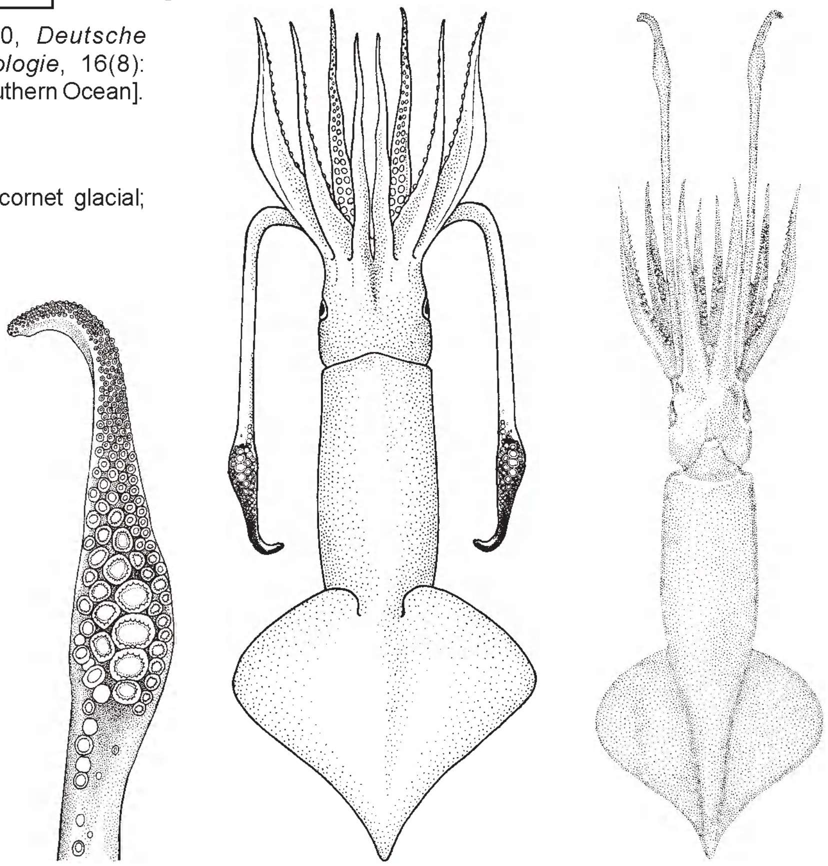

tentacular club dorsal view ventral view

Fig. 357 *Psychroteuthis glacialis*

Diagnostic Features: Since the family and genus are monotypic the characters listed under the family currently are applicable.

Geographical Distribution: This species is circumglobal in Antarctic waters, principally south of the Antarctic Convergence (Fig. 358).

Habitat and Biology: ***Psychroteuthis glacialis*** is an oceanic species reported from less than 200 to 920 m, taken with benthic and bentho-pelagic trawls. Paralarvae and juveniles occur at or near the surface because they frequently are preyed upon by many species of seabirds, penguins and marine mammals. Likewise, adults as they undergo ontogenetic descent into the depths are a major prey species for deeper-diving forms. Among its predators are the following: seabirds, such as the sooty albatross, grey-headed albatross, white-chinned petrel; penguins, like the Emperor penguin, Adelie penguin, gentoo penguin; pinnipeds, as the southern elephant seal, Weddell seal, Ross seal, Antarctic fur seal; odontocete cetaceans, such as the southern bottlenose whale and sperm whale; fishes, like the albacore tuna and other large species. In turn, ***P. glacialis*** preys on krill, *Euphausia superba*. Size-frequency data indicate that the species has a 2-year life cycle; males mature earlier and at a smaller size than females. Paralarvae, especially, show a strong similarity to paralarvae of Histioteuthidae, especially with regard to the shape of the fins, tentacular club with suckers much smaller than those on the arms and the anteriormost position in the mantle cavity of the digestive gland.

Size: The maximum mantle length reported is 440 mm.

Interest to Fisheries: Currently no specific direct interest as a fishery resource exists, but the species is of major importance as prey for both exploited and unexploited predatory species. Furthermore, since the musculature is firm, non-ammoniacal, and since the species is large (up to 440 mm mantle length) and apparently very abundant, it should be considered a potentially valuable resource. This seems more likely now that deep trawling activities continue to probe mesopelagic and upper bathypelagic depths.

Local Names: None available.

Literature: Filippova (1972, 1992 [1991]), Roper *et al.* (1969b), Nesis (1982, 1987), Piatkowski (1989, 2008).

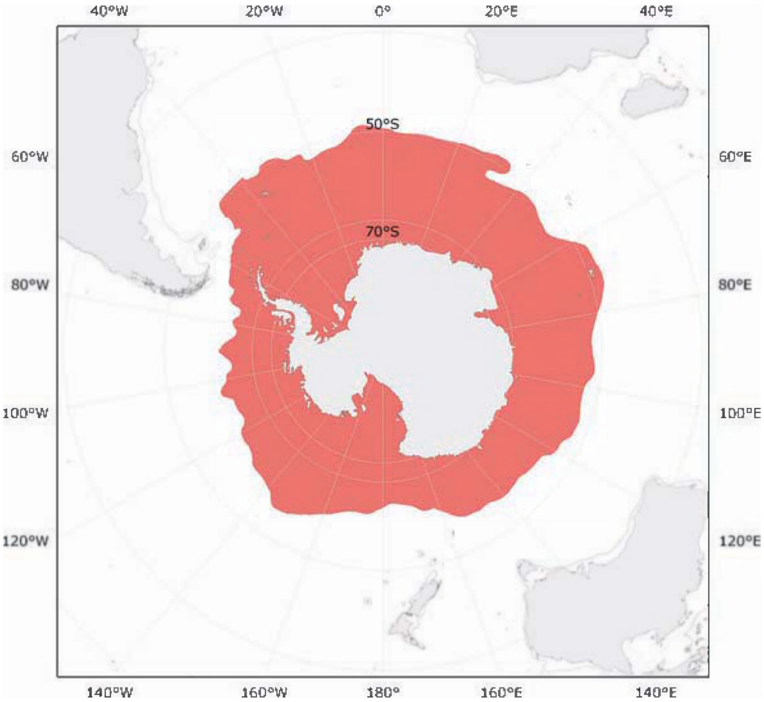


Fig. 358 *Psychroteuthis glacialis*

🟥 Known distribution

2.27 Family PYROTEUTHIDAE Pfeffer, 1912

by Clyde F.E. Roper and Patrizia Jereb

Pyroteuthidae Pfeffer, 1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2F(a): 815pp, 48 plates [189].

Type Genus: *Pyroteuthis* Hoyle, 1904.

FAO Names: En – Fire squids; **Fr** – Encornet feu; **Sp** – Fuegolurias.

Diagnostic Features: Buccal crown with 7 or 8 supports. Buccal connectives attach to dorsal margins of arms IV. Secondary buccal connectives attach to ventral margins of arms I and II. Gladius with small, strongly pointed conus and elongate cone field; rostrum absent. Straight mantle-funnel locking apparatus; biserial armature on arms. **Hooks present on arms I to III (at least)**; hook presence on tentacular club varies with genus; armature on manus always in 4 series. **Photophores present on viscera, eyeballs, and tentacles**. Photophores absent from fins, mantle, funnel, head, and arms. Nidamental glands present; oviducal glands normal on one side, may be reduced or absent on other side. **Oviduct single, unpaired**. **Right or left arm IV hectocotylized**. **Fins subterminal; posterior lobes distinct**. Tail not fleshy but acute, supported by needle-like terminal conus of gladius; vesicles absent. Nuchal folds absent. **Tentacles with permanent constriction and angular bend near base**; stalk "ligament" and vein leave tentacle distal to base and not in membrane. Ink sac embedded in digestive gland.

Size: Small-sized squid; maximum mantle length 50 mm.

Geographical Distribution: The species of this family are broadly distributed worldwide throughout the major oceans and the Mediterranean Sea in tropical and temperate waters. They are epipelagic as paralarvae and juveniles, then as adults they descend to upper mesopelagic habitats, from which they undergo diel vertical migrations into the epipelagic zone at night.

Habitat and Biology: Pyroteuthids are among the more common squids found in the midwaters of the open ocean. They are epipelagic as paralarvae and juveniles, then as adults they descend to upper mesopelagic habitats, from which they undergo diel vertical migrations into the epipelagic zone at night.

Remarks: The Pyroteuthidae was raised to full familial level together with its sister taxa, formerly subfamilies, Enoploteuthinae and Ancistroteuthinae by Clarke (1988b). Young *et al*. (1998b) present the history of these familial changes, diagnostic features of their genera, a list of currently accepted species and their distributions. A phylogenetic study confirmed the validity of dividing the group into 3 families (Young and Harman, 1998). The 2 genera currently recognized in the family Pyroteuthidae are ***Pyroteuthis*** and ***Pterygioteuthis***, species of which are very broadly cosmopolitan in tropical to temperate waters, principally as members of the upper mesopelagic realm. All species undergo diel vertical migrations into the epipelagic waters at night.

Key to the genera of Pyroteuthidae

1a. Hooks present on tentacular clubs and on arms IV; hooks on club arranged in 1 series, on arms in 2 series over entire length; relatively numerous; 12 photophores on ventral side of eyeball (none lidded), 9 large (of different sizes) and 3 small; 10 photophores in mantle cavity include 3 in a row transverse to the longitudinal axis of body at the level of gills; 6 or 7, sometimes 8, photophores on tentacular stalk of young and adults; right ventral arm hectocotylized; without a tooth plate; only left oviduct developed; right oviduct may be present but significantly reduced . . . . **Genus *Pyroteuthis* Hoyle, 1904**

1b. Hooks absent on tentacular club; no hooks, or not more than 2 hooks, on arms IV; hooks few, only in 1 or 2 series in middle of arms I to III; 14 ro 15 photophores on ventral side of eyeball (1 lidded), 10 large and 4 or 5 small; 8 photophores in mantle cavity, including only 1 at level of gills on longitudinal axis of body; 4 photophores on tentacular stalk; left ventral arm hectocotylized, with a tooth plate; only right oviduct developed in females . . . . **Genus *Pterygioteuthis* Fischer, 1896**

Literature: Roper *et al*. (1969b), Young *et al*. (1998b), Sweeney and Young (2003z), Lindgren *et al*. (2008).

Pyroteuthis Hoyle, 1904

Pyroteuthis Hoyle, 1904, *Bulletin of the Museum of Comparative Zoology, Harvard*, 43(1): 1–71 [42].

Type Species: *Pyroteuthis margaritifera* (Rüppel, 1844).

Frequent Synonyms: *Charibditeuthis* Vivanti, 1912; *Ioteuthion* Pfeffer, 1912 (pars); *Pterygonepion* Pfeffer, 1912.

Diagnostic Features: **More than 13 hooks per arm, in 2 transverse series**; **hooks present on arms IV**. Tentacular club with **1 series of hooks and 3 series of suckers on manus**. **Twelve photophores on ventral surface of eyeballs**. Eyeball photophore number 6 (= lidded photophore) absent. Six or 7 separated photophores embedded along tentacular stalk. Oviducts are paired; left oviduct reduced in size. **Right arm IV hectocotylized**; **toothed plate absent**.

Remarks: Three species of ***Pyroteuthis*** currently are recognized (***P. margaritifera***, ***P. addolux***, ***P. serrata***). However, because entities are so widely distributed and exhibit marked variation, most notably in ***P. margaritifera***, for example, it seems probable that a considerable species complex is involved.

Pyroteuthis margaritifera (Rüppel, 1844)

Fig. 359

Enoploteuthis margaritifera Rüppel, 1844, *Giornale del Gabinetto Letteràrio di Messina*, 5(27–28): 129–135 [130, fig.1]. [Type locality: Messina, Sicily, southern central Mediterranean Sea].

Frequent Synonyms: *Pyroteuthis (Pterygonepion) mediterranea* Pfeffer, 1912; *Charibditeuthis maculata* Vivanti, 1912; *Pyroteuthis margaritifera aurantica* Joubin, 1924.

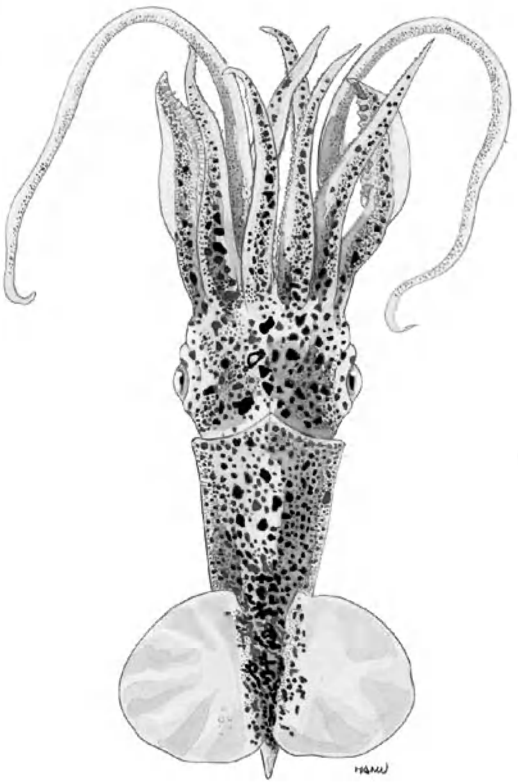
FAO Names: En – Jewel enope squid; **Fr** – Encornet-bijouter; **Sp** – Enoploluria joyera.

Diagnostic Features: Longitudinal membrane of hectocotylus on right arm IV long, about 33% of arm length (measured from first proximal hook); membrane begins distal to seventh to ninth pair of hooks. Normally no additional small photophores on tentacular stalk between first (proximal) and second photophores (but present in southern and western Australian specimens). **Arms long, very strong**; all, including arms IV, bear **hooks in 2 series, almost to tips**. **Tentacular clubs with 1 central series of 3 or 5 hooks and 2 series of suckers**.

Size: The maximum mantle length reaches to 50 mm.

Geographical Distribution: This species is cosmopolitan in tropical, subtropical to temperate waters of all oceans and the Mediterranean Sea (where it is the sole representative of the genus) (Fig. 360).

Habitat and Biology: The upper mesopelagic zone is the daytime adult habitat; adults then undergo diel vertical migration into epipelagic waters at night. For example, off Bermuda, closing-net studies showed that *P. margaritifera* occurs principally at 375 to 500 m during the day and ascends to 75 to 175 m at night. Open net studies off the Canary Islands placed animals at 400 to 800 m during the day and at 50 to 100 m to 200 m at night. In the South Pacific Ocean the species is common in the mixed waters of the subtropical frontal zone and the sub-Antarctic waters. The species occurs in the eastern Mediterranean Sea/northern Aegean Sea in the mesobathyal basins.



dorsal view

Fig. 359 ***Pyroteuthis margaritifera***

Interest to Fisheries: The species is of no interest to fisheries at the present time.

Local Names: ITALY: Totanello perlifero.

Literature: Young (1972a), Roper and Young (1975), Alexeyev (1994a), Lindgren *et al.* (2008).

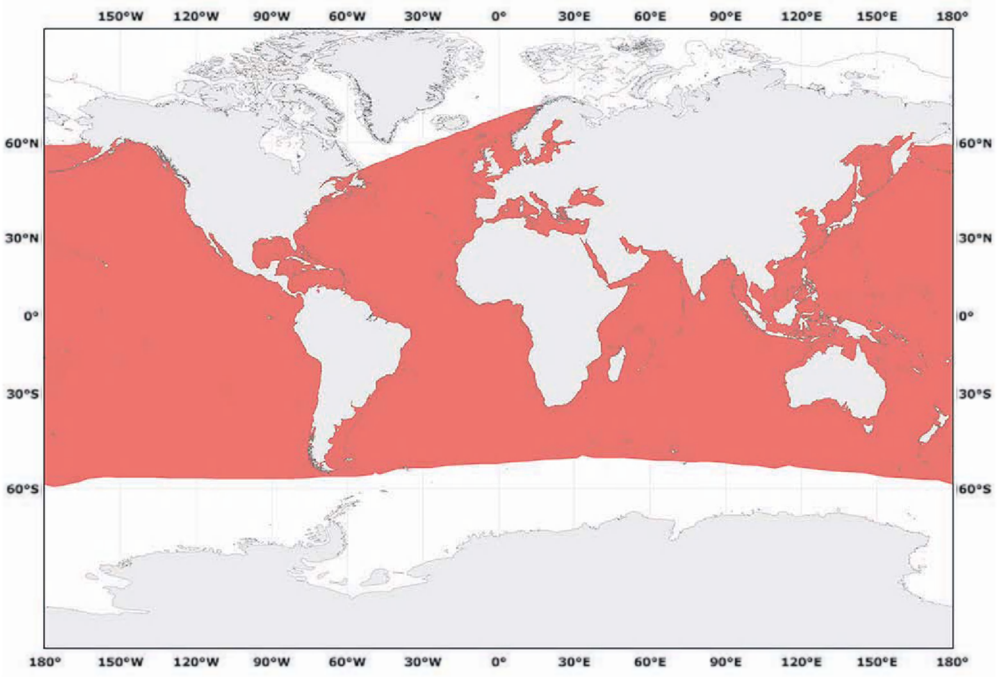


Fig. 360 ***Pyroteuthis margaritifera***

🟥 Known distribution

Pyroteuthis addolux Young, 1972

Plate X, 62

Pyroteuthis addolux Young, 1972a, *Smithsonian Contributions to Zoology*, 97: 1–159 [22, pls. 3 B, 4 I-Q, S]. [Type locality: 31°39'N, 133°16'W, eastern North Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length is 50 mm.

Geographical Distribution: This species occurs in the eastern sector of the central North Pacific Ocean from Hawaii to California as well as in the California Current.

Habitat and Biology: Adults are mesopelagic inhabitants that probably undergo ascent into the epipelagic zone at night.

Interest to Fisheries: No interest in a commercial fishery exists at present.

Literature: Young (1972a), Young (1978), Lindgren *et al*. (2008).

Pyroteuthis serrata Riddell, 1985

Pyroteuthis serrata Riddell, 1985, *Fisheries Research Bulletin, New Zealand*, 27: 1–52 [10, figs 3, 4a, b, d, f]. [Type locality: Kermadec Islands, northeast of New Zealand's North Island, western South Pacific Ocean].

Frequent Synonyms: None.

Size: The maximum mantle length reaches 40 mm.

Geographical Distribution: This species occurs off New Zealand north of the tropical convergence, around 30°S.

Habitat and Biology: The species inhabits mesopelagic to epipelagic zones and presumably is a diel vertical migrator.

Interest to Fisheries: None.

Literature: Riddell (1985).

Pterygioteuthis Fischer, 1896

Plate X, 63

Pterygioteuthis Fischer, 1896, *Journal de Conchyliologie, Paris*, 43(4): 205–211, pl. IX [210].

Type Species: *Pterygioteuthis giardi* Fischer, 1896.

Frequent Synonyms: *Ioteuthion* Pfeffer, 1912 (pars).

Diagnostic Features: Very few arm hooks exist, located only in middle portions of arms I to III, in 1 or 2 transverse series; **a maximum of 2 hooks on arms IV**, sometimes none. **Tentacular clubs without hooks**. **Fourteen or 15 photophores on ventral surface of eyeballs**, 10 large, 4 or 5 small; eyeball photophore number 6 is lidded. Four photophores embedded on tentacular stalk. Only right oviduct developed. **Left arm IV hectocotylized**; **toothed plate present**.

Remarks: Three species currently are recognized: ***Pterygioteuthis giardi***, ***P. gemmata*** and ***P. microlampas***. Each species is very broadly distributed in its own particular pattern, throughout the tropical, subtropical (occasionally temperate) Atlantic, Pacific and Indian Oceans and the Mediterranean Sea. Given such broad distributions, considerable geographic variation exists, some of which has been recognized as subspecific in nature; with continued exploration additional taxa could be described.

Pterygioteuthis giardi Fischer, 1896

Fig. 361

Pterygioteuthis giardi Fischer, 1896, *Journal de Conchyliologie, Paris*, 43(4): 205–211 [211, pl. IX: figs 1–7]. [Type locality: off Cape San Francisco, Galapagos Islands, south of Guaylas, eastern Equatorial Pacific].

Frequent Synonyms: *Pyroteuthis (Pterygonepion) planctonica* Pfeffer, 1912.

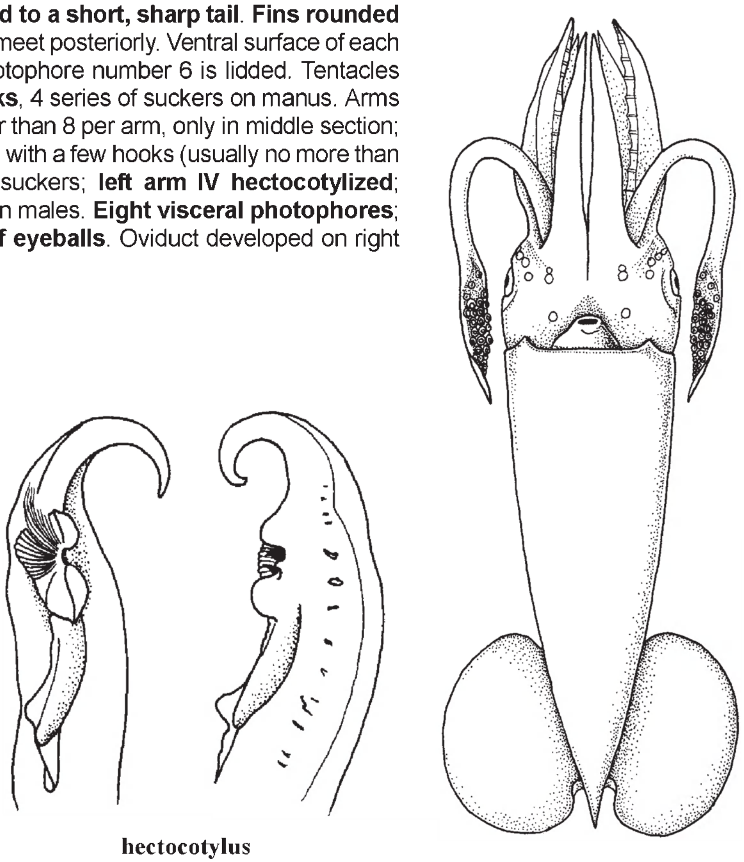
FAO Names: En – Roundear enope squid; **Fr** – Encornet boubou; **Sp** – Enoploluria orejuda.

Diagnostic Features: Mantle small, acutely tapered to a short, sharp tail. **Fins rounded with large anterior and posterior lobes**; fins do not meet posteriorly. Ventral surface of each **eye studded with 15 iridescent photophores**; photophore number 6 is lidded. Tentacles long, thin. **Tentacular clubs compact, without hooks**, 4 series of suckers on manus. Arms short, strong; arms I to III with 2 series of hooks, fewer than 8 per arm, only in middle section; **hooks absent from arms IV, except on adult males** with a few hooks (usually no more than 2), but no suckers; arms IV in females devoid of suckers; **left arm IV hectocotylized**; **toothed plate present**; 1 or 2 hooks on right arm IV in males. **Eight visceral photophores**; **15 photophores** on ventral and posterior **surface of eyeballs**. Oviduct developed on right side only; **left oviduct absent**.

Size: The maximum mantle length attained is 40 mm.

Geographical Distribution: This species/subspecies complex is distributed worldwide as a cosmopolitan tropical- subtropical form in oceanic waters. It is mesopelagic and ascends into the epipelagic zone at night. This is the sole species of the genus reported so far for the Mediterranean Sea (Fig. 362).

Habitat and Biology: This is a predominantly oceanic species with a depth distribution that ranges from just below the surface to about 500 m. It is known to undertake diel vertical migrations: off Bermuda it is found in 250 to 500 m by day and in 50 to 250 m at night. Off Hawaii it is a facultative inhabitant of the mesopelagic boundary zone. The species is preyed upon by large dolphins (e.g. *Tursiops truncatus*) and pelagic fishes.


hectocotylus

ventral view

Fig. 361 *Pterygioteuthis giardi*

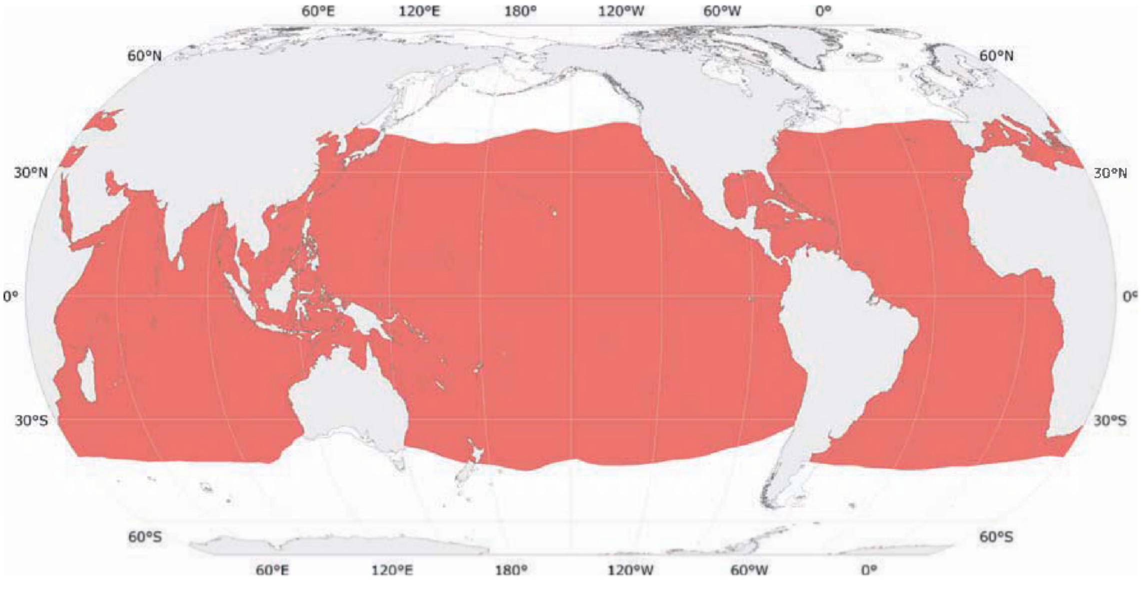


Fig. 362 *Pterygioteuthis giardi*

🟥 Known distribution

Interest to Fisheries: No interest to fisheries exists at present.

Remarks: Nesis (1982, 1987) distinguishes 2 subspecies: ***Pterygioteuthis giardi giardi*** (Atlantic) and ***P. giardi hoylei*** (Indo-Pacific) based on differences in the size of the hooks on the right arm IV of males. These forms were first given this taxonomic status by Pfeffer (1912) based on descriptions by Hoyle (1904) of the latter form from the eastern Equatorial Pacific. A careful study, however, of speciation in this taxa has never been made (Young and Mangold, 1996b)

Local Names: ITALY: Totanello orecchiuto.

Literature: Young (1972a,b), Clarke and Lu (1975), Young and Mangold (1996b), Lindgren *et al*. (2008).

Pterygioteuthis gemmata Chun, 1908

Pterygioteuthis gemmata Chun, 1908, *Zoologischer Anzeiger*, 33(2): 86–89 [87]. [Type locality: 5°51'N, 21°40'W, North Atlantic Ocean].

Frequent Synonyms: ?*Pyroteuthis (Ioteuthion) schnehageni* Pfeffer, 1912.

Size: The maximum mantle length reaches 40 mm.

Geographical Distribution: ***Pterygioteuthis gemmata*** is principally an anti-equatorial species in the Atlantic, Pacific and Indian Oceans. It is not recorded from the Mediterranean Sea to date.

Habitat and Biology: Adults are mesopelagic at 300 to 600 m during the day off southern California, then they ascend into the upper 200 m of the epipelagic zone during nightly vertical migrations. In the Canary Basin the species occurs at 50 to 100 m to 200 m at night and descends to 400 to 800 m during the day.

Interest to Fisheries: No interest exists at present.

Literature: Young (1972a,b), Cairns (1976), Nesis (1993d), Arkhipkin (1997b).

Pterygioteuthis microlampas Berry, 1913

Pterygioteuthis microlampas Berry, 1913b, *Proceedings of the United States National Museum*, 45(1966): 563–566 [566]. [Type locality: Kaiwi Channel, Hawaiian Islands, central North Pacific].

Frequent Synonyms: None.

Geographical Distribution: This species occurs in the central Pacific Ocean and the South Pacific Ocean, north of the tropical convergence.

Literature: Arnold and Young (1974), Bower *et al*. (1999c).

2.28 Family THYSANOTEUTHIDAE Keferstein, 1866

by Clyde F.E. Roper and Patrizia Jereb

Thysanoteuthidae Keferstein, 1866, *In* Bronn, H.G., *Die Klassen und Ordnungen des Thierreichs wissenschftlich dargestellt in Wort und Bild, 1862–1866, Weichtier (Malacozoa)*, 3(2): 1307–1464 [1445].

Type Genus: *Thysanoteuthis* Troschel, 1857.

FAO Names: En – Rhomboid squids, Diamondback squids; **Fr** – Chipilouas; **Sp** – Chipirones

Diagnostic Features: Mantle is very muscular, powerful (in adults to 60 to 85% body weight) with bluntly rounded posterior end and highly developed collagenous tunic system; mantle thickness in adults up to 50 mm (6.5% mantle length); width 25% of length. **The long, broad, very muscular rhomboidal fins extend entire length of mantle**, not fused together along dorsal midline; greatest fin width at anterior two-thirds to three-fourths of fin length; **fin width 75 to 85% of fin/mantle length in adults**. Head width similar to mantle width. Funnel strongly muscular, accompanied with prominent funnel groove. Mantle-funnel and mantle nuchal locking apparatus unique, well developed, the most characteristic familial traits. **Funnel-locking apparatus subtriangular with rounded angles, long, narrow longitudinal groove, short, broad transverse groove, knobs at juncture of grooves; forms a "sideways-T" shape**: ⊣; **large and robust, its length is from 13 to 15% mantle length**. Mantle component with ridges of corresponding form. **Nuchal locking apparatus extremely well developed**, with 2 large, swollen, hook-like knobs on mantle component that interlock with 2 conforming depressions and knobs on the nuchal component. Buccal connective formula DDVV. Arms with no sexual dimorphism in shape or external morphological traits in adults, but differences occur in length of arms III in immature squids of 120 to 450 mm mantle length (arms III length in males 75 to 110% of mantle length, in females about 50% mantle length). Arm formula III.II.IV.I (or IV = I). **Arms relatively short, strongly muscled, with 2 series of suckers (no hooks) and well-developed wide protective membranes expanded on long cirri-like trabeculae**; especially well developed on arms III, less so on arms II; arms I to III with distinct aboral keels. Arm sucker rings with 20 to 26 sharp conical teeth. **Tentacles relatively short, strongly muscled; tentacular clubs widened, relatively long; manus with 4 series of suckers that extend together to tip of dactylus**; **carpal-locking apparatus extends proximally along stalk as 2 series of alternating knobs and suckers**. Suckers on manus of clubs with 15 to 29 fine, strongly pointed, conical teeth. **Left ventral arm (IV) hectocotylized**. In mature males the hectocotylized distal region occupies from 13 to 20 sucker rows and 30 to 35% of the arm length. The modified part of the arm has tiny untoothed suckers with smooth horny rings and 2 oval glandular enlargements. The male reproductive system is characterized by a very long, narrow Needham's sac (40 to 60% mantle length) and a long muscular penis; the female system has hypertrophied oviducal glands (40 to 52% mantle length) with a very large lancet-like second section (30 to 40% mantle length) and relatively small oviducts, with distribution of the main ovarian afferent and efferent blood vessels in mesentery protruding dorsally into the ovary. **One well-developed anal photophore on ink sac near anal papilla in young squid from 60 to 350 mm mantle length; photophore gradually reduced, non-functional in adults**. The gladius very unusual for oegopsid squids. Pro-ostracum very wide, greatest width near anterior margin of gladius; rachis narrow with short anterior free lobes; lateral plates (the first paired elements from the rachis) narrow with hyperbolic anterior margins; wings (the second paired elements from the rachis) gradually widen anteriorly, their width about equal to the width of the rachis plus the lateral plates; anterior lobes of wings protrude beyond the lateral plates almost to the level of the anterior margin of the rachis; the conus is greatly reduced, cup-shaped; the rostrum is absent; the anterior, enlarged part of the gladius bends strongly toward the ventral side of the mantle and protrudes into the mantle cavity; consequently, the dorsal and lateral parts of the inner complex of organs are covered by the curved wings of the gladius, and the gills are situated between the gladius wings and the inner surface of the mantle. **The radula has 7 transverse rows of teeth**. The beak is very characteristic with small, robust rostra on both mandibles; rostrum of lower jaw pointed; jaw angle is distinct, sharp, with a shoulder tooth; the hood is short with a curve on the ventral edge; a well-pronounced transparent strip present; the shape of the beak closely resembles that of ***Architeuthis*** but differences exist: the form of the rostrum (no small hook on rostrum); the jaw edge to wing angle is more acute and beak size is smaller when the wings begin to darken.

Size: Large nektonic squid; adult size attains 100 cm or even 130 cm mantle length.

Interest to Fisheries: A strong local interest exists for the fishery in the Sea of Japan and in waters around Okinawa and Taiwan Province of China.The high commercial value makes it an important target species in Japan.

Remarks: This family now is considered to be monotypic. Formerly, 2 genera, ***Thysanoteuthis*** Troschel, 1857 and ***Cirrobrachium*** Hoyle, 1904, were included in the family. However, ***Cirrobrachium*** was declared to be a junior synonym of ***Thysanoteuthis*** (Nigmatullin and Arkhipkin, 1998: 158). Based on an analysis of gladius morphology of recent and extinct squids 3 evolutionary lines were distinguished: myopsid, oegopsid and thysanoteuthid (Bizikov, 1996). The thysanoteuthid gladius is archaic and unique among the squids: it most resembles gladii of Jurassic Loligosepiida. As a result, Bizikov (1996: 231–233) removed ***Thysanoteuthis*** from the suborder **Oegopsida** and created for it a new suborder, **Thysanoteuthida**, within the order **Teuthida**. The rest of the oegopsid squids remained in the suborder, **Oegopsida**. This opinion also is supported by some archaic and distinct features in the structure of the female reproductive system, spermatozoa, hectocotylus (Nigmatullin, *et al*., 1991a; Nigmatullin and Arkhipkin, 1998) and statocyst (Young, 1989; Nixon and Young, 2003) that seem more closely related to **Myopsida** than to **Oegopsida**.

Literature: Roper *et al*. (1984), Nesis (1982, 1987, 1992a) Guerra (1992), Nigmatullin *et al*. (1995), Nigmatullin and Arkhipkin (1998), Sweeney and Young (2003aa).

Thysanoteuthis Troschel, 1857

Thysanoteuthis Troschel, 1857, *Archiv für Naturgeschichte, Berlin*, 23(1): 40–76 [69].

Type Species: *Thysanoteuthis rhombus* Troschel, 1857.

Frequent Synonyms: *Cirrobrachium* Hoyle, 1904.

Diagnostic Features: The family is monotypic and generic characteristics are the same as given for the family.

Remarks: See remarks given for family.

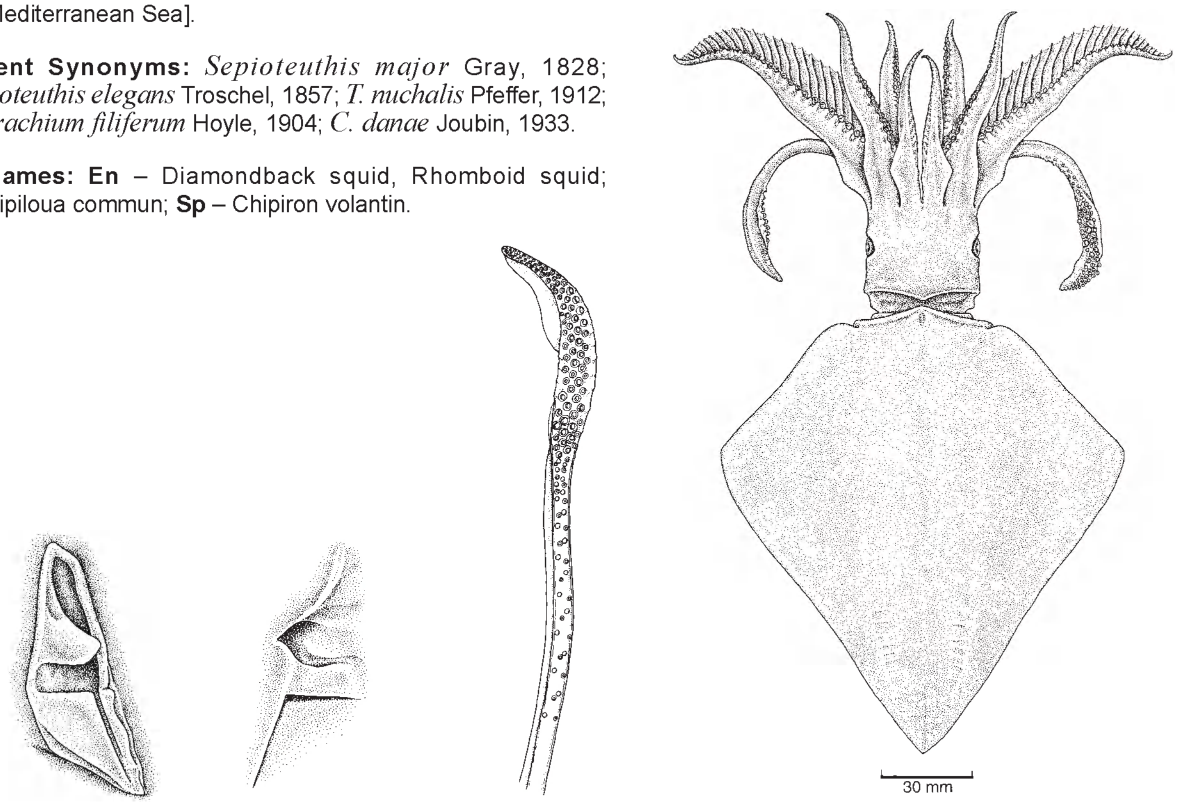
Thysanoteuthis rhombus Troschel, 1857

Fig. 363

Thysanoteuthis rhombus Troschel, 1857, *Archiv für Naturgeschichte*, 23(1): 40–76 [70, pls. 4, 5]. [Type locality: Messina, Sicily, Mediterranean Sea].

Frequent Synonyms: *Sepioteuthis major* Gray, 1828; *Thysanoteuthis elegans* Troschel, 1857; *T. nuchalis* Pfeffer, 1912; *Cirrobrachium filiferum* Hoyle, 1904; *C. danae* Joubin, 1933.

FAO Names: En – Diamondback squid, Rhomboid squid; **Fr** – Chipiloua commun; **Sp** – Chipiron volantin.



funnel-locking apparatus tentacular club dorsal view

Fig. 363 *Thysanoteuthis rhombus*

Diagnostic Features: ***Thysanoteuthis rhombus*** is monotypic, so the characters detailed at the family level are diagnostic. The most characteristic traits are the long, broad rhomboidal fins that occupy the entire length of mantle, the ⊣-shaped mantle-funnel locking cartilages, the presence of the anterior intestinal (anal) photophore in immature squid and the unique shape and structure of the gladius.

Size: The maximum mantle length of both sexes is the same, 100 cm, possibly to 130 cm, and the maximum body weight known is 24 to 30 kg, probably more. Maximum size of a sexed and measured male is 85 cm mantle length and of a female is 82 cm mantle length.

Geographical Distribution: ***Thysanoteuthis rhombus*** is a cosmopolitan species, a common circumglobal inhabitant of warm tropical and subtropical open waters of the world oceans, the Mediterranean Sea and the Caribbean Sea. It also reaches higher latitudes, the temperate boreal and notalian regions, transported by warm currents, e.g. the Tsushima, Kuroshio, Agulhas, Brazil Currents and the Gulf Stream. Thus, with the Tsushima Current, it penetrates into the Sea of Japan to 41°57'N to 140°57'E, and with the Agulhas Current to the Cape of Good Hope area. It inhabits open oceanic waters and only rarely approaches the shelf zone driven there by warm currents in the peripheral range of the species. It avoids the oligotrophic central waters of the open ocean. It occupies epipelagic to upper mesopelagic depths, and it undergoes diel vertical migrations (Fig. 364).

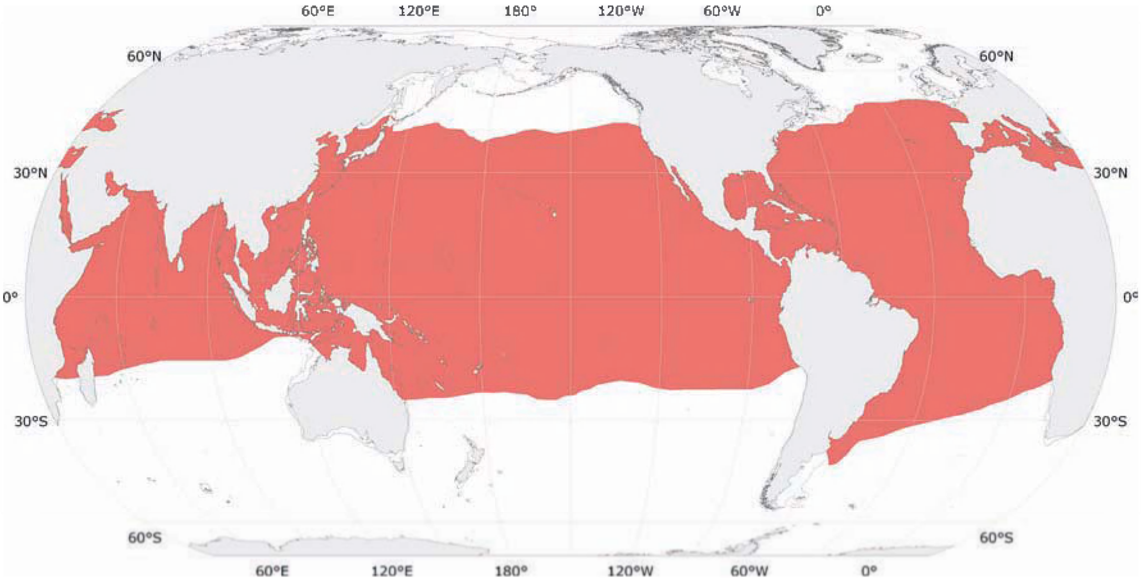


Fig. 364 ***Thysanoteuthis rhombus***

🟥 Known distribution

Habitat and Biology: ***Thysanoteuthis rhombus*** is an epipelagic to mesopelagic species that inhabits open oceanic waters in excess of 400 m bottom depth where surface water temperature principally is greater than 20°C. Paralarvae and juveniles live in the epipelagic zone. Subadults and adults (300 to 850 mm mantle length) make daily vertical migrations in the upper 600 to 800 m. At night most of the population migrates toward the surface (0 to 50 m), then in daytime descends to depths from 400 to 800 m, mainly 450 to 650 m. Distribution and migration depend on the surface circulation of oceanic waters. Despite its eunektonic appearance, ***T. rhombus*** is a relatively passive migrant that undertakes long seasonal migrations in the warm waters of peripheral oceanic currents. Consequently, it is characterized paradoxically as a planktonic nekteur. During most of its life cycle it does not swim actively. Rather, it propels itself slowly by gentle undulation of its long, broad, diamond-shaped fins. However, when it encounters danger, ***T. rhombus*** is capable of a powerful reactive jet of short duration. This low-energy life style enables the rhomboid squid to maintain very high growth rates, among the highest of all squids. By the age of 300 days the squid reach 800 mm mantle length and 17.5 kg body weight. Males reach maturity mainly at 400 to 550 mm mantle length (age 170 to 200 days), and females mature at 550 to 650 mm mantle length (age 230 to 250 days). The life span is 1 year. Spawning lasts throughout the year in tropical waters and during the warm season in peripheral regions. Needham's sac stores from 10 to 40 spermatophores 60 to 100 mm long. The potential fecundity of females is from 2.5 to 5 million oocytes. The development of oocytes is asynchronous. The size of ripe eggs is from 1.6 to 1.8 mm. Maximum egg numbers in oviducts is up to 140 000; spawned egg masses contain from 32 000 to 75 000 embryos. Spawning is intermittent, with multiple fillings and evacuations of the oviducts. In females 8 to 30 seminal receptacles are located on the ventral part of the buccal membrane. Mating occurs in the "head to head" position. The pelagic egg mass is a large cylinder (0.6 to 2 m long, 0.11 to 0.3 m diameter) of transparent gelatinous mucus with pink-violet embryos that are distributed in a double spiral in the outer layer. Hatching size is 1.4 to 1.6 mm mantle length. Development includes a paralarval stage. No pronounced geographical variability occurs in the main morphological features and ecological-population parameters (e.g. size and age at maturity). The same phenomenon is observed for genetic variability: mitochondrial DNA sequences differ very little between conspecific individuals from the western and eastern Pacific Ocean. The population density is low, mainly from 0.01 to 100 specimens per km^2. Total minimum estimated biomass within the vast geographical range of the species is only about 1.5 to 2.5 million tonnes only. The greatest abundance occurs in the productive zones of the open ocean and in coastal areas at the periphery of the range, mainly in the southwestern part of the Sea of Japan. The social organization is unique among squids. It consists of pairs formed of same-sized males and females that occur at an immature stage of less than 100 mm mantle length, and they probably remain together constantly during their lifetimes (monogamy). Small schools of pairs may be locally common. Arm length and probably the anal photophore play the key role in pair formation in immature squids. The reproductive and behavioural strategies are adaptations to low population density and inactive life style. Juveniles feed on crustaceans, small cephalopods and fishes in subsurface waters, but subadults and adults feed mainly in daytime in deep-water layers mostly from 400 to 650 m on dense concentrations of non-active midwater fishes. Predators include different species of ommastrephid squids, dolphin fish (*Coryphaena*), lancet fish (*Alepisarus* 2 species), various species of tuna, e.g. *Thunnus albacares*, *T. obesus*, *T. alalunga*, *Katsuwanus pelamis*, swordfish, *Gempylus serpens*, sharks and mammals (e.g. dolphins, rough-toothed dolphin (*Steno bredanensis*), false killer whale, sperm whale).

Interests to Fisheries: The flesh is firm and flavorful and a significant fishery exists in the coastal waters of the Sea of Japan and around Okinawa. Its high commercial value makes it an important target species in these waters. The only commercial fishery for this species is in Japan and locally in Taiwan. This species has a very high quality, tender meat that yields a very high price (about 0.7 to 2 million yen per tonne), a highly profitable fishery. Catches are not reflected in FAO statistics. The ***T. rhombus*** fishery began in the Sea of Japan off Hyogo Prefecture in 1962 as a nighttime fishery from small boats using baited hooks. In 1967, angling gear called “taru-nagashi”, comprising a buoy and a vertical line with 1 or 2 attached jigs, was introduced as a daytime fishery. Annual catches varied from 0 to 2 tonnes to 232 tonnes (1964), 619 tonnes (1967) and 516 tonnes (1972). In 1990 to 1995 total annual Japanese catches varied between 1 613 tonnes and 2 670 tonnes, then in 1998 it decreased to 200 tonnes and in 2001 peaked to almost 6 000 tonnes. Since 1998 annual catches averaged close to 4 900 tonnes. The main fishing grounds (90% of catch) are situated in the Sea of Japan, Okinawa Prefecture, and Kagoshima Prefecture. A small fishery also occurs near the Ogasawara Islands (2 to 7 tonnes in 1995 to 2000). Currently ***T. rhombus*** is caught in the Sea of Japan using “taru-nagashi” and inshore stationary trap nets. The fishing grounds occur at bottom depths of 100 to 500 m, where the jigs are set in midwater near the 100 m zone. The Sea of Japan fishery runs from July to February, with peak catches in September to December. In Hyogo Prefecture, the fishery typically starts in August and peaks in October. In Toyama, Kyoto and Hyogo, the peak catches occur in October to December when the squid are 200 to 700 mm mantle length. The fishery started in Okinawa Prefecture in 1989 with the same type of fishing gear as used in the Sea of Japan. Catches in Okinawa peaked in 2003 at 2 300 tonnes; these usually comprise about half of the national catch. Highest catches occur in March to April when adult squid of 700 to 850 mm mantle length are caught. This is primarily a daytime fishery with “hata-nagashi” gear, which consists of several jigs fished at depth on a line attached to several buoys with flags at the surface. The gear is set to about 500 m depth near the salinity minimum layer. The fishery employs boats smaller than 5 tonnes during the daytime and each boat uses 15 to 20 sets of fishing gear. This squid also has the potential for a valuable fishery resource in the different parts of its range as bycatch whenever squid and finfish pelagic trawl fisheries develop in slope and oceanic areas, especially in highly productive frontal zones.

Local Names: ARGENTINA: Calamar rombo; CANARY ISLANDS: Calamar de lo alto, Calamar obispo; FRANCE: Chipilona, Chipiloua commun; ITALY: Totano rombo; JAPAN: Common – Sode-ika and more local – Aka-ika, Beni-ika (the Oki Islands), Taru-ika (area near Wakasa Bay), Kannon-ika (Toyama Prefecture) and Sei-ika (Okinawa Prefecture); KOREA: Nal-Ge-O-Jing-Eo; MEXICO (the Gulf of California): Calamar de aleta corrida; PERU: Calamar diamante; UKRAINE: Kal’mar-romb; SPAIN: Chipirone, Chipiron volantin; SOUTH AFRICA: Diamond squid; UK: Diamondback squid; USA: Diamondback squid; TAIWAN: Líng-qí-yóu.

Literature: Roper *et al.* (1984), Nigmatullin *et al.* (1995), Nigmatullin and Arkhipkin (1998), Takeda and Tanda (1998), Bower and Miyahara (2005), Miyahara *et al.* (2005).

3. LIST OF NOMINAL SPECIES

The following list gives information (horizontally) in the order (i) the scientific name as it originally appeared, in alphabetical order according to the specific name; (ii) the author(s); (iii) date of publication; and (iv) present allocation.

NOMINAL SPECIES	PRESENT ALLOCATION
ANCISTROCHEIRIDAE Pfeffer, 1912	
Enoploteuthis lesueurii d'Orbigny, 1842	*Ancistrocheirus lesueurii*
ARCHITEUTHIDAE Pfeffer, 1900	
Architeuthis dux Steenstrup, 1857	*Architeuthis dux*
Megateuthis martensi Hilgendorf, 1880	*Architeuthis martensi*
Mouchezis sanctipauli Velain, 1877	*Architeuthis sanctipauli*
AUSTRALITEUTHIDAE Lu, 2005	
Australiteuthis aldrichi Lu, 2005	*Australiteuthis aldrichi*
BATHYTEUTHIDAE Pfeffer, 1900	
Bathyteuthis abyssicola Hoyle, 1885	*Bathyteuthis abyssicola*
Bathyteuthis bacidifera Roper, 1968	*Bathyteuthis bacidifera*
Bathyteuthis berryi Roper, 1968	*Bathyteuthis berryi*
BATOTEUTHIDAE Young and Roper, 1968	
Batoteuthis skolops Young and Roper, 1968	*Batoteuthis skolops*
BRACHIOTEUTHIDAE Pfeffer, 1908	
Brachioteuthis beanii Verrill, 1881	*Brachioteuthis beanii*
Brachioteuthis bowmani Russell, 1909	*Brachioteuthis bowmani*
Brachioteuthis picta Chun, 1910	*Brachioteuthis picta*
Slosarczykovia circumantarctica, Lipinski 2001	*Slosarczykovia circumantarctica*
Slosarczykovia linkovskyi, Lipinski, 2001	*Brachioteuthis linkovskyi*
Tracheloteuthis behni Steenstrup, 1882	*Brachioteuthis behnii*
Tracheloteuthis riisei Steenstrup, 1882	*Brachioteuthis riisei*
CHIROTEUTHIDAE Gray, 1849	
Asperoteuthis lui Salcedo-Vargas 1999	*Asperoteuthis lui*
Asperoteuthis mangoldae Young, Vecchione and Roper, 2007	*Asperoteuthis mangoldae*
Chiropsis mega Joubin, 1932	*Chiroteuthis mega*
Chiroteuthis acanthoderma Lu, 1977	*Chiroteuthis acanthoderma*
Chiroteuthis calyx Young, 1972	*Chiroteuthis calyx*
Chiroteuthis imperator Chun, 1908	*Chiroteuthis imperator*
Chiroteuthis joubini, Voss 1967	*Chiroteuthis joubini*
Chiroteuthis picteti Joubin, 1894	*Chiroteuthis picteti*
Chiroteuthis spoeli, Salcedo-Vargas, 1996	*Chiroteuthis spoeli*
Doratopsis exophthalmica Chun, 1908	*Planctoteuthis exophthalmica*
Doratopsis lippula Chun, 1908	*Planctoteuthis lippula*
Loligopsis bonplandi Verany, 1839	*Grimalditeuthis bonplandi*
Loligopsis veranii Ferussac, 1834	*Chiroteuthis veranyi*
Mastigoteuthis levimana Lönnberg, 1896	*Planctoteuthis levimana*
Valbyteuthis danae Joubin, 1931	*Planctoteuthis danae*

NOMINAL SPECIES	PRESENT ALLOCATION
Valbyteuthis oligobessa Young, 1972	*Planctoteuthis oligobessa*
CHTENOPTERYGIDAE Grimpe, 1922	
Chtenopteryx canariensis Salcedo-Vargas and Guerrero-Kommritz, 2000	*Chtenopteryx canariensis*
Chtenopteryx sepioloides Rancurel, 1970	*Chtenopteryx sepioloides*
Sepioteuthis sicula Verany, 1851	*Chtenopteryx sicula*
CRANCHIIDAE Prosch, 1847	
Ascocranchia joubini Voss, 1962	*Helicocranchia joubini*
Bathothauma lyromma Chun, 1906	*Bathothauma lyromma*
Belonella borealis Nesis, 1972	*Taonius borealis*
Carymoteuthis oceanica Voss, 1960	*Megalocranchia oceanica*
Cranchia maculata Leach, 1817	*Teuthowenia maculata*
Cranchia (Owenia) megalops Prosch, 1847	*Teuthowenia megalops*
Cranchia scabra Leach, 1817	*Cranchia scabra*
Crystalloteuthis glacialis Chun, 1906	*Galiteuthis glacialis*
Desmoteuthis pellucida Chun, 1910	*Teuthowenia pellucida*
Drechselia danae Joubin, 1931	*Leachia danae*
Egea inermis Joubin, 1933	*Egea inermis*
Galiteuthis armata Joubin, 1898	*Galiteuthis armata*
Galiteuthis phyllura Berry, 1911	*Galiteuthis phyllura*
Helicocranchia pfefferi Massy, 1907	*Helicocranchia pfefferi*
Leachia cyclura Lesueur, 1821	*Leachia cyclura*
Leachia dislocata Young, 1972	*Leachia dislocata*
Leachia reinhardti Steenstrup, 1856	*Liocranchia reinhardti*
Liguriella podophthalma Issel, 1908	*Liguriella podophthalma*
Liocranchia valdiviae Chun 1910	*Liocranchia valdiviae*
Loligo pavo Lesueur, 1821	*Taonius pavo*
Megalocranchia maxima Pfeffer, 1884	*Megalocranchia maxima*
Megalocranchia papillata Voss, 1960	*Helicocranchia papillata*
Mesonychoteuthis hamiltoni Robson, 1925	*Mesonychoteuthis hamiltoni*
Pyrgopsis atlantica Degner, 1925	*Leachia atlantica*
Pyrgopsis lemur Berry, 1920	*Leachia lemur*
Sandalops melancholicus Chun, 1906	*Sandalops melancholicus*
Taonidium pacificum Robson, 1948	*Galiteuthis pacifica*
Taonius suhmi Hoyle, 1886	*Galiteuthis suhmi*
Toxeuma belone Chun, 1906	*Taonius belone*
Zygaenopsis pacifica Issel, 1908	*Leachia pacifica*
CYCLOTEUTHIDAE Naef, 1923	
Cycloteuthis akimushkini Filippova, 1968	*Cycloteuthis akimushkini*
Cycloteuthis sirventi Joubin, 1919	*Cycloteuthis sirventi*
Discoteuthis discus Young and Roper, 1969	*Discoteuthis discus*
Discoteuthis laciniosa Young and Roper, 1969	*Discoteuthis laciniosa*

NOMINAL SPECIES	PRESENT ALLOCATION
ENOPLOTEUTHIDAE Pfeffer, 1900	
Abralia (Micrabralia) affinis Pfeffer, 1912	*Abraliopsis affinis*
Abralia andamanica Goodrich, 1896	*Abralia andamanica*
Abralia astrolineata Berry, 1914	*Abralia astrolineata*
Abralia astrostricta Berry, 1909	*Abralia astrostricta*
Abralia fasciolata Tsuchiya, 1991	*Abralia fasciolata*
Abralia gilchristi Robson, 1924	*Abralia gilchristi*
Abralia grimpei Voss, 1959	*Abralia grimpei*
Abralia heminuchalis Burgess, 1992	*Abralia heminuchalis*
Abralia lineata Goodrich, 1896	*Abraliopsis lineata*
Abralia marisarabica Okutani, 1983	*Abralia marisarabica*
Abralia multihamata Sasaki, 1929	*Abralia multihamata*
Abralia omiae Hidaka and Kubodera, 2000	*Abralia omiae*
Abralia redfieldi Voss, 1955	*Abralia redfieldi*
Abralia renschi Grimpe, 1931	*Abralia renschi*
Abralia robsoni Grimpe, 1931	*Abralia robsoni*
Abralia siedleckyi Lipinski, 1983	*Abralia siedleckyi*
Abralia similis Okutani and Tsuchiya, 1987	*Abralia similis*
Abralia spaercki Grimpe, 1931	*Abralia spaercki*
Abralia steindachneri Weindl, 1912	*Abralia steindachneri*
Abralia trigonura Berry, 1913	*Abralia trigonura*
Abraliopsis atlantica Nesis, 1982	*Abraliopsis atlantica*
Abraliopsis chuni Nesis, 1982	*Abraliopsis chuni*
Abraliopsis falco Young, 1972	*Abraliopsis falco*
Abraliopsis felis McGowan and Okutani, 1968	*Abraliopsis felis*
Abraliopsis pacificus Tsuchiya and Okutani, 1990	*Abraliopsis pacificus*
Abraliopsis scintillans Berry, 1911	*Watasenia scintillans*
Abraliopsis tui Riddell, 1985	*Abraliopsis tui*
Enoploteuthis anapsis Roper, 1964	*Enoploteuthis anapsis*
Enoploteuthis chunii Ishikawa, 1914	*Enoploteuthis chunii*
Enoploteuthis dubia Adam, 1960	*Abralia dubia*
Enoploteuthis galaxias Berry, 1918	*Enoploteuthis galaxias*
Enoploteuthis higginsi Burgess, 1982	*Enoploteuthis higginsi*
Enoploteuthis hoylei Pfeffer, 1884	*Abraliopsis hoylei*
Enoploteuthis jonesi Burgess, 1982	*Enoploteuthis jonesi*
Enoploteuthis leptura magnoceani Nesis, 1982	*Enoploteuthis leptura magnoceani*
Enoploteuthis migrato Burgess, 1982	*Enoploteuthis obliqua*
Enoploteuthis migratory Rancurel, 1970	*Enoploteuthis reticulata*
Enoploteuthis octolineata Burgess, 1982	*Enoploteuthis octolineata*
Enoploteuthis semilineata Alexeyev, 1994	*Enoploteuthis semilineata*
Enoploteuthis veranyi Rüppel, 1844	*Abralia veranyi*

NOMINAL SPECIES	PRESENT ALLOCATION
Loligo lepturo Leach, 1817	*Enoploteuthis leptura leptura*
Onychoteuthis armatus Quoy and Gaimard, 1832	*Abralia armata*
Onychoteuthis morisi Verany, 1839	*Abraliopsis morisii*
GONATIDAE Hoyle, 1886	
Berryteuthis magister nipponensis Okutani and Kubodera, 1987	*Berryteuthis magister nipponensis*
Berryteuthis magister shevtsovi Katugin, 2000	*Berryteuthis magister shevtsovi*
Eogonatus tinro Nesis, 1972	*Eogonatus tinro*
Gonatopisis okutanii Nesis, 1972	*Gonatopisis okutanii*
Gonatopsis borealis Sasaki, 1923	*Gonatopsis borealis*
Gonatopsis japonicus Okiyama, 1969	*Gonatopsis japonicus*
Gonatopsis makko Okutani and Nemoto, 1964	*Gonatopsis makko*
Gonatopsis octopedatus Sasaki, 1920	*Gonatopsis octopedatus*
Gonatus anonychus Pearcy and Voss, 1963	*Berryteuthis anonychus*
Gonatus antarcticus Lönnberg, 1898	*Gonatus antarcticus*
Gonatus berryi Naef, 1923	*Gonatus berryi*
Gonatus californiensis Young, 1972	*Gonatus californiensis*
Gonatus madokai Kubodera and Okutani, 1977	*Gonatus madokai*
Gonatus magister Berry, 1913	*Berryteuthis magister*
Gonatus onyx Young, 1972	*Gonatus onyx*
Gonatus oregonensis Jefferts, 1985	*Gonatus oregonensis*
Gonatus pyros Young, 1972	*Gonatus pyros*
Gonatus steenstrupi Kristensen, 1981	*Gonatus steenstrupi*
Gonatus ursabrunae Jefferts, 1985	*Gonatus ursabrunae*
Onychoteuthis fabricii Lichtenstein, 1818	*Gonatus fabricii*
Onychoteuthis kamtschatica Middendorff, 1849	*Gonatus kamtschaticus*
HISTIOTEUTHIDAE Verrill, 1881	
Calliteuthis celetaria celetaria Voss, 1960	*Histioteuthis celetaria celetaria*
Calliteuthis celetaria pacifica Voss, 1962	*Histioteuthis celetaria pacifica*
Calliteuthis corona Voss and Voss, 1962	*Histioteuthis corona corona*
Calliteuthis (Meleagroteuthis) heteropsis Berry, 1913	*Histioteuthis heteropsis*
Calliteuthis inermis Taki, 1964	*Histioteuthis corona inermis*
Calliteuthis meleagroteuthis Chun, 1910	*Histioteuthis meleagroteuthis*
Calliteuthis miranda Berry, 1918	*Histioteuthis miranda*
Calliteuthis reversa Verrill, 1880	*Histioteuthis reversa*
Cranchia bonnellii Ferussac, 1834	*Histioteuthis bonnellii*
Histiopsis atlantica Hoyle, 1885	*Histioteuthis atlantica*
Histiopsis hoylei Goodrich, 1896	*Histioteuthis hoylei*
Histiothauma oceani Robson, 1948	*Histioteuthis oceani*
Histioteuthis corona berryi Voss, 1969	*Histioteuthis corona berryi*
Histioteuthis corona cerasina Nesis, 1971	*Histioteuthis corona cerasina*
Histioteuthis eltaninae Voss, 1969	*Histioteuthis eltaninae*

NOMINAL SPECIES	PRESENT ALLOCATION
Histioteuthis macrohista Voss, 1969	*Histioteuthis macrohista*
Stigmatoteuthis arcturi Robson, 1948	*Histioteuthis arcturi*
JOUBINITEUTHIDAE Naef, 1922	
Chiroteuthis portieri Joubin, 1916	*Joubiniteuthis portieri*
LEPIDOTEUTHIDAE Pfeffer, 1912	
Lepidoteuthis grimaldii Joubin, 1895	*Lepidoteuthis grimaldii*
LOLIGINIDAE Lesueur, 1821	
Alloteuthis africana Adam 1950	*Alloteuthis africana*
Doryteuthis pickfordi Adam, 1954	*Uroteuthis pickfordi*
Doryteuthis reesi Voss, 1962	*Uroteuthis reesi*
Doryteuthis sibogae Adam, 1954	*Uroteuthis (Photololigo) sibogae*
Loligo abulati Adam, 1955	*Uroteuthis (Photololigo) abulati*
Loligo beka Sasaki, 1929	*Loliolus (Nipponololigo) beka*
Loligo bengalensis Jothinayagam, 1987	*Uroteuthis (Photololigo) bengalensis*
Loligo bleekeri Keferstein, 1866	*Heterololigo bleekeri*
Loligo brevis Blainville, 1823	*Lolliguncula (Lolliguncula) brevis*
Loligo chinensis Gray, 1849	*Uroteuthis (Photololigo) chinensis*
Loligo diomedeae Hoyle, 1904	*Lolliguncula (Loliolopsis) diomedeae*
Loligo duvaucelii D'Orbigny, 1835	*Uroteuthis (Photololigo) duvaucelii*
Loligo edulis Hoyle, 1885	*Uroteuthis (Photololigo) edulis*
Loligo forbesii Steenstrup, 1856	*Loligo forbesii*
Loligo gahi d'Orbigny, 1835	*Doryteuthis (Amerigo) gahi*
Loligo hardwickei Gray, 1849	*Loliolus (Loliolus) hardwickei*
Loligo japonica Hoyle, 1885	*Loliolus (Nipponololigo) japonica*
Loligo ocula Cohen, 1976	*Doryteuthis (Amerigo) ocula*
Loligo opalescens Berry, 1911	*Doryteuthis (Amerigo) opalescens*
Loligo pealeii Lesueur, 1821	*Doryteuthis (Amerigo) pealeii*
Loligo plei Blainville, 1823	*Doryteuthis (Doryteuthis) plei*
Loligo reynaudii Orbigny, 1839–1841	*Loligo reynaudii*
Loligo roperi Cohen, 1976	*Doryteuthis (Doryteuthis) roperi*
Loligo sanpaulensis Brakoniecki, 1984	*Doryteuthis sanpaulensis*
Loligo sepioidea Blainville, 1823	*Sepioteuthis sepioidea*
Loligo singhalensis Ortmann, 1891	*Uroteuthis (Photololigo) singhalensis*
Loligo subulata Lamarck, 1798	*Alloteuthis subulata*
Loligo sumatrensis D'Orbigny, 1835	*Loliolus (Nipponololigo) sumatrensis*
Loligo surinamensis Voss, 1974	*Doryteuthis (Amerigo) surinamensis*
Loligo uyii Wakiya and Ishikawa, 1921	*Loliolus (Nipponololigo) uyii*
Loligo vossi Nesis, 1982	*Uroteuthis (Photololigo) vossi*
Loligo vulgaris Lamarck, 1798	*Loligo vulgaris*
Loliolus affinis Steenstrup, 1856	*Loliolus (Loliolus) affinis*
Loliolus noctiluca Lu, Roper, and Tait, 1985	*Uroteuthis (Aestuariolus) noctiluca*

NOMINAL SPECIES	PRESENT ALLOCATION
Lolliguncula argus Brakoniecki and Roper, 1985	*Lolliguncula (Lolliguncula) argus*
Lolliguncula mercatoris Adam, 1941	*Afrololigo mercatoris*
Lolliguncula panamensis Berry, 1911	*Lolliguncula (Lolliguncula) panamensis*
Pickfordiateuthis bayeri Roper and Vecchione, 2001	*Pickfordiateuthis bayeri*
Pickfordiateuthis pulchella Voss, 1953	*Pickfordiateuthis pulchella*
Pickfordiateuthis vossi Brakoniecki, 1996	*Pickfordiateuthis vossi*
Pteroteuthis arabica Ehrenberg, 1831	*Uroteuthis (Photololigo) arabica*
Sepia media Linnaeus, 1758	*Alloteuthis media*
Sepioteuthis australis Quoy and Gaimard, 1832	*Sepioteuthis australis*
Sepioteuthis lessoniana Ferussac in Lesson, 1831	*Sepioteuthis lessoniana*
Uroteuthis bartschi Rehder, 1945	*Uroteuthis (Uroteuthis) bartschi*
Uroteuthis (Photololigo) machelae Roeleveld and Augustine, 2005	*Uroteuthis (Photololigo) machelae*
Uroteuthis robsoni Alexeyev, 1992	*Uroteuthis (Photololigo) robsoni*
LYCOTEUTHIDAE Pfeffer, 1908	
Lampadioteuthis megaleia Berry, 1916	*Lampadioteuthis megaleia*
Nematolampas regalis Berry, 1913	*Nematolampas regalis*
Nematolampas venezuelensis Arocha, 2003	*Nematolampas venezuelensis*
Onychoteuthis lorigera Steenstrup, 1875	*Lycoteuthis lorigera*
Oregoniateuthis springeri Voss, 1956	*Lycoteuthis springeri*
Selenoteuthis scintillans Voss, 1959	*Selenoteuthis scintillans*
MAGNAPINNIDAE Vecchione and Young, 1998	
Magnapinna atlantica Vecchione and Young, 2006	*Magnapinna atlantica*
Magnapinna pacifica Vecchione and Young, 1998	*Magnapinna pacifica*
Mastigoteuthis talismani Fischer and Joubin, 1907	*Magnapinna talismani*
MASTIGOTEUTHIDAE Verrill, 1881	
Chiroteuthis famelica Berry, 1909	*Mastigoteuthis famelica*
Chiroteuthoides hastula Berry, 1920	*Mastigoteuthis hastula*
Echinoteuthis danae Joubin, 1933	*Mastigoteuthis danae*
Mastigoteuthis agassizii Verrill, 1881	*Mastigoteuthis agassizii*
Mastigoteuthis atlantica Joubin, 1933	*Mastigoteuthis atlantica*
Mastigoteuthis cordiformis Chun, 1908	*Mastigoteuthis cordiformis*
Mastigoteuthis dentata Hoyle, 1904	*Mastigoteuthis dentata*
Mastigoteuthis glaukopis Chun, 1908	*Mastigoteuthis glaukopis*
Mastigoteuthis hjorti Chun, 1913	*Mastigoteuthis hjorti*
Mastigoteuthis inermis Rancurel, 1972	*Mastigoteuthis inermis*
Mastigoteuthis iselini MacDonald and Clench, 1934	*Mastigoteuthis iselini*
Mastigoteuthis latipinna Sasaki, 1916	*Mastigoteuthis latipinna*
Mastigoteuthis magna Joubin, 1913	*Mastigoteuthis magna*
Mastigoteuthis microlucens Young, Lindgren and Vecchione, 2008	*Mastigoteuthis microlucens*
Mastigoteuthis okutanii Salcedo-Vargas, 1997	*Mastigoteuthis okutanii*
Mastigoteuthis psychrophila Nesis, 1977	*Mastigoteuthis psychrophila*

NOMINAL SPECIES	PRESENT ALLOCATION
Mastigoteuthis pyrodes Young, 1972	*Mastigoteuthis pyrodes*
Mastigoteuthis tyroi Salcedo-Vargas, 1997	*Mastigoteuthis tyroi*
NEOTEUTHIDAE Naef, 1921	
Alluroteuthis antarcticus Odhner, 1923	*Alluroteuthis antarcticus*
Narrowteuthis nesisi Young and Vecchione, 2005	*Narrowteuthis nesisi*
Neoteuthis thielei Naef, 1921	*Neoteuthis thielei*
Nototeuthis dimegacotyle Nesis and Nikitina, 1986	*Nototeuthis dimegacotyle*
OCTOPOTEUTHIDAE Berry, 1912	
Ancistrocheirus megaptera Verrill, 1885	*Octopoteuthis megaptera*
Octopodoteuthis danae Joubin, 1931	*Octopodoteuthis danae*
Octopoteuthis deletron Young, 1972	*Octopoteuthis deletron*
Octopodoteuthis indica Naef, 1923	*Octopodoteuthis indica*
Octopodoteuthis nielseni Robson, 1948	*Octopoteuthis nielseni*
Octopoteuthis rugosa Clarke, 1980	*Octopoteuthis rugosa*
Octopoteuthis sicula Rüppell, 1844	*Octopoteuthis sicula*
Taningia danae Joubin, 1931	*Taningia danae*
OMMASTREPHIDAE Steenstrup, 1857	
Illex oxygonius, Roper, Lu and Mangold, 1969	*Illex oxygonius*
Loligo bartramii Lesueur, 1821	*Ommastrephes bartramii*
Loligo coindetii Verany, 1839	*Illex coindetii*
Loligo eblanae Ball, 1841	*Todaropsis eblanae*
Loligo illecebrosus Lesueur, 1821	*Illex illecebrosus*
Loligo oualaniensis Lesson, 1830	*Sthenoteuthis oualaniensis*
Loligo sagittata Lamarck, 1798	*Todarodes sagittatus*
Martialia hyadesi Rochebrune and Mabille, 1889	*Martialia hyadesi*
Ommastrephes argentinus Castellanos, 1960	*Illex argentinus*
Ommastrephes gigas d'Orbigny 1835	*Dosidicus gigas*
Ommastrephes gouldi McCoy, 1888	*Nototodarus gouldi*
Ommastrephes hawaiiensis Berry, 1912	*Nototodarus hawaiiensis*
Ommastrephes pteropus Steenstrup, 1855	*Sthenoteuthis pteropus*
Ommastrephes sloanii Gray, 1849	*Nototodarus sloanii*
Ornithoteuthis volatilis (Sasaki 1915)	*Ornithoteuthis volatilis*
Ornithoteuthis volatilis antillarum Adam, 1957	*Ornithoteuthis antillarum*
Sepia pelagica Bosc, 1802	*Hyaloteuthis pelagica*
Symplectoteuthis luminosa Sasaki, 1915	*Eucleoteuthis luminosa*
Todarodes angolensis Adam, 1962	*Todarodes angolensis*
Todarodes filippovae, Adam 1975	*Todarodes filippovae*
Todarodes pacificus (Steenstrup, 1880)	*Todarodes pacificus*
Todarodes pusillus Dunning, 1988	*Todarodes pusillus*
ONYCHOTEUTHIDAE Gray, 1849	

NOMINAL SPECIES	PRESENT ALLOCATION
Kondakovia longimana Filippova, 1972	*Kondakovia longimana*
Loligo banksi Leach, 1817	*Onychoteuthis banksii*
Moroteuthis knipovitchi Filippova, 1972	*Onykia knipovitchi*
Moroteuthis lönnbergi Ishikawa and Wakiya, 1914	*Onykia lönnbergi*
Moroteuthis robsoni Adam, 1962	*Onykia robsoni*
Notonykia africanae Nesis, Roeleveld and Nikitina, 1998	*Notonykia africanae*
Notonykia nesisi Bolstad, 2007	*Notonykia nesisi*
Ommastrephes robusta Verrill, 1876,	*Onykia robusta*
Onychoteuthis borealijaponicus Okada, 1927	*Onychoteuthis borealijaponica*
Onychoteuthis ingens Smith, 1881	*Onykia ingens*
Onychoteuthis lichtensteini Férussac, 1835	*Ancistroteuthis lichtensteini*
Onychoteuthis meridiopacifica Rancurel and Okutani, 1990	*Onychoteuthis meridiopacifica*
Onychoteuthis platyptera d'Orbigny, 1834 (1834-1837)	*Onykia platyptera*
Onykia carriboea Lesueur, 1821	*Onykia carriboea*
Onykia rancureli Okutani, 1981	*Onykia rancureli*
Teleoteuthis appellöfi Pfeffer, 1900	*Onykia appellöfi*
Teleoteuthis compacta Berry, 1913	*Onychoteuthis compacta*
Teleoteuthis intermedia Pfeffer, 1912	*Onykia intermedia*
Teleoteuthis verrilli Pfeffer, 1900	*Onykia verrilli*
Walvisteuthis virilis Nesis and Nikitina, 1986	*Walvisteuthis virilis*
PHOLIDOTEUTHIDAE Voss, 1956	
Pholidoteuthis adami Voss, 1956	*Pholidoteuthis adami*
Tetronychoteuthis massyae Pfeffer, 1912	*Pholidoteuthis massyae*
PROMACHOTEUTHIDAE Naef, 1912	
Promachoteuthis megaptera Hoyle, 1885	*Promachoteuthis megaptera*
Promachoteuthis sloani Young, Vecchione and Piatkowski 2006	*Promachoteuthis sloani*
Promachoteuthis sp. B Young, Vecchione and Roper, 2007	*Promachoteuthis sp. B*
Promachoteuthis sp. D Young, Vecchione and Roper, 2007	*Promachoteuthis sp. D*
Promachoteuthis sulcus Young, Vecchione and Piatkowski 2006	*Promachoteuthis sulcus*
PSYCHROTEUTHIDAE Thiele, 1920	
Psychroteuthis glacialis Thiele, 1920	*Psychroteuthis glacialis*
PYROTEUTHIDAE Pfeffer, 1912	
Enoploteuthis margaritifera Rüppel, 1844	*Pyroteuthis margaritifera*
Pterygioteuthis giardi Fischer, 1896	*Pterygioteuthis giardi*
Pterygioteuthis gemmata Chun, 1908	*Pterygioteuthis gemmata*
Pterygioteuthis microlampas Berry, 1913	*Pterygioteuthis microlampas*
Pyroteuthis addolux Young, 1972	*Pyroteuthis addolux*
Pyroteuthis serrata Riddell, 1985	*Pyroteuthis serrata*
THYSANOTEUTHIDAE Keferstein, 1866	
Thysanoteuthis rhombus Troschel, 1857	*Thysanoteuthis rhombus*

4. LIST OF SPECIES BY MAJOR FISHING AREAS

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Australiteuthis aldrichi	36											●				●				
Loligo vulgaris	40			●		●	●		●											
Loligo forbesii	43			●		●	●													
Loligo reynaudii	46								●											
Afrololigo mercatoris	48					●			●											
Alloteuthis media	50			●		●	●													
Alloteuthis africana	52					●			●											
Alloteuthis subulata	53			●		●	●													
Doryteuthis (Doryteuthis) plei	55				●			●												
Doryteuthis (Doryteuthis) roperi	57				●															
Doryteuthis (Amerigo) gahi	58							●											●	
Doryteuthis (Amerigo) ocula	61				●															
Doryteuthis (Amerigo) opalescens	62														●		●			
Doryteuthis (Amerigo) pealeii	64		●		●															
Doryteuthis (Amerigo) surinamensis	68				●															
Doryteuthis sanpaulensis	69							●												
Heterololigo bleekeri	71													●						
Loliolus (Loliolus) hardwickei	73										●	●				●				
Loliolus (Loliolus) affinis	75											●				●				
Loliolus (Nipponololigo) beka	76											?		●		●				
Loliolus (Nipponololigo) japonica	77													●		●				
Loliolus (Nipponololigo) sumatrensis	78											●		●		●				
Loliolus (Nipponololigo) uyii	80													●		●				
Lolliguncula (Lolliguncula) brevis	81		●		●			●												
Lolliguncula (Lolliguncula) argus	84																●		●	
Lolliguncula (Lolliguncula) panamensis	85																●		●	
Lolliguncula (Loliolopsis) diomedeae	86																●		●	
Pickfordiateuthis pulchella	88				●			●												
Pickfordiateuthis bayeri	89				●															
Pickfordiateuthis vossi	90																●			
Sepioteuthis sepioidea	91				●			●												
Sepioteuthis australis	93											●						●		
Sepioteuthis lessoniana	95						●				●	●		●		●		●		
Uroteuthis (Uroteuthis) bartschi	99											●				●				
Uroteuthis (Aestuariolus) noctiluca	100											●				●				
Uroteuthis (Photololigo) edulis	101										●	●		●		●				
Uroteuthis (Photololigo) abulati	103										●									
Uroteuthis (Photololigo) arabica	104										●									
Uroteuthis (Photololigo) bengalensis	105											●								
Uroteuthis (Photololigo) chinensis	106											●		●		●				
Uroteuthis (Photololigo) duvaucelii	108										●	●		●		●				

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Uroteuthis (Photololigo) machelae	110										●									
Uroteuthis (Photololigo) robsoni	111										●									
Uroteuthis (Photololigo) sibogae	112								●			●		●		●				
Uroteuthis (Photololigo) singhalensis	113										●	●		●		●				
Uroteuthis (Photololigo) vossi	114										●					●				
Uroteuthis pickfordi	116										?	●				●				
Uroteuthis reesi	117															●				
Ancistrocheirus lesueurii	119		●	●	●	●	●	●	●		●	●		●		●	●	●	●	
Architeuthis dux	122		●	●	●		●													
Architeuthis martensi	122													●	●		●			
Architeuthis sanctipauli	123							●	●		●	●						●	●	
Bathyteuthis abyssicola	125					●	●	●	●	●	●	●	●			●	●	●	●	●
Bathyteuthis bacidifera	126										●					●	●			
Bathyteuthis berryi	126														●		●			
Batoteuthis skolops	127							●		●		●	●					●	●	
Brachioteuthis riisei	130	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Brachioteuthis picta	132				●	●		●	●		●	●		●		●	●	●	●	
Brachioteuthis beanii	133		●																	
Brachioteuthis behnii	133							●	●		●	●								
Brachioteuthis bowmani	133			●	●															
Brachioteuthis linkovskyi	134							●												
Slosarczykovia circumantarctica	134									●			●							●
Chiroteuthis veranyi	137		●	●	●	●	●	●	●		●	●	●			●	●	●	●	●
Chiroteuthis calyx	138													●	●		●			
Chiroteuthis imperator	138										●	●				●	●	●		
Chiroteuthis joubini	138										●	●					●			
Chiroteuthis mega	139														●	●				
Chiroteuthis picteti	139										●	●		●		●	●			
Chiroteuthis spoeli	139										●									
Asperoteuthis acanthoderma	140				●			●	●		●	●		●		●				
Asperoteuthis lui	141																	●		
Asperoteuthis mangoldae	141																●			
Grimalditeuthis bonplandi	142		●	●	●	●		●	●		●	●		●		●	●	●	●	
Planctoteuthis exophthalmica	143					●					●									
Planctoteuthis danae	144		●	●	●	●		●	●		●	●		●		●	●	●	●	
Planctoteuthis levimana	145		●	●																
Planctoteuthis lippula	145								●											
Planctoteuthis oligobessa	145														●	●	●			
Chtenopteryx sicula	146		●	●	●	●	●	●	●		●	●		●		●	●		●	
Chtenopteryx canariensis	147					●														
Chtenopteryx sepioloides	147															●	●			
Cranchia scabra	151		●	●	●	●	●	●	●		●	●		●		●	●	●	●	
Leachia cyclura	153										●	●				●				
Leachia atlantica	154		●		●			●												

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Leachia danae	154																●		●	
Leachia dislocata	154																●		●	
Leachia lemur	155				●															
Leachia pacifica	155											●		●		●	●			
Liocranchia reinhardti	156		●	●	●	●		●	●		●	●		●		●	●	●	●	
Liocranchia valdiviae	157								●		●	●				●	●			
Taonius pavo	159		●	●	●	●		●	●		●									
Taonius belone	160										●	●		●		●	●		●	
Taonius borealis	160													●	●		●			
Bathothauma lyromma	161		●	●	●	●		●	●		●	●		●		●	●	●	●	
Egea inermis	162		●	●	●	●		●			●	●		●		●	●		●	
Galiteuthis armata	164		●	●	●	●	●													
Galiteuthis glacialis	165									●			●							●
Galiteuthis pacifica	165											●				●	●		●	
Galiteuthis phyllura	165													●	●		●			
Galiteuthis suhmi	166									●			●							●
Helicocranchia pfefferi	167		●	●	●	●		●	●		?	?		?			?	?	?	
Helicocranchia joubini	168				●	●		●	●							●				
Helicocranchia papillata	168				●	●														
Liguriella podophthalma	169		●	●	●	●		●	●	●	●	●	●	●		●	●	●	●	●
Meagalocranchia maxima	171							●	●		●			●						
Meagalocranchia oceanica	172		●	●	●	●		●	●											
Mesonychoteuthis hamiltoni	173									●			●							●
Sandalops melancholicus	174		●	●	●	●		●	●		●	●		●		●	●	●	●	
Teuthowenia megalops	176		●	●	●		●													
Teuthowenia maculata	178			●		●			●											
Teuthowenia pellucida	178							●	●	●	●	●								
Cycloteuthis sirventi	180		●	●	●	●	●	●			●	●		?		?				
Cycloteuthis akimushkini	181							●	●	●	●	●	●							●
Discoteuthis discus	181		●	●	●	●		●	●		●	●		●		●	●	●	●	
Discoeuthis laciniosa	182		●	●	●	●		●	●		●	●		●		●	●	●	●	
Enoploteuthis leptura leptura	184				●	●		●	●			●		●		●				
Enoploteuthis leptura magnoceani	185										●	●		●		●	●			
Enoploteuthis anapsis	185				●															
Enoploteuthis chunii	186													●						
Enoploteuthis galaxias	186															●		●		
Enoploteuthis higginsi	186										●	●				●	●			
Enoploteuthis jonesi	187															●	●			
Enoploteuthis obliqua	187																●			
Enoploteuthis octolineata	187															●	●			
Enoploteuthis reticulata	188											●				●				
Enoploteuthis semilineata	188																		●	
Abralia armata	189											●				●				
Abralia andamanica	190										●	●		●		●				

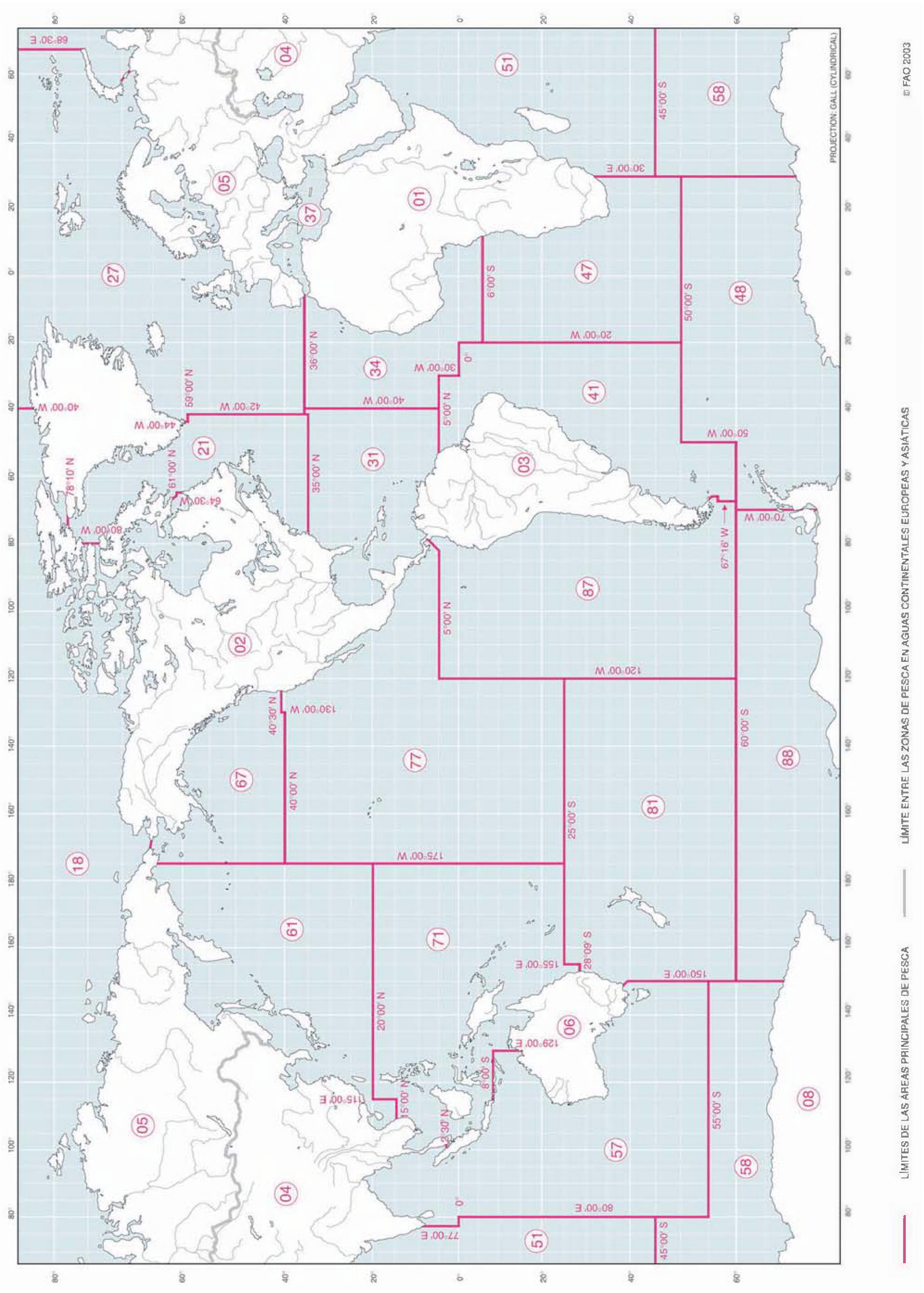
SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Abralia astrolineata	190											●						●		
Abralia astrostricta	190													●		●	●			
Abralia dubia	190										●									
Abralia fasciolata	191										●									
Abralia grimpei	191				●															
Abralia heminuchalis	191																●			
Abralia marisarabica	191										●									
Abralia multihamata	192													●		●				
Abralia omiae	192															●				
Abralia redfieldi	192		●		●	●		●	●											
Abralia renschi	192										●	●								
Abralia robsoni	193													●						
Abralia siedleckyi	193								●											
Abralia similis	193											●		●		●	●			
Abralia spaercki	193											●				●				
Abralia steindachneri	194										●	●								
Abralia trigonura	194													●			●			
Abralia veranyi	194		●	●	●	●	●													
Abraliopsis hoylei	195										●	●		●		●		●		
Abraliopsis affinis	196																●		●	
Abraliopsis atlantica	196					●			●											
Abraliopsis chuni	196										●	●				●				
Abraliopsis falco	196																●		●	
Abraliopsis felis	197													●	●					
Abraliopsis gilchristi	197								●		●							●		
Abraliopsis lineata	197										●	●								
Abraliopsis morisii	197		●	●	●	●	●													
Abraliopsis pacificus	198													●			●			
Abraliopsis tui	198																	●		
Watasenia scintillans	199													●						
Gonatus fabricii	203		●	●										●	●					
Gonatus kamtschaticus	204													●	●					
Gonatus madokai	206													●	●					
Gonatus steenstrupi	207		●	●																
Berryteuthis magister	209													●	●		●			
Berryteuthis anonychus	211													●	●					
Gonatopsis octopedatus	213													●						
Gonatopsis borealis	215													●	●		●			
Gonatopsis japonicus	216													●						
Gonatopsis makko	218													●	●					
Gonatus antarcticus	219								●	●			●						●	●
Gonatus berryi	219													●	●		●			
Gonatus californiensis	219														●		●			
Gonatus onyx	220													●	●		●			

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Gonatus oregonensis	220														●		●			
Gonatus pyros	220													●	●		●			
Gonatus ursabrunae	221														●					
Berryteuthis magister nipponensis	221													●						
Berryteuthis magister shevtsovi	221													●						
Eogonatus tinro	222													●	●					
Gonatopsis okutanii	222													●	●					
Histioteuthis bonnellii	226			●		●	●		●		●	●						●		
Histioteuthis hoylei	228										●	●		●	●	●	●	●	●	
Histioteuthis miranda	229								●		●	●						●		
Histioteuthis reversa	231		●	●	●	●	●													
Histioteuthis arcturi	232		●		●	●		●	●											
Histioteuthis atlantica	232							●	●		●	●						●	●	
Histioteuthis celetaria celetaria	233			●	●	●		●	●											
Histioteuthis celetaria pacifica	233								●		●	●				●	●		●	
Histioteuthis corona berryi	233																●			
Histioteuthis corona cerasina	234																●		●	
Histioteuthis corona corona	234		●	●	●	●		●	●											
Histioteuthis corona inermis	234													●						
Histioteuthis eltaninae	235							●	●	●		●						●		●
Histioteuthis heteropsis	235																●		●	
Histioteuthis macrohista	235							●	●		●	●						●		
Histioteuthis meleagroteuthis	236		●	●	●	●		●	●		●	●		●		●	●	●	●	
Histioteuthis oceani	236															●	●		●	
Joubiniteuthis portieri	237		●	●	●	●		●	●		●	●		●		●	●	●	●	
Lepidoteuthis grimaldii	239		●	●				●	●		●	●		●		●	●	●		
Lycoteuthis lorigera	242							●	●		●	●						●	●	
Lycoteuthis springeri	243				●															
Nematolampas regalis	244																	●		
Nematolampas venezuelensis	245				●	●														
Solenoteuthis scintillans	245		●	●	●	●														
Lampadioteuthis megaleia	246		●	●		●												●		
Magnapinna pacifica	248																●			
Magnapinna atlantica	249				●	●														
Magnapinna talismani	249					●														
Mastigoteuthis agassizii	252		●	●	●	●														
Mastigoteuthis atlantica	253		●	●	●	●														
Mastigoteuthis cordiformis	253											●		●		●				
Mastigoteuthis danae	253		●	●	●	●														
Mastigoteuthis dentata	253										●			●		●	●	●	●	
Mastigoteuthis famelica	254																●			
Mastigoteuthis glaukopis	254					●			●		●			●						
Mastigoteuthis hjorti	254		●		●	●			●		●								●	
Mastigoteuthis magna	254		●		●	●								●						

SPECIES	page	GEOGRAPHICAL DISTRIBUTION																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Mastigoteuthis microlucens	255																●			
Mastigoteuthis psychrophila	255									●			●							●
Mastigoteuthis pyrodes	255																●			
Mastigoteuthis tyroi	256										●									
Neoteuthis thielei	258		●	●	●	●		●	●					●	●		●			
Alluroteuthis antarcticus	259									●			●							●
Narrowteuthis nesisi	260					●														
Nototeuthis dimegacotyle	261																		●	
Octopoteuthis sicula	264		●	●	●	●	●	●	●		●	●		●		●	●	●	●	
Taningia danae	265		●	●	●	●	●	●	●		●	●		●	●	●	●	●	●	
Octopoteuthis danae	267				●	●														
Octopoteuthis deletron	267													?	●		●		●	
Octopoteuthis indica	267								●		●									
Octopoteuthis megaptera	268		●		●	●						●				●		●		
Octopoteuthis nielseni	268																●		●	
Octopoteuthis rugosa	268					●			●		●	●								
Illex illecebrosus	280		●	●	●															
Illex argentinus	285							●												
Illex coindetii	290			●	●	●	●	●	●											
Illex oxygonius	292		●		●	?														
Ommastrephes bartramii	295		●	●	●	●	●	●	●		●	●		●	●			●	●	
Dosidicus gigas	300														●		●		●	
Eucleoteuthis luminosa	305							●	●		●	●		●		●	●	●	●	
Hyaloteuthis pelagica	307			●	●	●		●	●					●		●	●	●	●	
Ornithoteuthis volatilis	309								?		●	●		●		●	●	●		
Ornithoteuthis antillarum	312		●		●	●		●	●											
Sthenoteuthis oualaniensis	314										●	●		●		●	●	●	●	
Sthenoteuthis pteropus	318		●		●	●		●	●											
Todarodes sagittatus	322	●		●		●	●													
Todarodes angolensis	325								●											
Todarodes filippovae	326							●	●	●	●	●	●					●	●	●
Todarodes pacificus	328													●	●					
Todarodes pusillus	333											●				●				
Martialia hyadesi	334							●	●	●		●	●					●	●	●
Nototodarus sloanii	337																	●		
Nototodarus gouldi	340											●						●		
Nototodarus hawaiiensis	343								●		●	●		●		●	●		●	
Todaropsis eblanae	345			●		●	●		●		●	●		●		●		●		
Onychoteuthis banksii	350		●	●	●	●	●	●	●		●	●		●	●	●	●	●	●	
Onychoteuthis borealijaponica	352													●	●		●			
Ancistroteuthis lichtensteini	354				●	●	●	●	●							●		●		
Notonykia africanae	355							●	●		●	●						●	●	
Notonykia nesisi	356									●			●	●				●		●
Onykia carriboea	357				●	●		●	●		●	●		●		●	●		●	

SPECIES	page	**GEOGRAPHICAL DISTRIBUTION**																		
		MAJOR FISHING AREAS FOR STATISTICAL PURPOSES																		
		18	21	27	31	34	37	41	47	48	51	57	58	61	67	71	77	81	87	88
		ARC	WNA	ENA	WCA	ECA	MED	WSA	EDA	ANC	WIO	EIO	ANE	WNP	ENP	WCP	ECP	WSP	ESP	ANW
Onykia ingens	359							●	●	●		●	●					●	●	
Onykia knipovitchi	360									●			●							●
Onykia lönnbergi	362										●	●		●		●				
Onykia robsoni	363							●	●			●						●		
Onykia robusta	364													●	●		●			
Kondakovia longimana	365							●	●	●			●					●		●
Onychoteuthis compacta	368																●			
Onychoteuthis meridiopacifica	368															●	●			
Walvisteuthis virilis	367		●	●	●	●		●	●		●	●		●	●	●	●		●	
Pholidoteuthis massyae	371							●	●		●	●						●	●	
Pholidoteuthis adami	372		●		●			●												
Promachoteuthis megaptera	375													●						
Promachoteuthis sloani	376			●																
Promachoteuthis sulcus	376								●											
Promachoteuthis sp.B	376			?														?	●	
Promachoteuthis sp.D	376								●											
Psychroteuthis glacialis	378									●			●							●
Pyroteuthis margaritifera	380		●	●	●	●	●	●	●		●	●		●	●	●	●	●	●	
Pyroteuthis addolux	381																●			
Pterygioteuthis serrata	381																	●		
Pterygioteuthis giardi	382		●	●	●	●	●	●	●		●	●		●		●	●	●	●	
Pterygioteuthis gemmata	383		●	●				●	●		●	●		●	●			●	●	
Pterygioteuthis microlampas	383													●		●	●			
Thysanoteuthis rhombus	385		●	●	●	●	●	●	●		●	●		●		●	●		●	

MAJOR FISHING AREAS FOR STATISTICAL PURPOSES



5. REFERENCES*

AAVV. 1998. Squid culture 'a must' in Thailand, *Fish Faming International*, 25(2): 8.

AAVV. 1998. Market squid: What we know and what we need to know for effective management. *Reports of the California Cooperative Oceanic Fisheries Investigations*, 39: 53–54.

Anon. 1989. Falkland Islands Interim Conservation and Management Zone Fisheries Report 87–88. *Falkland Islands Government, Stanley*, 45 pp.

Anon. 1991. Fishery potential of north eastern Atlantic squid stocks. *Copenhagen Denmark ICES*, 5 pp.

Anon. 2000. Analysis and evaluation of the fisheries of the most commercially important cephalopod species in the Mediterranean Sea. *Final Report (Contract No 97/0054)*, 196 pp.

Anon. 2001. The squid fishery in crisis; scientists link poor squid catches to El Niño; squid research is back on track [Three squid sectors]. *Fish Ind News South Africa*, 2(4): 5, 6, 8.

Anon. 2004. Report of the working group on cephalopod fisheries and life history. *Working Group on Cephalopogs, ICES Council Meeting* /G:02.

Anon. 2005. First documentation of the Roper inshore squid, *Loligo roperi* (Cohen 1976), in the Gulf of Mexico. *Gulf of Mexico Science*, 23(1): 132–135.

Aasgard, T. 1987. Squid as feed for salmonids. *Aquaculture*, 61(3–4): 259–273.

Abdel-Aziz, S.H. 1994. Observations on the biology of the common torpedo (*Torpedo torpedo*, Linnaeus, 1758) and marbled electric ray (*Torpedo marmorata*, Risso, 1810) from Egyptian Mediterranean waters. *Australian Journal of Marine and Freshwater Research*, 45: 693–704.

Abitia-Cardenas, L.A., F. Galvan-Magana, F.J. Gutierrez-Sanchez, J. Rodriguez-Romero, B. Aguilar-Palomino & A. Moehl-Hitz. 1999. Diet of blue marlin *Makaira mazara* off the coast of Cabo San Lucas, Baja California Sur, Mexico. *Fisheries Research*, 44(1): 95–100.

Abitia-Cardenas, L.A., A. Muhlia-Melo, V. Cruz-Escalona & F. Galvan-Magana. 2002. Trophic dynamics and seasonal energetics of striped marlin *Tetrapturus andax* in the southern Gulf of California, Mexico. *Fisheries Research*, 57(3): 287–295.

Abollo, E., C. Gestal, A. Lopez, A.F. Gonzalez, A. Guerra & S. Pascual. 1998. Squid as trophic bridges for parasite flow within marine ecosysterms: The case of *Anisakis simplex* (Nematoda: Anisakidae), or when the wrong way can be right. *South African Journal of Marine Science*, 20: 223–232.

Abolmasova, G.I. 1978. Skorost' obmena u nekotorykh vidov bespozvonochnykh iz Sredizemnogo morya (Metabolic rates in some invertebrates from the Mediterranean Sea). *Biologiya Morya, Kiev*, (46): 25–9 (in Russian).

Abolmasova, G.I. & Yu.S. Belokopytin. 1987. A study of energy metabolism in captive epipelagic squid *Sthenoteuthis pteropus* St. at different swimming speeds. *Ehkologiya Morya*, 27: 75–78.

Abolmasova, G.I. & A.Ya. Stolbov. 1991. A study of the rate of energy metabolism in the squid (*Sthenoteuthis pteropus* St.) at low temperatures with consideration for hydrostatic pressure. *Ehkologiya Morya.*, 37: 73–76.

Acha, E.M, H.W. Mianzan, R.A. Guerrero, M. Favero & J. Bava. 2004. Marine fronts at the continental shelves of austral South America Physical and ecological processes. *Journal of Marine Systems*, 44: 83–105.

***Adam, W.** 1938. Zur Kenntnis von *Sepioteuthis loliginiformis* (Ruppell & Leuckart, 1828). *Archiv für Molluskenskunde*, 70: 52–59.

Adam, W. 1939a. The Cephalopoda in the Indian Museum, Calcutta. *Records of the Indian Museum*, 41: 61–100.

***Adam, W.** 1939b. Cephalopoda, I. Le genre *Sepioteuthis* Blainville, 1824. *Siboga Expedition Monographie*, 55a: 1–33.

***Adam, W.** 1941. Cephalopoda. *In*: Résultats scientifiques des croisières du Navire-école Belge "Mercator". Volume III. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, series 2, 21: 83–162.

Adam, W. 1942. Cephalopods of the Red Sea. *Bulletin of the Institute of Oceanography*, 822: 1–20.

---

[*] References cited in this document are preceeded by an asterisk (*)

⋆**Adam, W.** 1950a. Notes sur les Céphalopodes, XXII. Deux nouvelles espèces de la côte Africaine Occidentale. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 26(45): 1–9.

⋆**Adam, W.** 1950b. Un cephalopode nouveau: *Pholidoteuthis boshmai* gen. et sp. nov. *Koninklijke Nederlandse Academie von Wetenschappen*, 53(10): 1592–1598.

⋆**Adam, W.** 1952. Céphalopodes. *Résultats Scientifiques, Expédition Océanographique Belge dans les Eaux Cotières Africaines de l'Atlantique Sud (1948–1949)*, 3(3): 1–142.

⋆**Adam, W.** 1954. Cephalopoda. Partie III. IV. Cephalopodes a l'exclusion des genres *Sepia*, *Sepiella* et *Sepioteuthis*. Siboga Expedition, *Monographie*, 55(c): 123–193, 40 figs, 4 pls.

⋆**Adam, W.** 1955. Cephalopodes. In: Résultats scientifiques des campagnes de la "Calypso"I: Campagnes 1951–1952 en Mer Rouge. *Annales de l'Institut Oceanographique, Paris*, 30: 185–194.

Adam, W. 1957. Notes sur les Céphalopodes. XXIII– Quelques espèces des Antilles. *Bulletin du Institut royal des Sciences naturelles de Belgique*, 33(7): 1–10, 1 pl.

⋆**Adam, W.** 1959. Les Cephalopodes de la mer Rouge. *Mission Robert Ph. Dollfus en Egypte, Resultats Scientifiques*, 3(28): 125–193.

⋆**Adam, W.** 1960a. Cephalopoda from the Gulf of Aquaba. Contributions to the knowledge of the Red Sea No. 16. *Bulletin of the Sea Fishery Research Station, Haifa*, 26: 3–26.

⋆**Adam, W.** 1960b. Notes sur les Cephalopodes XXIV: Contribution a la connaissance de l'hectocotyle chez les Ommastrephidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 36(19): 1–10.

⋆**Adam, W.** 1962. Céphalopodes de l'Archipel du Cap-Vert, de l'Angola et du Mozambique. *Memorias da Junta de Investigacoes do Ultramar*, (2ª Série)33: 9–64, 2 pls.

Adam, W. 1972. Notes on cephalopods. XXV. Contribution to the knowledge of *Chaunoteuthis mollis* Appellof, 1891. *Bulletin de l'Institute royal des Sciences naturelles de Belgique*, 48(12): 1–7.

Adam, W. 1973. Cephalopoda from the Red Sea. Contributions to the knowledge of the Red Sea No 47. *Bulletin of the Sea–Fish Research Station, Haifa*, 60: 9–47.

⋆**Adam, W.** 1975. Notes sur les Cephalopodes. XXVI. Una nouvelle espèce de *Todarodes* (*Todarodes filippovae* sp. nov.) de l'Ocean Indien. *Bulletin de l' Institut royal des Sciences naturelles de Belgique*, 50 (9): 1–10.

Adam, W. 1983. Cephalopoda from West and South Africa. *Atlantide Report*, 13: 151–180.

Adams, A. & L. Reeve. 1848 [1848–1850]. Mollusca Part 1. The zoology of the voyage of H.M.S. "Samarang" under the command of Captain Sir Edward Belcher during the years 1843–46. Paris, 88 pages, 24 pls.

Adcock, G.J., G.R. Carvalho, P.G. Rodhouse & P.W. Shaw. 1999a. Highly polymorphic microsatellite loci of the heavily fished squid genus *Illex* (Ommastrephidae). *Molecular Ecology*, 8(1): 165–167.

Adcock, G.J., P.W. Shaw, P.G. Rodhouse & G.R. Carvalho. 1999b. Microsatellite analysis of genetic diversity in the squid *Illex argentinus* during a period of intensive fishing. *Marine Ecology Progress Series*, 187: 171–178.

Agnew, D.J. 2002. Critical aspects of the Falkland Islands pelagic ecosystem: distribution, spawning and migration of pelagic animals in relation to oil exploration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 12(1): 39–50.

Agnew, D.J., J.R. Beddington & S.L. Hill. 2002. The potential use of environmental information to manage squid stock. *Canadian Journal of Fishery and Aquatic Science*, 59: 1851–1857.

Agnew, D.J., S.L. Hill & J.R. Beddington. 2000. Predicting the recruitment strength of an annual squid stock: *Loligo gahi* around the Falkland Islands. *Canadian Journal of Fishery and Aquatic Science*, 57: 2479–2487.

Agnew, D.J., C.P. Nolan & S. des Clers. 1998a. On the problem of identifying and assessing populations of Falkland Island squid *Loligo gahi*. *South African Journal of Marine Science*, 20: 59–66.

Agnew, D.J., R. Baranowski, J.R. Beddington, S. des Clers & C.P. Nolan. 1998b. Approaches to assessing stocks of *Loligo gahi* around the Falkland Islands. *Fisheries Research Amsterdam*, 35(3): 155–169.

Agnew, D.J., S.L. Hill, F.R. Beddington, L.V. Purchase & R.C. Wakeford. 2005. Sustainability and management of southwest Atlantic squid fisheries. *Bulletin of Marine Science*, 76(2): 579–594.

Ahmad, T. & Usman [no–initials–given] 1997. Bigfin squid culture: The Indonesian experience *Proceedings of the seventh Workshop of the Tropical Marine Mollusc Programme TMMP on Central and West Java, Indonesia conducted at IPB, UNDIP, LIPI, 11–22 November 1996, Part 1* Hylleberg, J. (ed.), 17(1): 285–287.

Ainley, D.G., L.B. Spear, S.G. Allen & C.A. Ribic. 1996. Temporal and spatial patterns in the diet of the common murre in California waters. *Condor*, 4: 691–705.

Akao, N., S. Tsukidate, Y. Mori, T. Kajiyama, K. Kondo & K. Fujita. 1995. The lethal effect of freezing on spirurid nematode larvae in firefly squids, *Watasenia scintillans*. *Japan Journal of Parasitology*, 44(4): 321–324.

***Akasaki, T., M. Nikaido, K. Tsuchiya & S. Segawa.** 2006. Extensive mitochondrial gene arrangements in coleoid Cephalopoda and their phylogenetic implications. *Molecular Phylogenetics and Evolution*, 38(3): 648–658.

***Akimushkin, I.I.** 1963. Cephalopods of the seas of the U.S.S.R. *Academy of Sciences of the U.S.S.R., Institute of Oceanology, Mocow*, 235 pp., 60 figs [In Russian].

Akiyama, S., S. Kaihara & T. Arimoto. 2004a. Capture characteristics of a trammel net for oval squid *Sepioteuthis lessoniana* in Tateyama Bay, Chiba Prefecture. *Bulletin of the Japanese Society of Scientific Fisheries*, 70(6): 865–871.

Akiyama, S., S. Kaihara, T. Arimoto & T. Toaki. 2004b. Size selectivity of a trammel net for oval squid *Sepioteuthis lessoniana*. *Fisheries Science*, 70(6): 945–951.

Akulin, V.N., S.P. Kasyanov, V.G. Rybin, A.E. Karaulov & M.I. Yurjeva. 2005. Hydrobionts' lipids research. *Transactions of the Pacific Research Fisheries Center*, 141: 335–347.

Akyol, O. & G. Metin. 2001. An investigation on determination of some morphological characteristics of cephalopods in Izmir Bay (Aegean Sea). *Journal of Fisheries and Aquatic Sciences*, 18(3–4): 357–365.

Akyol, O. & H. Sen. 2004. A new large pelagic squid record for the Northern Aegean Sea of Turkey; neon flying squid, *Ommastrephes bartramii* (LeSueur, 1821). *Turkish Journal of Fisheries and Aquatic Sciences*, 4(2): 111–113.

***Aldred, R.G.** 1974. Structure, growth and distribution of the squid *Bathothauma lyromma* Chun. *Journal of Marine Biological Association United Kingdom*, 54: 995–1006.

***Aldrich, F.A.** 1991. The history and evolution of the Newfoundland squid jigger, and jigging. *Journal of Cephalopod Biology*, 2(1): 23–30.

***Aldrich, F.A.** 1992. Some aspects of the systematics and biology of squid of the genus *Architeuthis* based on the study of specimens from Newfoundland waters. *Bulletin of Marine Science*, 49(1–2): 457–481.

Alejo-Plata, M.C., G. Cerdenares Ladron de Guevara & J.E. Herrera Galindo. 2001. Cefalopodos loliginidos en la fauna de acompanamiento del camaron. (The loliginid cephalopods in the shrimp by catch). *Ciencia y Mar*, 5(13): 41–46.

Alexandronets, Yu.A., Yu.I. Magaras & C.M. Nigmatullin. 1983. Distribution pattern and range structure in nektonic oceanic squids, family Ommastrephidae, in the open ocean in connection with macroscale circulations. *In* Ya.I. Starobogatov & K.N. Nesis, eds. *Taxonomy and ecology of cephalopods*. Leningrad: Zoological Institute of the Academy of Sciences USSR Publication: 99–102 (In Russian).

***Alexeyev, D.O.** 1989. Advantages and limitations of using the gladius in diagnosis of species and genera of the loliginid family. *Zoologicheskij Zhurnal*, 68: 36–42.

***Alexeyev, D.O.** 1992 [1991]. Systematics and phylogeny of bioluminescent Loliginidae. *Bulletin of Marine Science*, 49: 660.

***Alexeyev, D.O.** 1992. Systematic position of photophore-bearing squids of the family Loliginidae (Cephalopoda, Myopsida). *Zoologicheskij Zhurnal*, 71(11): 12–23, 2 figs.

***Alexeyev, D.O.** 1994a. New data on the distribution and biology of squids in the South Pacific. *Ruthenica*, 4(2): 151–166.

***Alexeyev, D.O.** 1994b. *Enoploteuthis (Paraenoploteuthis) semilineata*, a new species of squid (Cephalopoda, Oegopsida, Enoploteuthidae) from the South Pacific. *Ruthenica*, 4(2): 167–171.

Alexeyev, D.O., V.A. Bizikov & D.N. Khromov. 1989. Underwater observations on behavior and distribution of squid *Berryteuthis magister* and other cephalopods in the northwest Pacific Ocean. *Moscow, VNIRO*, p. 66. [Russian with English abstract].

Allan, J. 1945. Planktonic cephalopod larvae from eastern Australian coasts. *Records of the Australian Museum*, 21(6): 317–350.

*__Ally, J.R.R. & S.A. Keck.__ 1978. A biochemical-genetic population structure study of market squid, *Loligo opalescens* , along the California coast. *In*: Biological, oceanographic and acoustic aspects of the market squid, *Loligo opalescens* Berry. *California Department of Fish and Game*; Long Beach, CA (USA). 1978: 113–121.

Alonso, M.K., E.A. Crespo, S.N. Pedraza, N.A. Garcia & M.A. Coscarella. 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin*, 98(2): 250–263.

Alonso, M.K., S.N. Pedraza, A.C.M. Schiavini, R.N.P. Goodall & E.A. Crespo. 1999. Stomach contents of false killer whales (*Pseudorca crassidens*) stranded on the coasts of Strait of Magellan, Tierra del Fuego. *Marine Mammal Science*, 15(3): 712–724.

Amaratunga, T. 1987. Population biology. *In*: P.R. Boyle, ed. *Cephalopod Life Cycles. Vol. II. Academic Press*, London, 239–252 pp.

Amelekhina, A.M. & G.V. Zuev. 1988. [Cephalopods.] *In*: G.V. Zuev, ed. *Macroplankton and Nekton of the Tropical Atlantic*, Naukova Dumka, Kiev, 37–44 pp. [In Russian].

*__Amelekhina, A.M., A.D. Gubanova, S.M. Ignatyev, V.V. Melnikov, I.Yu. Prusova, V.A. Skryabin & I.Yu. Tamoikin.__ 1990. [Zooplankton]. *In*: G.V Zuev, ed. *Productivity of Equatorial Atlantice*, Naukova Dumka, Kiev. 77–98 pp. [In Russian].

Amir, O.A., P. Berggren, S.G.M. Ndaro & N.S. Jiddawi. 2005. Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania. *Estuarine, Coastal and Shelf Science*, 63(3): 429–437.

*__Anderson, C.I.H. & P.G. Rodhouse.__ 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. *Fisheries Research (Amsterdam)*, 54(1): 133–143.

*__Anderson, C.I.H. & P.G. Rodhouse.__ 2002. Distribution of juvenile squid in the Scotia Sea in relation to regional oceanography. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. *Bulletin of Marine Science*, 71(1): 97–108.

Anderson, E.J. & E.M. Demont. 2005. The locomotory function of the fins in the squid *Loligo pealei*. *Marine and Freshwater Behaviour and Physiology*, 38(3): 169–189.

Anderson, E.J. & M.A. Grosenbaugh. 2005. Jet flow in steadily swimming adult squid. *Journal of Experimental Biology*, 208(6): 1125–1146.

*__Anderson F.E.__ 1996. Preliminary cladistic analyses of relationships among loliginid squids (Cephalopoda: Myopsida) based on morphological data. *American Malacological Bulletin*, 12: 113–128.

Anderson, F.E. 1999. Phylogenetic relationships and biogeography of the loliginid squids (Mollusca: Cephalopoda) based on DNA sequence data, morphology and allozymes. *Dissertation Abstracts International Part B: Science and Engineering*, 59(8): 3950.

*__Anderson F.E.__ 2000a. Phylogenetic relationships among loliginid squids (Cephalopoda: Myopsida) based on analyses of multiple data sets. *Zoological Journal of the Linnean Society*, 130: 603–633.

*__Anderson F.E.__ 2000b. Phylogeny and historial biogeography of the loliginid squids (Mollusca: Cephalopoda) based on mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution*, 15: 191–214.

*__Anderson, F.E., V. Laptikhovsky, A. Pilsits & G. Bello.__ 2006. Phylogeny and population genetics of *Alloteuthis* (Loliginidae) and discovery of criptic species. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 34.

Anderson, F.E., T. Valinassab, C.W. Ho, K.S. Mohamed, P.K. Asokan, G.S. Rao, P. Nootmorn, C. Chotiyaputta, M. Dunning & C.C. Lu. 2007. Phylogeography of the pharaoh cuttle *Sepia pharaonis* based on partial mitochondrial 16S sequence data. *Reviews in Fish Biology and Fisheries*, 17(2–3): 345–352.

*__Anderson, F.E., A. Pilsits, S. Clutts, V. Laptikhovsky, G. Bello, E. Balguerias, M. Lipinski, C. Nigmatulin, J.M.F. Pereira, U. Piatkowski, J.P. Robin, A. Salman & M.G. Tasende.__ 2008. Systematics of *Alloteuthis* (Cephalopoda: Loliginidae) based on molecular and morphometric data. *Journal of Experimental Marine Biology and Ecology*, 364: 99–109.

Ando, K., Y. Sato, K. Miura, Y. Chinzei & S. Ogawa. 1992. Further observation on the larva of the suborder Spirurina suspected as the causative agent of creeping eruption. *Japan Journal of Parasitology*, 41(5): 384–389.

Ando, M., E. Takenaga, S. Hamase & A. Yamane. 2005. Effect of super-chilling storage on maintenance of quality and freshness of Swordtip squid *Loligo edulis*. *Food Science and Technology Research*, 11(3): 355–361.

Andre, M., T. Johansson, E. Delory & M. Van Der Schaar. 2007. Foraging on squid: the sperm whale mid-range sonar. *Journal of the Marine Biological Association of the United Kingdom*, 87(1): 59–67.

Andriguetto, J.M., Jr. 1989. *Abundância, distribução, habitus alimentares e ciclo reproductivo de Loligo sanpaulensis (Cephalopoda: Myopsida) na plataforma costiera e talude superior do Rio Grande do Sul, Brasil*. M.Sc. Thesis, Universidade Federal do Paranà, Curitiba.

Andriguetto, J.M., Jr. & M. Haimovici. 1988. Effects of fixation and preservation methods on the morphology of a loliginid squid (Cephalopoda: Myopsida). *American Malacological Bulletin*, 6(2): 213–217.

***Andriguetto, J.M., Jr. & M. Haimovici.** 1991. Abundance and distribution of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda, Loliginidae) in southern Brazil. *Scientia Marina*, 55: 611–618.

***Andriguetto, J.M., Jr. & M. Haimovici.** 1996. Reproductive cycle of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda; Loliginidae) in southern Brazil. *Scientia Marina*, 60: 443–450.

***Andriguetto, J.M., Jr. & M. Haimovici.** 1997. Feeding habits of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda, Loliginidae) in southern Brazil. *Nefritica*, 11(1–2): 63–76.

***Angelescu, V., F.S. Gnieri & A. Nani.** 1958. La merluza del mar Argentino (biologia e taxonomia). Servicio de Hidrografia Naval, Buenos Aires, Documento H 1004: 224 pp. (+ 4 maps and 14 pls).

Antonelis, G.A., Jr, M.S. Lowry, D.P. DeMaster & C.H. Fiscus. 1987. Assessing northern elephant seal feeding habits by stomach levage. *Marine Mammal Science*, 3(3): 308–322.

Antonelis, G.A., E.H. Sinclair, R.R. Ream & B.W. Robison. 1997. Inter-island variation in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. *Journal of Zoology*, 242(3): 435–451.

Antonetti, P., G. Sigovini, M. Gerotto, M. Palonta & A. Troncon. 1994. Levels of cadmium and selenium in some species of cephalopod molluscs fished in the Adriatic Sea during the years 1988, 1989 and 1991. Il Pesce 1: 63–69.

Aoki, M., H. Imai, T. Naruse & Y. Ikeda. 2008. Low genetic diversity of Oval squid, *Sepioteuthis* cf. *lessoniana* (Cephalopoda: Loliginidae), in Japanese waters, inferred from a mitochondrial DNA non-coding region. *Pacific Science*, 62(3): 403–411.

***Appellöf, A.** 1886. Japanska Cephalopoder. *Svenska Vetenskaps-Akademiens Handlingar, Stockholm*, 21(13): 5–40.

***Appellöf, A.** 1890. Teuthologische Beitrage I: *Chtenopteryx* n.g., *Veranya sicula* Krohn, *Calliteuthis* Verrill. *Bergens Museums Aarsberetning*, 1889(3): 1–34.

Appellöf, A. 1891. Teuthologische Beitrage II. *Chaunoteuthis* n.g. Oegopsidarum. *Bergens Museums Aarsberetning*, 1890(1): 1–29, 4 pls.

Arancibia, F.H. & V.H. Robotham. 1984. Growth and age of the squid (*Loligo gahi* Orbigny) in the southern region of Chile (Teuthoidea–Loliginidae). *Investigación Pesquera, Santiago,*, 31: 71–79.

Arancibia, H. & S. Neira. 2005. Redation on common hake (*Merluccius gayi*) by jumbo squid (*Dosidicus gigas*) in central Chile (33–39 DGS). *ICES Council Meeting documents Copenhagen*, No. 2005.

***Arango, C.P. & J.M. Diaz.** 1996. First record of the pigmy squid, *Pickfordiateuthis pulchella* (Cephalopoda: Myopsida: Loliginidae), from the Caribbean Coast of Colombia. *Boletin de Investigaciones Marinas y Costeras,* 25: 107–109.

Arata, J. & J.C. Xavier. 2003. The diet of black-browed albatrosses at the Diego Ramirez Islands, Chile. *Polar Biology*, 26(10): 638–647.

Arata, J., G. Robertson, J. Valencia, J.C. Xavier & C.A. Moreno. 2004. Diet of grey-headed albatrosses at the Diego Ramirez Islands, Chile: ecological implications. *Antarctic Science*, 16(3): 263–275.

Araya, H. 1967. Resources of common squid, *Todarodes pacificus* Steenstrup, in the Japanese water. *Fisheries Research Series (16). Japanese Association for Marine Resources Conservation*, 60 pp.

Araya, H. 1976. Migration and fishing ground of winter subpopulation of the squid, *Todarodes pacificus* Steenstrup, in the northern waters of Japan. *Bulletin of the Hakkaido Regional Fisheries Research Laboratory,* 41: 119–129.

Araya, H. 1983. Fishery, biology and stock assessment of *Ommastrephes bartramii* in the North Pacific Ocean. *Memoirs of the National Msueum of Victoria*, 44: 269–283.

Araya, H. & T. Ishii. 1972. Population structure of common squid in the waters around Hokkaido. *Research Report of the Technical Council of Agriculture, Forestry and Fisheries*, 57: 192–205.

Araya, H & M. Ishii. 1974. Information on the fishery and ecology of the squid *Doryteuthis bleekeri* Keferstein, in the waters of Hokkaido. *Bulletin of the Hokkaido Regional Fisheries Laboratory*, 40: 1–13.

Arfelli, C.A., A.F. de Amorim & A.R.G. Tomas. 1991. First record of a giant squid *Architeuthis* sp. Steenstrup, 1857 (Cephalopoda, Architeuthidae) in Brazilian waters. *Bolletin de Institut Pesca, São Paulo*, 18: 83–88.

Arguelles, J., P.G. Rodhouse, P. Villegas & G. Castillo. 2001. Age, growth and population structure of the jumbo flying squid *Dosidicus gigas* in Peruvian waters. *Fisheries Research*, 54(1): 51–61.

Arizmendi-Rodriquez, D.I, L.S. Abitia-Cardenas, F. Galvan-Magana & I. Trejo-Escamilla. 2006. Food habits of sailfish *Istiophorus platypterus* off Mazatlan, Sinaloa, Mexico. *Bulletin of Marine Science*, 79(3): 777–791.

Arkhipkin, A.I. 1990. Edad y crecimiento del calamar (*Illex argentinus*). *Frente Maritimo*, 6A: 25–35.

Arkhipkin, A.I. 1993. Statolith microstructure and maximum age of *Loligo gahi* (Myopsida: Loliginidae) on the Patagonian Shelf. *Journal of the Marine Biological Association of the United Kingdom*, 73: 979–982.

***Arkhipkin, A.I.** 1994. Age, growth and maturation of the squid *Enoploteuthis leptura* (Oegopsida: Enoploteuthidae) from the central-east Atlantic. *Journal of Molluscan Studies*, 60(1): 1–8.

Arkhipkin, A.I. 1995. Age, growth and maturation of the European squid *Loligo vulgaris* (Myopsidae, Loliginidae) on the west Saharan Shelf. *Journal of the Marine Biological Association of the United Kingdom*, 75: 593–604.

Arkhipkin, A.I. 1996a. Age and growth of the squid *Abraliopsis pfefferi* (Legopsida: Enoploteuthidae) from the central-east Atlantic based on statolith microstructure. *Scientia Marina Barcelona*, 60(2–3): 325–330.

***Arkhipkin, A.I.** 1996b. Statolith microstructure and age of early stages of planktonic squids *Galiteuthis phyllura* and *Belonella borealis* (Oegopsida, Cranchiidae) from the northern North Pacific. *Journal of Plankton Research*, 18(1): 123–132.

***Arkhipkin, A.I.** 1996c. Age and growth of planktonic squids *Cranchia scabra* and *Liocranchia reinhardti* (Cephalopoda, Cranchiidae) in epipelagic waters of the central-east Atlantic. *Journal of Plankton Research*, 18(9): 1675–1683.

***Arkhipkin, A.I.** 1997a. Age and growth of the mesopelagic squid *Ancistrocheirus lesueurii* (Oegopsida: Ancistrocheiridae) from the central-east Atlantic based on statolith microstructure. *Marine Biology*, 129(1): 103–111.

***Arkhipkin, A.I.** 1997b. Age of the micronektonic squid *Pterygioteuthis gemmata* (Cephalopoda: Pyroteuthidae) from the central-east Atlantic based on statolith growth increments. *Journal of Molluscan Studies*, 63(2): 287–290.

Arkhipkin, A.I. 1997c. Geographical variation in growth and maturation of the squid *Illex coindetii* (Oegopsida, Ommastriphidae) off the northwest African coast. *Journal of the Marine Biological Association of the United Kingdom*, 76: 1091–1106.

Arkhipkin, A.I. 2000. Intrapopulation structure of winter-spawned Argentine shortfin squid, *Illex argentinus* (Cephalopoda, Ommastrephidae), during its feeding period over the Patagonian Shelf. *Fishery Bulletin*, 98: 1–13.

Arkhipkin, A.I. 2003a. Interannual changes in spatial distribution and abundance of the Patagonian squid *Loligo gahi* in the southwest Atlantic. *Theme Session Q. Regional Long-Term Changes in the Spatial Distribution, Abundance and Migration of Pelagic and Demersal Resources. ICES Council Meeting documents*: [np]

***Arkhipkin, A.I.** 2003b. Towards identification of the ecological lifestyle in nektonic squid using statolith morphometry. *Journal of Molluscan Studies*, 69(3): 171–178.

Arkhipkin, A.I. 2004. Diversity in growth and longevity in short-lived animals: squid of the suborder Oegopsina. *Marine Freshwater Research*, 55: 341–355.

Arkhipkin, A.I. 2006. Nektonic squid as biological pumps between oceanic ecosystems. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 23.

***Arkhipkin, A.I. & V.A. Bizikov.** 1997. Statolith shape and microstructure in studies of systematics, age and growth in planktonic paralarvae of gonatid squids (Cephalopoda, Oegopsida) from the western Bering Sea. *Journal of Plankton Research*, 19(12): 1993–2030.

Arkhipkin, A.I & V.A. Bizikov. 2000. Role of the statolith in functioning of the acceleration receptor system in squids and sepioids. *Journal of Zoology*, 250(1): 31–55.

***Arkhipkin, A.I. & H. Björke.** 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. *Polar Biology*, 22(6): 357–365.

Arkhipkin, A.I. & H. Björke. 2000. Statolith shape and microstructure as indicators of ontogenetic shifts in the squid *Gonatus fabricii* (Oegopsida, Gonatidae) from the Norwegian Sea. *Polar Biology*, 23: 1–10.

Arkhipkin, A.I & P.P. Fedulov. 1986. Diel movements of juvenile *Illex illecebrosus* and other cephalopods in the shelf waterslope water frontal zone off the Scotian Shelf in spring. *Journal of Northwestern Atlantic Fishery Science*, 7(1): 15–24.

Arkhipkin, A.I. & A.A. Fetisov. 2000. Population structure and growth of the squid *Illex illecebrosus* (Cephalopoda: Ommastrephidae) off Nova Scotia, northwest Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 80(2): 367–368.

Arkhipkin A. & A. Golub. 2000. Aberrant structure of the statolith postnuclear zone in the squid *Todarodes sagittatus* (cephalopoda: Ommastrephidae). *Journal of the Marine Biological Association of the United Kingdom*, 80: 183–184.

Arkhipkin, A.I. & V.V. Laptikhovsky. 2000. Age and growth of the squid *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) on the north-west African shelf. *Journal of the Marine Biological Association of the United Kingdom*, 80: 747–748.

***Arkhipkin, A.I. & V.V. Laptikhovsky.** 2006. Life cycle of *Gonatus antarcticus*, Lönnberg, 1898 in the southwest Atlantic. Cephalopod International Advisory Council Symposium 2006, Abstract: p.71.

Arkhipkin, A.I. & D.A.J. Middleton. 2002a. Inverse patterns in abundance of *Illex argentinus* and *Loligo gahi* in Falkland waters: possible interspecific competition between squid? *Fisheries Research*, 59(1–2): 181–196.

Arkhipkin, A.I. & D.A.J. Middleton. 2002b. Sexual segregation in ontogenetic migrations by the squid *Loligo gahi* around the Falkland Islands. *Bulletin of Marine Science*, 71: 109–127.

Arkhipkin, A.I. & D.A.J. Middleton. 2003. In-situ monitoring of the duration of embryonic development in the squid *Loligo gahi* (Cephalopoda: Loliginidae) on the Falkland Shelf. *Journal of Molluscan Studies*, 69(2): 123–133.

Arkhipkin, A.I. & A.B. Mikheev. 1992. Age and growth of the squid *Sthenoteuthis pteropus* (Oegopsida: Ommastrephidae) from the central-east Atlantic. *Journal of Experimental Marine Biology and Ecology*, 163(2): 261–276.

Arkhipkin, A.I. & S.I. Murzov. 1990. Age and growth patterns of the micronektonic squid *Abraliopsis atlantica*. *Soviet Journal of Marine Biology*, 16(5): 19–25.

***Arkhipkin A. & N. Nekludova.** 1993. Age, growth and maturation of the loliginid squids *Alloteuthis africana* and *A. subulata* on the West African shelf. *Journal of the Marine Biological Association of the United Kingdom*, 73: 949–961.

***Arkhipkin, A.I. & C.M. Nigmatullin.** 1997. Ecology of the oceanic squid *Onychoteuthis banksi* and the relationship between the genera *Onychoteuthis* and *Chaunoteuthis* (Cephalopoda: Onychoteuthidae). *Journal of the Marine Biological Association of the United Kingdom*, 77(3): 839–869.

Arkhipkin, A.I. & J.A.A. Perez. 1998. Life history reconstruction. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. *Squid recruitment dynamics. The genus* Illex *as a model, the commercial* Illex *species and influences on variability. FAO Fisheries Technical Paper*, 376: 157–180.

Arkhipkin, A.I. & Z.N. Scherbich. 1991. Intraspecific growth and structure of the squid, *Illex argentinus* (Ommastrephidae) in winter and spring in the southwestern Atlantic. *Scientia Marina*, 55: 619–627. (in Spanish).

Arkhipkin, A.I. & B.A. Seibel. 1999. Short communication. Statolith microstructure from hatchlings of the oceanic squid, *Gonatus onyx* (Cephalopoda, Gonatidae) from the Northeast Pacific. *Journal of Plankton Research*, 21(2): 401–404.

***Arkhipkin, A.I. & A.S. Shchetinnikov.** 1989. [Fauna and distribution of juveniles and adult pelagic cephalopods in the Gulf of Guinea.] *Zoologicheskii Zhurnal*, 68(8): 26–32. [In Russian with English summary].

Arkhipkin, A.I. & N.V. Silvanovich. 1997. Age, growth and maturation of the squid *Martialia hyadesi* (Cephalopoda, Ommastrephidae) in the southwest Atlantic. *Antarctic Science*, 9(4): 373–380.

***Arkhipkin, A.I., V.A. Bizikov & A.V. Verkhunov.** 1998a. Distribution and growth in juveniles of the squid *Berryteuthis magister* (Cephalopoda, Gonatidae) in the western Bering Sea. *Sarsia*, 83(1): 45–54.

Arkhipkin, A., P. Brickle & V. Laptikhovsky. 2003. Variation in the diet of the Patagonian toothfish with size, depth and season around the Falkland Islands. *Journal of Fish Biology*, 63(2): 428–441.

Arkhipkin, A.I., P. Jereb & S. Ragonese. 1998b. Age determination of *Illex coindetii* from the Strait of Sicily by statolith increments analysis. *In*: A.I.L. Payne, M.R. Lipinski & M.A.C. Roeleveld, eds. Cephalopod Biodiversity, Ecology and Evolution. *South African Journal of Marine Science*, 20: 233–240.

Arkhipkin, A.I., P. Jereb & S. Ragonese. 2000a. Growth and maturation in two successive seasonal groups of the short-finned squid, *Illex coindetii* from the Strait of Sicily (central Mediterranean). *ICES–International Council for the Exploration of the Sea Journal of Marine Science*, 57(1): 31–41.

*__Arkhipkin, A.I., V. Laptikhovsky & A. Golub.__ 1999. Population structure and growth of the squid *Todarodes sagittatus* (Cephalopoda: Ommastrphidae) in north-west African waters. *Journal of the Marine Biological Association of the United Kingdom*, 79(3): 467–477.

*__Arkhipkin, A.I., V. Laptikhovsky & D.A.J. Middleton.__ 2000b. Adaptations for cold water spawning in loliginid squid: *Loligo gahi* in Falkland waters. *Journal of Molluscan Studies*, 66(4): 551–564.

*__Arkhipkin, A.I., Yu.A. Loktionov & A.S. Shchetinnikov.__ 1988. Conditions leading to the formation of local patches of the squid, *Sthenoteuthis pteropus*, in the western Gulf of Guinea. *Okeanologiya*, 28(1): 140–145. (In Russian with English summary).

Arkhipkin, A.I., V.A. Bizikov, V.V. Krylov & K.N. Nesis. 1996. Distribution, stock structure, and growth of the squid *Berryteuthis magister* (Berry, 1913) (Cephalopoda, Gonatidae) during summer and fall in the western Bering Sea. *Fishery Bulletin*, 94(1): 1–30.

Arkhipkin, A.I., S.E. Campana, J. FitzGerald & S.R. Thorrold. 2004a. Spatial and temporal variation in elemental signatures of statoliths from the Patagonian longfin squid (*Loligo gahi*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61(7): 1212–1224.

*__Arkhipkin, AI., V.V Laptikhovsky, A.M. Sirota & R. Grzebielec.__ 2006. The role of the Falkland Current in the dispersal of the squid *Loligo gahi* along the Patagonian Shelf. *Estuarine, Coastal and Shelf Science*, 67(1–2): 198–204.

Arkhipkin, A.I., D.A.J. Middleton, A.M. Sirota & R. Grzebielec. 2004b. The effect of Falkland Current inflows on offshore ontogenetic migrations of the squid *Loligo gahi* on the southern shelf of the Falkland Islands. *Estuarine, Coastal and Shelf Science*, 60(1): 11–22.

*__Arkhipkin, A.I., V.V. Laptikhovsky, C.M. Nigmatullin, A.V. Bespyatykh & S.A. Murzov.__ 1998c. Growth, reproduction and feeding of the tropical squid *Ornithoteuthis antillarum* (Cephalopoda, Ommastrephidae) from the central-east Atlantic. *Scientia Marina Barcelona*, 62(3): 273–288.

Arkhipin, A.I., A.M. Sirota, V.V. Laptikhovsky, R. Grzebielec & D.A.J. Middleton. 2002. The effect of Falkland Current inflows on offshore ontogenetic migrations of the squid *Loligo gahi* on the southern shelf of the Falkland Islands, ICES Council Meeting Documents.

Arkhipkin, A.I., R. Grzebielec, A.M. Sirota, A.V. Remeslo, I.A. Polishchuk & D.A. Middleton. 2004c. The influence of seasonal environmental changes on ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf. *Fisheries Oceanography*, 13(1): 1–9.

Arkhipkin, A., P. Brickle, V. Laptikhovsky, L. Butcher, E. Jones, M. Potter & D. Poulding. 2001. Variation in the diet of the red cod with size and season around the Falkland Islands (south west Atlantic). *Journal of the Marine Biological Association of the United Kingdom*, 81(6): 1035–1040.

Arnold, J.M. 1962. Mating behaviour and social structure in *Loligo pealii*. *Biological Bulletin*, 123(1): 53–57.

Arnold, J.M. 1965. Normal embryonic stages of the squid *Loligo pealii* (LeSueur). *Biological Bulletin*, 128: 24–32.

Arnold, J.M. & R. O'Dor. 1990. In vitro fertilization and embryonic development of oceanic squid. *Journal of Cephalopod Biology*, 1(2): 21–36.

Arnold, J.M. & R. O'Dor. 1992. In vitro artificial fertilization and embryonic development of oceanic squid for developmental studies, paralarval identification and culture. *Bulletin of Marine Science*, 49(1–2): 660 p.

Arnold, J.M. & L.D. Williams-Arnold. 1977. Cephalopoda: Decapoda. *In*: A.C. Giese & J.S. Pearse, eds. *Reproduction of Marine Iinvertebrates*. London and New York, *Academic Press*, 4: 243–290.

*__Arnold, J.M. & R.E. Young.__ 1974. Ultrastructure of a cephalopod photophore. I. Structure of a photogenetic tissue. *Biology Bulletin*, 147(3): 507–521.

Arnold, J.M., R.E. Young & M.V. King. 1974. Ultrastructure of a cephalopod photophore. II. Iridophores as reflectors and transmitters. *Biology Bulletin*, 147(3): 522–534.

Arnold, J.M., W.C. Summers, D.L. Gilbert, R.S. Manalis, N.W. Daw & R.J. Lasek. 1974. A guide to laboratory use of the squid *Loligo pealei*. *Woods Hole, Marine Biological Laboratory*, 74 pp.

Arnould, J.P.Y., D.M. Trinder & C.P. McKinley. 2003. Interactions between fur seals and a squid jig fishery in southern Australia. *Marine and Freshwater Research*, 54(8): 979–984.

Arocha, F. 1986. Biologia y pesqueria de los cefalopodos de interes commercial en la region nororiental de Venezuela. Mater's Thesis, Universidad Oriente, Cumana, Venezuela, 76 p.

Arocha, F. 1989. Cephalopod resources of Venezuela. *Marine Fisheries Review*, 51: 47–51.

*****Arocha, F.** 2003. A new species of *Nematolampas* (cephalopoda: Oegopsida) from the Western Central Atlantic with an overview of the family Lycoteuthidae. *Bulletin of Marine Science*, 72: 941–953.

*****Arocha, F. & L.J. Urosa.** 1991. Some biological studies of *Loligo plei* and occurrence of *Loligo pealii* (Cephalopoda, Myopsida) in northeastern Venezuela. *Acta Cientifica Venezuelana*, 42(3): 145–152.

Arocha, F., L. Marcano & R. Cipriani. 1991. Cephalopods trawled from Venezuelan waters by the R/V Dr. Fridtjof Nansen in 1988. *Bulletin of Marine Science*, 49(1–2): 231–234.

*****Arvanitidis, C., D. Koutsoubas, J.-P. Robin, J. Pereira, A. Moreno, M. Cunha, V. Valavanis & A. Eleftheriou.** 2002. A comparation of the fishery biology of three *Illex coindetii* Vérany, 1839 (Cephalopoda: Ommastrephidae) populations from the European Atlantic and Mediterranean Waters. *Bulletin of Marine Science*, 71(1): 129–146.

Ashirin, Z.S. & A.B. Ibrahim. 1992. Preliminary squid survey in coastal waters off Kuala Terengganu, Malaysia. *Asian Fisheries Science*, 5: 261–264.

Asokan, P.K. & V.S. Kakati. 1991. Embryonic development and hatching of *Loligo duvaucelii* Orbigny (Loliginidae, Cephalopoda) in the laboratory. *Indian Journal of Fisheries*, 38: 201–206.

Atkinson, B.G. 1973. Squid nidamental gland extract: isolation of a factor inhabiting ciliary activity. *Journal of Experimental Zoology*, 184(3): 335–340.

Augustyn, C.J. 1983. The biomass and biology of the long-finned squid *Loligo reynaudii* in the Agulhas Bank region. Fifth National Oceanographic Symposium. 24–28 January 1983. Rhodes University, Grahamstown. Abstracts. Council for Scientific and Indust. *Res. South Africa; Sancor South Africa*, 1983. p. H 9 .

Augustyn, C.J. 1986. The squid jigging fishery on the South African south coasts. *South African Shipping News and Fishing Industry Review*, 41: 24–26.

Augustyn, C.J. 1990. Biological studies on the chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. *South African Journal of Marine Science*, 9: 11–26.

*****Augustyn, C.J.** 1991a. The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the west coast of South Africa. *South African Journal of Zoology*, 26(4): 164–181.

*****Augustyn, C.J.** 1991b. Migration cycle of the chokker squid *Loligo vulgaris reynaudii*. *Bulletin of Marine Science*, 49(1–2): 660.

*****Augustyn, C.J. & W.S. Grant.** 1988. Biochemical and morphological systematics of *Loligo vulgaris vulgaris* Lamarck and *Loligo vulgaris reynaudii* d'Orbigny nov. comb. (Cephalopoda: Myopsida). *In*: R.T. Hanlon ed. "International symposium on Life history, Systematics and Zoogeography of Cephalopods in honor of Sir Stillman Berry". *American Malacological Union Symposium Proceedings*. 29(1): 215–233.

Augustyn, C.J. & B.A. Roel. 1998. Fisheries biology, stock assessment, and management of the chokka squid (*Loligo vulgaris reynaudii*) in South African waters: An overview. *Reports of California Cooperative Oceanic Fisheries Investigations*, 39: 71–80

Augustyn, C.J., M.R. Lipinski & W.H.J. Sauer. 1992. Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann & R. Hilborn, eds. "Benguela Trophic Functioning", 12: 903–918.

Augustyn, C.J., B.A. Roel & K.L. Cochrane. 1993. Stock assessment in the chokka squid *Loligo vulgaris reynaudii* fishery off the coast of South Africa. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology*, 3–14.

*****Augustyn, C.J., M.R. Lipinski, W.H.H. Sauer, M.J. Roberts & B.A. Mitchell-Innes.** 1994. Chokka squid on the Agulhas Bank: Life history and ecology. *South African Journal of Science*, 90(3): 143–154.

Aurioles Gamboa, D. & F.J. Camacho Rios. 2007. Diet and feeding overlap of two otariids, *Zalophus californianus* and *Arctocephalus townsendi*: implications to survive environmental uncertainty. *Aquatic Mammals*, 33(3): 315–326.

Austin, C.R., C. Lutwak-Mann & T. Mann. 1964. Spermatophores and spermatozoa of the squid *Loligo pealii*. *Proceedings of the Royal Society, Series B: Biological Sciences*, 161: 143–152.

***Auteri, R., P. Mannini & C. Volpi.** 1987. Biological parameters estimation of *Alloteuthis media* (Linnaeus, 1758) (Cephalopoda, Loliginidae) sampled off Tuscany coast. *Quaderni del Museo di Storia Naturale di Livorno*, 8: 119–129.

Aydin, K.Y., K.W. Myers & R.V. Walker. 2000. Variation in summer distribution of the prey of Pacific salmon (*Oncorhynchus* spp.) in the offshore Gulf of Alaska in relation to oceanographic conditions, 1994–98. *NPAFC Bulletin, Japan*, 2: 43–54.

Aydin, K.Y., F.A. McFarlane, J.R. King, B.A. Megrey & K.W. Myers. 2005. Linking oceanic food webs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. *Deep Sea Research (Part II, Topical Studies in Oceanography)*, 52(5–6): 757–780.

Ayensa, M.G., M.P. Montero, A.J. Borderias & J.L. Hurtado. 2002. Influence of some protease inhibitors on gelation of squid muscle. *Journal of Food Science*, 67(5): 1636–41.

Baba, O., T. Taniuchi & Y. Nose. 1987. Depth distribution and food habits of three species of small squaloid sharks off Choshi. *Bulletin of Japanese Society of Scientific Fishery*, 53(3): 417–424.

Baddyr, M. 1988. The biology of the squid *Loligo vulgaris* in relation to the artisanal fishing site of Tifnit, Morocco. Ph.D. Thesis, Institut Agronomique et Vètèrinaire Hassan II. Rabat, Morocco, 93 p.

Baddyr, M. 1991. Biology of the squid *Loligo vulgaris* in relation to the artisanal fishing site of Tifnit, Morocco. *Bulletin of Marine Science*, 49(1–2): 661.

Badenhorst, J.H. 1974. The morphology and histology of the male genital system of the squid *Loligo reynaudii* (d'Orbigny). *Annals of the University of Stellenbosch Series A*, 49(1): 1–36.

***Baeg, G.H., Y. Sakurai & K. Shimazaki.** 1992. Embryonic stages of *Loligo bleekeri* Keferstein (Mollusca: Cephalopoda). *Veliger*, 35(3): 234–241.

Baird, R.W., K.M. Langelier & P.J. Stacey. 1989. First records of false killer whales, *Pseudorca crassidens*, in Canada. *Canada Field Naturalist*, 103(3): 368–371.

Bakun, A. & J. Csirke. 1998. Environmental processes and recruitment variability. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 105–124.

Balch, N., R.H. O'Dor & P. Helm. 1985. Laboratory rearing of rhynchoteuthions of the ommastrephid squid *Illex illecebrosus* (Mollusca: Cephalopoda). *In*: K.M. Mangold & S.V. Boletsky, eds. *Biology and Distribution of Early Juvenile Cephalopods*, 35(3–4): 243–246.

Balgos, M.C. & D. Pauly. 1998. Age and growth of the squid *Sepioteuthis lessoniana* in N.W. Luzon, Philippines. *South African Journal of Marine Science*, 20: 449–452

Ball, D., L. Morris, J. Hindell & A. Coots. 2004. Development of a Fisheries Habitat Suitability Model utilising a Geographic Information System. VDPI, Queenscliff, Vic. (Australia), vp. Apr 2004.

***Ball, R.** 1841. On a species of *Loligo*, found on the shore of Dublin Bay. *Proceedings of the Royal Irish Academy*, 1(19): 362–364.

Baltz, D.M & G.V. Morejohn. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. *The Auk*, 94(3): 526–543.

Baraff, L.S. & T.R. Loughlin. 2000. Trends and potential interactions between pinnipeds and fisheries of New England and the UnitedStates West Coast. *Marine Fisheries Review*, 62(4): 1–39.

Barbieri, E., J. Gulledge, D. Moser & C.C. Chien. 1996. New evidence for bacterial diversity in the accessory nidamental gland of the squid (*Loligo pealei*). *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 191(2): 316–317.

***Barbut, J.** 1783. The genera *Verium* exemplified by various specimens of the animals container in the orders of the Intestina et Mollusca Linnae I. 101 pp., 11 pls. London: J. Dixwell.

Barcia, I., M.L. Sanchez–Purrinos, M. Novo, A. Novas, J.F. Maroto & R. Barcia. 2008. Optimisation of *Dosidicus gigas* mantle proteolysis at industrial scale. *Food Chemistry*, 107(2): 869–875.

Bargu, S., C.L. Powell, Z. Wang, G.J. Doucette & M.W. Silver. 2008. Note on the occurrence of *Pseudo-nitzschia australis* and domoic acid in squid from Monterey Bay, CA (USA). *Harmful Algae*, 7(1): 45–51.

*** Baron, P.J.** 2001. First description and survey of the egg masses of *Loligo gahi* (d'Orbigny, 1835) and *Loligo sanpaulensis* (Brakoniecki, 1984) from coastal waters of Patagonia. *Journal of Shellfish Research*, 20: 289–295.

Baron, P.J. 2002. Embryonic development of *Loligo gahi* and modelling of hatching frequency distributions in Patagonia. *Bulletin of Marine Science*, 71(1): 165–173.

Baron, P.J. 2002. The embryonic development of *Loligo sanpaulensis*. *Bulletin of Marine Science*, 71: 1113–1114.

*** Baron, P.J.** 2003a. Embryonic development of the South American long-fin squid *Loligo sanpaulensis* Brakoniecki, 1984. *Journal of Molluscan Studies*, 69: 221–227.

*** Baron, P.J.** 2003b. The paralarvae of two South American sympatric squid: *Loligo gahi* and *Loligo sanpaulensis*. *Journal of Plankton Research*, 25(11): 1347–1358.

*** Baron, P.J. & M.E. Ré.** 2002a. Morphometry of the northern Patagonian sympatric populations of *Loligo sanpaulensis* and *Loligo gahi*. *Journal of the Marine Biological Association of the United Kingdom*, 82: 269–278.

*** Baron, P.J. & M.E. Ré.** 2002b. Reproductive cycle and population structure of *Loligo sanpaulensis* of the northeastern coast of Patagonia. *Bulletin of Marine Science*, 71: 175–186.

Barrett, R.T., M. Asheim & V. Bakken. 1997. Ecological relationships between two sympatric congeneric species, common murres and thick-billed murres, *Uria aalge* and *U. lomvia*, breeding in the Barents Sea. *Canadian Journal of Zoology*, 75(4): 618–631.

*** Barrientos, G.** 1987. Biological aspects of the squid *Lolliguncula tydeus* (Mollusca: Cephalopoda). [Aspectos biologicos del calamar *Lolliguncula tydeus* (Mollusca: Cephalopoda)]. Memoirs, 3rd National Meeting of Malacology and Conchology [Memorias 3 Reunion Nacional De Malacologia Y Conquiliologia], 262–282.

Barrientos, G. & A. Garcia-Cubas. 1997. Distribution and abundance of the family Loliginidae (Mollusca: Cephalopoda) in Mexican waters of the Gulf of Mexico. *Revista de la Sociedad Mexicana de Historia Natural*, 47: 123–139.

*** Barton, A.J. D.J. Agnew & L.V. Purchase.** 2004. The southwest Atlantic; achievements of bilateral management and the case for a multilateral arrangement. *Management of shared fish stocks*, pp. 202–222.

Bartol, I.K. & M. Vecchione. 1997. Distribution of the euryhaline squid *Lolliguncula brevis* in the Cheseapeake Bay: Relationships between movement patterns and physical gradients. *ICES Council Meeting Papers*, 1997/S: 12: 4 pp.

*** Bartol, I.K., R. Mann & M. Vecchione.** 2002. Distribution of the euryhaline squid *Lolliguncula brevis* in Chesapeake Bay: Effects of selected abiotic factors. *Marine Ecology Progress Series*, 226: 235–247.

Bartol, I.K., M.R. Patterson & R. Mann. 2001. Swimming mechanics and behaviour of the negatively buoyant, brief squid *Lolliguncula brevis*. *Journal of Experimental Biology*, 204: 3655–3682.

Basir, S. 2000. Biological features of an oceanic squid, *Sthenoteuthis oualaniensis*, in the South China Sea, Area 3: Western Philippines. Proceedings of the third Technical Seminar on Marine Fishery Resources Survey in the South China Sea, Area 3: Western Philippines, 41: 135–147.

Basson, M., J.R. Beddington, J.A. Crombie, S.J. Holden, L.V. Purchase & G.A. Tingley. 1996. Assessment and management techniques for migratory annual squid stocks: the *Illex argentinus* fishery in the Southwest Atlantic as an example. *Fisheries Research*, 28: 3–27.

Baylis, A.M.M., B. Page, K. Peters, R. McIntosh, J. McKensie & S. Goldsworthy. 2005. The ontogeny of diving behaviour in New Zealand fur seal pups (*Arctocephalus forsteri*). *Canadian Journal of Zoology*, 83(9): 1149–1161.

Bazzino, G., R.A. Quinones & W. Norbis. 2006. Environmental associations of shortfin squid *Illex argentinus* (Cephalopoda: Ommastrephidae) in the Northern Patagonian Shelf. *Fisheries Research (Amsterdam)*, 76(3): 401–416.

Bazzino, G., C. Salinas-Zavala & U. Markaida. 2007. Variability in the population structure of jumbo squid (*Dosidicus gigas*) in Santa Rosalia, central Gulf of California. *Ciencias Marinas*, 33(2): 173–186.

Beatson, E. 2007. The diet of pygmy sperm whales, *Kogia breviceps*, stranded in New Zealand: Implications for conservation. *Reviews in Fish Biology and Fisheries*, 17(2–3): 295–303.

Beatson, E., S. O'Shea & M. Ogle. 2007. First report on the stomach contents of long-finned pilot whales, *Globicephala milas*, stranded in New Zealand. *New Zealand Journal of Zoology*, 34(1): 51–56.

Beck, P.C. E.G. Dawe & J. Drew. 1994. An update of the fishery for short-finned squid (*Illex illecebrosus*) in the Newfoundland area during 1989–93 with descriptions of some biological characteristics and temperature trends. *NAFO Scientific Council Research Documents*, 94(37): 14 pp.

Beck, P.C. E.G. Dawe & J. Drew. 1998. An update of the fishery for short-finned squid (*Illex illecebrosus*) in the Newfoundland area during 1994–1997 with descriptions of some biological characteristics. *Science Council Research Document NAFO*, 98/55, 16 pp.

Beddington, J.R, A.A. Rosenberg, J.A. Crombie & G.P. Kirkwood. 1990. Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. *Fisheries Research*, 8: 351–365.

Begossi, A. & L.F.L. Duarte. 1988. New occurrence of *Sepioteuthis sepioidea* (Cephalopoda, Loliginidae) in the Brazilian coast. *Malacological Review*, 21(1–2): 133–134.

Belcari, P. 1996. Length-weight relationship in relation to sexual maturation of *Illex coindetii* (Cephalopoda: Ommastrephidae) in the northern Tyrrhenian Sea (Western Mediterranean). *Scientia Marina*, 60: 379–384.

***Belcari, P.** 1999a. *Alloteuthis media*. *In*: G. Relini, J. Bertrand & A. Zamboni, eds. Synthesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea*, 6(Suppl.1): 699–702.

***Belcari, P.** 1999b. *Alloteuthis subulata*. *In*: G. Relini, J. Bertrand & A. Zamboni, eds. Synthesis of the knowledge on bottom fishery resources in Central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea,* 6(Suppl.1): 703–705.

***Belcari, P.** 1999c. *Illex coindetii*. *In*: G. Relini, J. Bertrand & A. Zamboni, eds. Synthesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea,*6(Suppl.1): 715–718.

***Belcari, P.** 1999d. *Loligo forbesi*. *In*: G. Relini, J. Bertrand & A. Zamboni, eds. Synthesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea*, 6(Suppl.1): 706–709.

***Belcari, P.** 1999e. *Loligo vulgaris*. *In*: G. Relini, J. Bertrand & A. Zamboni, eds. Synthesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea*, 6(Suppl.1): 710–720.

Belcari, P. 1999f. *Ommastrephes bartramii*. *In*: G. Relini, J. Bertrand & A. Zamboni, eds. Synthesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea*, 6(Suppl.1): 721–724.

***Belcari, P.** 1999g. *Todarodes sagittatus* (Lamarck, 1798). *In*: G. Relini, J. Bertrand & A. Zamboni, eds. (1999) – Sintesi delle conoscenze sulle risorse da pesca dei fondi del Mediterraneo centrale (Italia e Corsica). *Biologia Marina Mediterranea*, 6(suppl. 1): 725–728.

Belcari, P. 1999h. *Todaropsis eblanae* (Ball, 1841). *In*: G. Relini, J. Bertrand & A. Zamboni, eds. Sintesi delle conoscenze sulle risorse da pesca dei fondi del Mediterraneo centrale (Italia e Corsica). *Biologia Marina Mediterranea*, 6(suppl. 1): 729–732.

Belcari, P. & P. Sartor. 1993. Bottom trawling teuthofauna of the Northern Tyrrhenian Sea. *Scientia Marina*, 57(2–3): 145–152.

Belcari, P., E. Fedi & C. Viva. 1989. Distribuzione e sex-ratio di *Illex coindetii* (Verany, 1839) (Cephalopoda, Oegopsida) nell'arcipelago toscano meridionale. *Nova Thalassia*, 10: 507–509.

Belcari, P. & P. Sartor & S. De Ranieri. 1998. I cefalopodi nello sbarcato commerciale con reti a strascico nel Mar Tirreno Settentrionale. *Biologia Marina Mediterranea*, 5(2): 318–325.

Belcari, P., P. Sartor, N. Nannini & S. De Ranieri. (1999). Relazione taglia-peso di *Todaropsis eblanae* (Cephalopoda–Ommastrephidae) nel Mar Tirreno settentrionale in funzione della maturità sessuale. Length-weight relationship of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) of the northern Tyrrhenian Sea in relation to sexual maturation. *Biologia Marina Mediterranea*, 6: 524–528.

Bellido, J.M., G.J. Pierce & J. Wang. 2001. Modelling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. *Fisheries Research*, 52(1–2): 3–39.

Bellido, J.M., J.M. Portela, J. Wang & G.J. Pierce. 2002. Trends in the pattern of discarding in the hake (*Merluccius hubbsi* and *Merluccius australis*) fishery in the SW Atlantic. *ICES Council Meeting Documents*.

Bello, G. 1985a. On a collection of cephalopods netted on mesobathyal grounds in the Gulf of Taranto. *Bollettino Malacologico*, 21(10–12): 275–280.

Bello, G. 1985b. Preliminary note on cephalopods in the stomach content of swordfish, *Xiphias gladius* L., from the Ionian and Adriatic seas. *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 29 (8): 231–232.

Bello, G. 1986. Catalogo dei Molluschi Cefalopodi viventi nel Mediterraneo. *Bollettino Malacologico*, 22: 197–214.

Bello, G. 1987. Elenco dei cefalopodi del Golfo di Taranto. *Atti Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 128: 173–179.

Bello, G. 1990. The cephalopod fauna of the Adriatic. *Acta Adriatica, 31(1–2): 275–291.*

Bello, G. 1991. Growth by weight versus growth by length in cephalopods. *In* P. Jereb, S. Ragonese & S. von Boletzky, eds. *Proceedings of the International Workshop held in the Istituto di Technologia, Della Pesca e del Pescato*. 1: 35–37.

Bello, G. 1992 [1991]. Role of cephalopods in the diet of the swordfish, *Xiphias gladius*, from the eastern Mediterranean Sea. *Bulletin of Marine Science*, 49(1–2): 312–324.

Bello, G. 1992a. Stomach contents of a Risso's Dolphin, *Grampus griseus*. Do dolphins compete with fishermen and swordfish, *Xiphias gladius*? European Research on Cetaceans. P.G.H. Evans, Ed. *Proceedings of the 6th Conference of the European Cetacean Society, Sandefjord*, 6: 199–201.

Bello, G. 1992b. Stomach content of a specimen of *Stenella coeruleoalba* (Cetacea: Delphinidae) from the Ionian Sea. *Atti Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 133: 41–48.

Bello, G. 1992c. On the validity, authorship, and publication date of the specific name *Ancistrocheirus lesueurii* (Cephalopoda: Ancistrocheiridae). *Veliger*, 35(2): 141–145.

Bello, G. 1993. Male specimen of *Illex coindetii* (Oegopsida: Ommastrephidae) with two functional gonoducts. *Journal of Cephalopod Biology*, 2(2): 1–2.

Bello, G. 1994. *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae) in the Adriatic Sea: evidence from predator stomach contents. *Bollettino Malacologico*, 30(1–4): 43–48.

Bello, G. 1997 [1996]. Teuthophagous predators as collectors of oceanic cephalopods: the case of the Adriatic Sea. *Bollettino Malacologico*, 32: 71–78.

Bello, G. 1998. *Chaunoteuthis mollis*: re-examination of a Mediterranean specimen and its identity with *Onychoteuthis banksii* (Cephalopoda: Onychoteuthidae). *Journal of the Marine Biological Association of the United Kingdom*, 78: 1027–1030.

Bello, G. 1999 [1998]. New records of *Thysanoteuthis rhombus* (Cephalopoda: Thysanoteuthidae) in the Mediterranean Sea. *Bollettino Malacologico*, 34: 125–128.

Bello, G. 1999. Cephalopods in the diet of albacore, *Thunnus alalunga*, from the Adriatic Sea. *Journal of Molluscan Studies*, 65(2): 233–240.

*__Bello, G.__ 2005. *Abraliopsis morisii* vs. *Abraliopsis pfefferi* (Cephalopoda: Enoploteuthidae): which is the right name? *Journal of Conchology*, 38(5): 561–565.

*__Bello, G. & V. Biagi.__ 1999. A large cranchiid squid (Cephalopoda: Teuthoidea) caught in the Mediterranean Sea. *Bollettino Malacologico*, 34(5–8): 69–70.

*__Bello, G. & R. Giannuzzi-Savelli.__ 1993. Case 2874. *Chtenopteryx* Appellof, 1890 (Mollusca, Cephalopoda): proposed confirmation as the correct original spelling. *Bulletin of Zoological Nomenclature*, 50(4): 270–272.

Bello, G. & C. Pipitone. 2002. Predation on cephalopods by the giant red shrimp *Aristaeomorpha foliacea*. *Journal of the Marine Biological Association of the United Kingdom*, 82(2): 213–218.

Bello, G., C. Pipitone & M. Arculeo. (1994). I cefalopodi dei fondi strascicabili del Golfo di Castellammare. *Bollettino Malacologico*, 30: 173–181.

Bello, G., A. Potoschi & A. Berdar. 1994. Adult of *Ancistrocheirus lesueurii* caught in the Straits of Messina (Cephalopoda: Ancistrocheiridae). *Bollettino Malacologico*, 29(9–12): 259–266.

Belman, B.W. 1978. Respiration and the effects of pressure on the mesopelagic vertically migrating squid *Histioteuthis heteropsis*. *Limnology and Oceanography*, 23(4): 735–739.

Bendik, A.B. 2001. Abundance explosion of the jumbo squid, *Dosidicus gigas*, on the high seas of the Peruvian region in relation to anomalous oceanographic patterns. *International Council for the Exploration of the Sea*, 134 pp.

Benjaminsen, T. & I. Christensenl. 1979. The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Foster). *In*: H.E. Winn, B.L. Olla, eds. Behavior of marine animals. Plenum Press, New York, pp. 143–164.

***Berdar, A. & G. Cavallaro.** 1975. Cephalopoda washed ashore along the beaches of the Sicilian coast of the Straits of Messina. *Memorie di Biologia Maina e Oceanografia*, 5(5): 121–138.

Berenbojm, B.I. 1991. Invertebrate resources and fishery prospects in the Barents Sea. *In*: A.L. Sorokin, ed. Multiple fishery research by PINRO in the northern basin: results and prospects, 1991: 166–171.

Berezinskij, L.A., Ch.M. Nigmatullin & R.M. Sabirov. 1996. To the question of the existence of photophore in squid *Thysanoteuthis rhombus* (Oegopsida) on the juvenile stage. VII conference of Hydrobiological Society of Russian Academy of Science. Proceedings of conference. Kazan: Poligraf Press. Vol. 1: 100–102 (In Russian).

Bergmann, M., S.K. Wieczorek, P.G. Moore & R.J.A. Atkinson. 2002. Utilisation of invertebrates discarded from the Nephrops fishery by variously selective benthic scavengers in the west of Scotland. *Marine ecology progress series*, 233: 185–198.

Bernard, F.R. 1980. Preliminary report on the potential commercial squid of British Columbia. *Canadian Technical Report of Fisheries and Aquatic Sciences*, 942: 51 pp.

***Berry, S.S.** 1909. Diagnosis of new cephalopods from the Hawaiian Islands. *Proceedings of the United States National Museum*, 37(1713): 407–419, 9 figs.

***Berry, S.S.** 1911a. Note on a new *Abraliopsis* from Japan. *Nautilus*, 25(8): 93–94.

***Berry, S.S.** 1911b. Preliminary notices of some new Pacific cephalopods. *Proceedings of the United States National Museum*, 40(1838): 589–592.

***Berry, S.S.** 1911c. A note on the genus *Lolliguncula*. *Proceedings of the Academy of Natural Science of Philadelphia*, 63(1): 100–105, text–figs 1–7, pl 7.

***Berry, S.S.** 1912. A catalogue of Japanese Cephalopoda. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 64(2): 380–444, 5 pls.

***Berry, S.S.** 1913a. Notes on some West American cephalopods. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 65: 72–77, 2 figs.

***Berry, S.S.** 1913b. Some new Hawaiian cephalopods. *Proceedings of the United States National Museum*, 45(1996): 563–566.

***Berry, S.S.** 1913c. *Nematolompas*, a remarkable new cephalopod from the South Pacific. *Biological Bulletin*, 25(3): 208–212, 1 fig.

***Berry, S.S.** 1914. Notes on a collection of cephalopods from the Kermadec Islands. *Transactions and Proceedings of the New Zealand Institute*, 46(24): 134–149, 4 figs, 4 pls.

***Berry, S.S.** 1916. Cephalopoda of the Kermadec Islands. *Proceedings of the Academy of Sciences Philadelphia*, pp. 45–70.

***Berry, S.S.** 1918. Report on the Cephalopoda obtained by the F.I.S. “Endeavour” in the Great Australian Bight and other southern Australian localities. Biological results of the fishing experiments carried on by the F.I.S. “Endeavour” 1909–14, 4(5): 201–298.

***Berry, S.S.** 1920a. Preliminary diagnosis of new cephalopods from the western Atlantic. *Proceedings of the United States National Museum*, 58(2335): 293–300, 1 pl.

***Berry, S.S.** 1920b. Light production in cephalopods, I. An introductory survey. *Biological Bulletin*, 38(3): 141–169.

***Berry, S.S.** 1926. A note on the occurrence and habits of a luminous squid (*Abralia veranyi*) at Madeira. *Biological Bulletin, Woods Hole*, 51(4): 257–268.

***Berry, S.S.** 1929. *Loliolopsis chiroctes*, a new genus and species of squid from the Gulf of California. *Transactions of the San Diego Society of Natural History*, 5(18): 263–282, 9 figs, 2 pls.

Bertignac, M., S. Cunningham & M. Zouiri. 1989. The Morrocan cephalopod fishery. Bio-economic modelling and management proposals. Proj/Pnud/Fao/Mor/86/019, 107 pp.

Besteiro, C. 1985. Fishery prospect expedition on the fishery of squid (*Todarodes sagittatus* (Lamarck, 1880) and red-fish (*Sebastes marinus* (Linneo, 1758) in the waters of the economic exclusive zone of Norway (August–November of 1981). *Trabajos Compostelanos de Biología*, 11: 61–102.

Bet-Sayad, W.V. & G.R. Parsons. 2007. Records of the giant North Pacific squid *Onykia robusta* (Cephalopoda: Onychoteuthidae). *Veliger*, 48(4): 243–246

Bettencourt, V. 1994. Estudo da estrutura da população de *Loligo vulgaris* (Lamarck, 1799) da costa sul de Portugal através da leitura dos anéis de crescimento nas estruturas duras, os estatólitos. MSc thesis, Universidade do Algarve (UCTRA), 70 pp.

Bettencourt, V. & A. Guerra. 2000. Growth increments and biomineralization process in cephalopod. *Journal of Experimental Marine Biology and Ecology*, 248(2): 191–205.

Bettencourt, V., M.L. Coelho & J.P. Andrade. 1995. The use of statoliths in age determination of the long-finned squid, *Loligo vulgaris* (Cephalopoda: Loliginidae). *Copenhagen Denmark ICES*.

Bettencourt, V., M.L. Coelho, J.P., Andrade & A. Guerra. 1996. Age and growth of the squid *Loligo vulgaris* off the south coast of Portugal, using statolith analysis. *Journal of Molluscan Studies*, 62: 359–366.

*****Bettinger, T.E., L. Goodwin & R.T. Burge.** 1985. Development of a Puget Sound fishery for the opal squid *Loligo opalescens* Berry. *Journal on Shellfish Research, 5(1): 49–50.*

Biagi, V. 1984. Spiaggiamenti di cefalopodi sulla costa livornese. *Quaderni del Museo di Storia Naturale diLivorno*, 5: 99–115.

Bidder, A.M. 1950. The digestive mechanism of the European squids *Loligo vulgaris*, *Loligo forbesi*, *Alloteuthis media* and *Alloteuthis subulata*. *Quarterly Journal of Microscopical Science*, 91: 1–43.

*****Bidder, A.M.** 1966. Feeding and digestion in cephalopods. *In* K.H. Wilbur & C.M. Young, eds. *Physiology of Mollusca, New York, London: Academic Press*. pp. 97–124.

Biemann, M.D. & U. Piatkowski. 2001. Amounts and composition of trace elements in the statoliths of loliginid squids and their relationships to environmental variables. *Copenhagen Denmark ICES*.

Biemann, M.D. & U. Piatkowski. 2002. Investigations on the winter population of *Loligo forbesi* (Cephalopoda: Loliginidae) from the North Sea. *Bulletin of Marine Science*, 71(2): 1114.

Bigelow, H.B. 1924. Plankton of the offshore waters of the Gulf of Maine. *Fish Bulletin*, 40: 112–116.

Bigelow, K.A. 1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. *Marine Ecological Program Services*, 82(1): 31–40.

Bigelow, K.A. 1994. Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific. *Fishery Bulletin*, 92(1): 13–25.

Biggs, J. & D. Epel. 2005. Egg capsule sheath of *Loligo opalescens* Berry: structure and association with bacteria. *Journal of Experimental Zoology*, 259(2): 263–267.

Bishop, A., M.B. Santos, S. Desormonts, G.J. Pierce & J.M. Portela. 2002. The trophic relationships of several commercial finfish species from the southwest Atlantic. *ICES Council Meeting Documents*.

Bizikov, V.A. 1991. A new method of squid age determination using the gladius. *In*: P. Jereb, S. Ragonese & S. von Boletsky, eds. Special publication. Squid age determination using statoliths. *Proceedings of the International Workshop held in the Istituto de Technologia Della*, 1: 127 pp.

Bizikov, V.A. 1995. Growth of *Sthenoteuthis oualaniensis*, using a new method based on gladius microstructure. *International Council for the Exploration of the Sea, Marine Symposium*, 199: 445–458.

*****Bizikov, V.A.** 1996. Atlas of morphology and anatomy of the gladius of squids. Moscow: VNIRO Publishing, 248 pp. (In Russian with English summaries of all 11 chapters).

Bizikov, V.A. 2002. Evolution of the shell in octopoda (Cirrata and Incirrata). *Bulletin of Marine Science*, 71(2): 1115.

Bizikov, V.A. & A.I. Arkhipkin. 1996. Distribution, population structure and prospects for fishery of the Commodore I. squid. *RYBN. KHOZ.* 1: 42–45.

Bizikov, V.A. & A.I. Arkhipkin. 1997. Morphology and microstructure of the gladius and statolith from the boreal Pacific giant squid *Moroteuthis robusta* (Oegopsida; Onychoteuthidae). *Journal of Zoology*, 241(3): 475–492.

*****Björke, H.** 1995. Norwegian investigations on *Gonatus fabricii* (Lichtenstein). *Copenhagen, Denmark ICES*. 13 pp.

Björke, H. 2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. *Fisheries Research*, 52(1–2): 113–120.

Björke, H. & H. Gjoesaeter. 1998. Who eats the larger *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea? *Copenhagen, Denmark ICES*, 11 pp.

Björke H, & H. Gjøsæter. 2004. Cephalopods in the Norwegian Sea. *In*: H.R. Skjoldal *et al*., eds. The Norwegian Sea Ecosystem. *Tapur Academic Press Trondheim*, pp. 371–394.

Björke, H. & K. Hansen. 1996. Recording of mature *Gonatus fabricii* (Lichtenstein) off the Norwegian coast. *Copenhagen, Denmark ICES*, 11 pp.

Björke, H., K. Hansen & R.C. Sundt. 1997. Egg masses of the squid *Gonatus fabricii* (Cephalopoda, Gonatidae) caught with pelagic trawl off northern Norway. *Sarsia*, 82(2): 149–152.

Black, G.A.P., T.W. Rowel & E.G. Dawe. 1987. Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealei* in the northwest Atlantic. *Canadian Special Publication of Fishery and Aquatic Science*, 100: 68 pp.

Blackburn, S., W.H.H. Sauer & M.R. Lipinski. 1998. The embryonic development of the chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845. *Veliger*, 41(3): 249–258.

***Blainville, H.D.** 1823. Memoire sur les especes du genre Calmar (*Loligo*, Lamarck). *Journal de Physique, de Chimie et d'Histoire Naturelle*, 96: 116–135.

***Blainville, H.D.** 1824. Mollusques, Mollusca (Malacoz.). *Dictionnaire des Sciences Naturelles*, 32: 1–394, atlas number 2 with 118 pls.

Blanco, C. & J.A. Raga. 2000 Cephalopod prey of two *Ziphius cavirostris* (Cetacea) stranded on the western Mediterranean coast. *Journal of the Marine Biological Association of the United Kingdom*, 80: 381–382.

Blanco, C., J. Aznar & J.A. Raga. 1995. Cephalopods in the diet of the striped dolphin *Stenella coeruleoalba* from the western Mediterranean during an epizootic in 1990. *Journal of Zoology*, 237(1): 151–158.

Blanco, C., M.A. Raduan & J.A. Raga. 2006. Diet of Risso's dolphin (*Grampus griseus*) in the western Mediterranean Sea. *Scientia Marina*, 70(3): 407–411.

Blanco C., O. Salomon & J.A. Raga. 1997. Stomach contents of *Ziphius cavirostris* stranded on the western Mediterranean coast. *European Research on Cetaceans*,11: 143.

Blanco C., O. Salomon & J.A. Raga. 2001 Diet of the bottlenose dolphin (*Tursiops truncatus*) in the western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 81: 1053–1058.

Bloodgood, R.A. 1977. The squid accessory nidamental gland: ultrastructure and association with bacteria. *Tissue Cell.*, 9(2): 197–208.

Bloomer, S. 1996. Hatchdate distributions of pelagic fish species and their relationship to the environment off South Africa. Some preliminary results of a Benguela Ecology Programme study. Summaries of contributions presented at the Workshop on West African Fisheries organized during the Advanced Course on Upwelling Systems Atlantic Ocean Eastern Boundary. A joint effort from IOC and European Union Mast Programme Las Palmas, Gran Canaria, Spain, 9–10 August 1995. Paris, France UNESCO, 43–44 pp.

Boal, J.G. & S.A. Gonzalez. 1998. Social behaviour of individual oval squids (Cephalopoda, Teuthoidea, Loliginidae, Sepioteuthis lessoniana) within a captive school. *Ethology*, 104(2): 161–178.

Boletzky, S.v. 1974. Elevage de Céphalopodes en aquarium. *Vie et Milieu*, 24 (2A): 309–340.

Boletzky, S.v. 1979. Observations on early post-embryonic development of *Loligo vulgaris* (Mollusca, Cephalopoda). *Rapp. Comm. Int. Mer. Médit.*, 25/26: 10 pp.

Boletsky, S.v. 1985. Cephalopods (Biscay Bay). *In*: L. Laubier & C. Monniot, eds. Deep sea benthic communities from the Gulf of Biscay. *Biogas Cruise*, 401–408.

Boletzky, S.v. 1987. On egg and capsule dimensions in *Loligo forbesi* (Mollusca: Cephalopoda): a note. *Vie Milieu*, 37: 187–192.

Boletsky, S.v. 1998. Cephalopod eggs and egg masses. *Oceanographic Marine Biological Annual Review*, 36: 341–371.

***Boletzky, S.v.** 1999. Breve mise au point sur la classification des cephalopodes actuels. *Bulletin de la Societé Zoologique de France*, 124(3) : 271–278.

Boletzky, S.v. & R.T. Hanlon. 1983. A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *In* C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Proceedings of the workshop on the biology and resource potential of cephalopods. Memorial National Museum of Victoria*. 44: 147–188.

Boletzky, S.v., L. Rowe & L. Aroles. 1973. Spawning and development of the eggs, in the laboratory, of *Illex coindetii*. *Veliger*, 15: 257–258.

Bolstad, K.S. 2006. Sexual dimorphism in the beaks of *Moroteuthis ingens* Smith, 1881 (Cephalopoda: Oegopsida: Onychoteuthidae). *New Zealand Journal of Zoology*, 33(4): 317–327.

***Bolstad, K.S.** 2007. Systematics and distribution of the New Zealand onychoteuthid fauna (Cephalopoda: Oegopsida), including a new species, *Notonykia nesisi* sp. nov. *Reviews in Fish Biology and Fisheries*, 17(2–3): 305–335.

Bolstad, K.S. & S. O'Shea. 2004. Gut contents of a giant squid *Architeuthis dux* (Cephalopoda: Oegopsida) from New Zealand waters. *New Zealand Journal of Zoology*, 31(1): 15–21.

***Bolstad, K.S., R.E. Young, M. Vecchione & K. Tsuchiya.** 2007. *Notonykia* Nesis, Roeleveld and Nikitina 1998. Version 09 July 2007 (under construction). http://tolweb.org/Notonykia/108188/2007.07.09 in The Tree of Life Web Project, http://tolweb.org/

Bone, Q., A. Pulsford & A.D. Chubb. 1981. Squid mantle muscle. *Journal of the Marine Biological Association of the United Kingdom*, 1981 61(2): 327–342.

Bone, Q., A. Packard & A.L. Pulsford. 1982. Cholinergic innervation of muscle fibres in squid. *Journal of the Marine Biological Association of the United Kingdom*, 62(1): 193–199.

Bonnaud, L., R. Boucher-Rodoni & M. Monnerot. 1996. Relationship of some coleoid cephalopods established by 3' end of the 16S rDNA and cytochrome oxidase III gene sequence comparison. *American Malacological Bulletin*, 12(1–2): 87–90.

***Bonnaud, L., P.G. Rodhouse & R. Boucher-Rodoni.** 1998. A phylogenetic study of the squid family Onychoteuthidae (Cephalopoda: Oegopsida). *Proceedings of the Royal Society of London, Series B*, 265: 1761–1770.

Booman, A. & R.P. Singh. 1986. A mechanical device to sort market squid, *Loligo opalescens*. *Marine Fisheries Review*, 48(2): 37–43.

Boongerd, S. & S. Chitrapong. 1990. Small-scale fishing for squids and related species (light attraction fishing). A report of the training study tour on squid fishing. Rayong and Chonburi, Thailand, 17–24 April 1990. Manila Philippines Asean UNDP FAO, 26–43 pp.

***Borges, T.C.** 1995. Discriminant analysis of geographic variation in hard structures of *Todarodes sagittatus* from the North Atlantic. *ICES Marine Science Symposium*, 433–440 pp.

***Borges, T.C. & J.C. Wallace.** 1993. Some aspects of the fishery biology of the ommastrephid squid *Todarodes sagittatus* (Lamarck, 1798) from the Northeast Atlantic. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology (Tokai University Press, Tokyo)*, 25–36 pp.

Börjesson, P., P. Berggren & B. Ganning. 2003. Diet of harbour porpoises in the Kattegat and Skagerrak sea: accounting for individual variation and sample size. *Marine Mammal Science*, 19(1): 38–58.

***Bosc, L.A.G.** 1802. Histoire naturelle des vers contenant leur descriptionet leurs moeurs; avec figures dessinees d'apres nature. 1: 324 pages. Paris: Déterville.

Boucaud-Camou, E. & C.F.E. Roper. 1995. Digestive enzymes in paralarval cephalopods. *Bulletin of Marine Science*, 57(2): 313–327.

Boucher-Rodoni, R. 1975. Rate of digestion in cephalopods *Eledone cirrhosa* (Lamarck) and *Illex illecebrosus* (Lesueur). *Cahiers Biologia Marina*, 16(2): 159–175.

Boucher-Rodoni, R. 1976. Histological study of the digestive tract of two cephalopods, *Eledone cirrosa* (Octopoda) and *Illex illecebrosus* (Teuthoidea), during digestion. *Cahiers Biologia Marina*, 17(3): 245–260.

Boumaaz, A. & A. Idelhaj. 1997. Selectivity of bottom trawlers in the exploitation of cephalopods from Moroccan South Atlantic waters. Annex 4 *In*: M. Lamboeuf, ed. Ad hoc Working Group on Cephalopods, 19–26 May 1997, Tenerife, Spain. Rome, Italy, FAO 63: 58–63.

Bowen, W.D. & G.D. Harrison. 1996. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Canadian Journal of Zoology*, 74(1): 125–135.

Bower, J.R. 1997. Estimated paralarval drift and inferred hatching sites for *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) near the Hawaiian Archipelago. *Fishery Bulletin*, 94: 398–411.

***Bower, J.R. & T. Ichii.** 2005. The red flying squid (*Ommastrephes bartramii*): a review of recent research and the fishery in Japan. *Fisheries Research (Amsterdam)*, 76(1): 39–55, figs. 1–7, tables 1–3.

***Bower, J.R. & K. Miyahara.** 2005. The diamond squid (*Thysanoteuthis rhombus*): A review of the fishery and recent research in Japan. *Fisheries Research*, 173: 1–11.

Bower, J.R. & Y. Sakurai. 1996. Laboratory observations on *Todarodes pacificus* (Cephalopoda: Ommastrephidae) egg masses. *American Malacological Bulletin*, 13: 65–71.

***Bower, J.R. & S. Takagi.** 2004. Summer vertical distribution of paralarval gonatid squids in the northeast Pacific. *Journal of Plankton Research*, 26(8): 851–857.

***Bower, J.R., J.M. Murphy & Y. Sato.** 2002. Latitudinal gradients in body size and maturation of *Berryteuthis anonychus* (Cephalopoda: Gonatidae) in the Northeast Pacific. *Veliger*, 45(4): 309–315.

Bower, J.R., Y. Sakurai, J. Yamamoto & H. Ishii. 1999a. Transport of the ommastrephid squid *Todarodes pacificus* under cold-water anesthesia. *Aquaculture*, 170(2): 127–130.

Bower, J.R., Y. Nakamura, K. Mori, J. Yamamoto, Y. Isoda & Y. Sakurai. 1999b. Distribution of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) paralarvae near the Kuroshio of southern Kyushu, Japan. *Marine Biology*, 135: 99–106.

***Bower, J.R., M.P. Seki, R.E. Young, K.A. Bigelow, J. Hirota & P. Flament.** 1999c. Cephalopod paralarvae assemblages in Hawaiian Islands waters. *Marine Ecology Progress Series*, 185: 203–212.

Bower, S.M. & L. Margolis. 1991. Potential use of helminth parasites in stock identification of flying squid, *Ommastrephes bartramii*, in the North Pacific waters. *Canadian Journal of Zoology*, 69: 1124–1126.

Boyle, P.R. (ed) . 1983. Cephalopod Life Cycles. Vol. I. Species Accounts. *Academic Press London*, 475 pp.

Boyle, P.R. 1986 Report on a specimen of *Architeuthis* stranded near Aberdeen, Scotland. *Journal of Molluscan Studies*, 52(1): 81–82.

Boyle, P.R. (ed). 1987. Cephalopod Life Cycles. Vol. II. Comparative Reviews. *Academic Press London*, 441 pp.

Boyle, P.R. & M.A.K. Ngoile. 1993. Assessment of maturity state and seasonality of reproduction in *Loligo forbesi* (Cephalopoda: Loliginidae) from Scottish waters. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in fishery biology. Tokai University Press, Tokyo*, 37–48.

***Boyle, P.R. & G.J. Pierce (eds).** 1994. Fishery biology of Northeast Atlantic squid. *Fisheries Research*, 21(1–2): 1–311.

***Boyle, P.R. & P. Rodhouse.** 2005. Cephalopods: ecology and fisheries. Blackwell Science Ltd., Oxford, UK, 452 pp.

Boyle, P.R., M.A. Collins & G.J. Pierce. 1995a. Patterns in reproduction and recruitment of *Loligo forbesi* around the British Isles. *Copenhagen Denmark ICES*, 11 pp.

Boyle, P.R., M.A. Collins & G.J. Pierce (eds). 2002. Cephalopod biomass and production, Parts 1 and 2. *Bulletin of Marine Science*, 71(1–2): 1–1146.

Boyle, P.R., M.A. Collins & G.R. Williamson. 1998. The cephalopod by-catch of deep-water trawling on the Hebrides slope. *Journal of the Marine Biological Association of United Kingdom*, 78(3): 1023–1026.

***Boyle, P.R., G.J. Pierce & L.C. Hastie** 1995b. Flexible reproductive strategies in the squid *Loligo forbesi*. *Marine Biology*, 121: 501–508.

Bradbury, H.E. 1971. A technique for demonstrating the blood vascular system of squid. *Canada Journal of Zoology*, 49(4): 505–506.

Bradbury, H.E. & F.A. Aldrich. 1971. The occurrence of morphological abnormalities in the oegopsid squid *Illex illecebrosus* (Lesueur, 1821). *Canadian Journal of Zoology*, 49(3): 377–379.

Bradshaw, M. 2006. Co-operative development of area-based management of southern calamari. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: 59 p.

Brakoniecki, T.F. 1980. *Lolliguncula tydeus*, a new species of squid (Cephalopoda; Myopsida) from the Pacific coast of central America. *Bulletin of Marine Science*, 30(2):424–430.

****Brakoniecki, T.F.** 1984a. *Loligo sanpaulensis*. *In*: C.F.E. Roper *et al*., eds. Cephalopods of the World. An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis,* No. 125, Volume 3: 102.

****Brakoniecki, T.F.** 1984b. A full descripition of *Loligo sanpaulensis*, Brakoniecki, 1984 and a redescription of *Loligo gahi* d'Orbigny, 1835, two species of squid (Cephalopoda: Myopsida) from the southwest Atlantic. *Bulletin of Marine Science*, 34(3):435–448.

****Brakoniecki, T.F.** 1986. A generic revision of the family Loliginidae (Cephalopoda; Myopsida) based primarily on the comparative morphology of the hectocotylus. Unpublished Ph.D. dissertation, University of Miami, Coral Gables, Florida, 163 pp.

****Brakoniecki, T.F.** 1996. A revision of the genus *Pickfordiateuthis* Voss, 1953 (Cephalopoda: Myopsida). *Bulletin of Marine Science*, 58(1): 9–28.

****Brakoniecki, T.F. & C.F.E. Roper.** 1985. *Lolliguncula argus*, a new species of loliginid squid (Cephalopoda: Myopsida) from the tropical eastern Pacific. *Proceedings of the Biological Society of Washington*, 98(1): 47–53.

Brandt, S.B. (1983). Pelagic squid associations with a warm-core eddy of the East Australian Current. *Australian Journal of Marine and Freshwater Research*, 34: 573–585.

Bravo-de-Laguna, J. & E. Balguerias Guerra. 1993. The Saharan fishery for cephalopods: A brief review. *Boletino del Instituto Espanol de Oceanografia*, 9(1): 203–213 ; *Brazil. Bulletin of Marine Science*, 71(2): 753–770.

Breen, P.A., R. Hilborn, M.N. Maunder & S.W. Kim. 2003. Effects of alternative control rules on the conflict between a fishery and a threatened sea lion (*Phocarctos hookeri*). *Canadian Journal of Fisheries and Aquatic Sciences*, 60(5): 527–541.

Breiby, A. & M. Jobling. 1985. Predatory role of the flying squid (*Todarodes sagittatus*) in North Norvegian waters. *NAFO Scientific Council Studies*, 9: 125–132.

Brickle, P., P.D. Olson, D. Timothy, J. Littlewood, A. Bishop & A.I. Arkhipkin. 2001. Parasites of *Loligo gahi* from waters off the Falkland Islands, with a phylogenetically based identification of their cestode larvae. *Canadian Journal of Zoology*, 79(12): 2289–2296.

Brierley, A.S., A.L. Allcock, J.P. Thorpe & R.D. Clarke. 1996. Biochemical genetic evidence supporting the taxonomic separation of *Loligo edulis* and *Loligo chinensis* Cephalopoda: Teuthoidea) from the genus *Loligo*. *Marine Biology*, 127(1): 97–104.

****Brierley, A.S., P.G. Rodhouse, J.P. Thorpe & M.R. Clarke.** 1993. Genetic evidence of population heterogeneity and cryptic speciation in the ommastrephid squid *Martialia hyadesi* from the Patagonian Shelf and Antarctic Polar Frontal Zone. *Marine Biology*, 116(4): 593–602.

****Brierley, A.S., R.S. Thorpe, G.J. Pierce, M.R. Clarke & P.R. Boyle.** 1995. Genetic variation in the neritic squid *Loligo forbesi* (Myopsida: Loliginidae) in the northeast Atlantic Ocean. *Marine Biology*, 12: 79–86.

Brinken, T. 1997. North Korea opens up. *FAO Eastfisheries Magazine*, 1997(1): 20–22.

Brito-Castillo, L., E. Alcantara-Razo, R. Morales-Azpeitia & C.A. Salinas-Zavala. 2000. Water temperatures in the Gulf of California in May and June 1996 and their relation to the capture of giant squid (*Dosicidicus gigas*) d'Orbigny, 1835. *Ciencia y mar*, 26(3): 413–440.

Brito-Castillo, L., E. Alcantara-Razo & C.A. Salinas-Zavala. 2002. Comments about the relationship between temperature and giant squid catches. *Ciencias Marinas*, 28(2): p. 221.

Brix, O., A. Colosimo & B. Giardina. 1994. Temperature dependence of oxygen binding to cephalopod haemocyanins: ecological implications. *Marine and Freshwater Behavior Physiology*, 25(103): 149–162.

Brix, O., A. Baardgard, A. Cau, A. Colosimo, S.G. Condo & B. Giardina. 1989. Oxygen-binding properties of cephalopod blood with special reference to environmental temperatures and ecological distribution. *Journal of Experimental Zoology*, 252(1): 34–42.

****Brock, J.** 1887. Indische Cephalopoden. *Zoologische Jahrbücher*, 2: 591–614.

****Brodziak, J.K.T.** 1998. Revised biology and management of long-finned squid (*Loligo pealei*) in the Northwest Atlantic. *Reports of California Cooperative Oceanic Fisheries Investigations*, 39: 61–70.

****Brodziak, J.K.T. & L. Hendrickson.** 1999. An analysis of environmental effects on survey catches of squid *Loligo pealei* and *Illex illecebrosus* in the Northwest Atlantic. *Fishery Bulletin*, 97: 9–24.

Brodziak, J.K.T. & W.K. Macy, III. 1996. Growth of long-finned squid, *Loligo pealei*, in the Northwest Atlantic. *Fishery Bulletin*, 94(2): 212–236.

***Brodziak, J.K.T. & A.A. Rosenberg.** 1993. A method to assess squid fisheries in the north-west Atlantic. *ICES Journal of Marine Science*, 50: 187–194.

Brown, E.R. & N.J. Abbott. 1993. Ultrastructure and permeability of the Schwann cell layer surrounding the giant axon of the squid. *Journal of Neurocytology*, 22(4): 283–298.

Brown, E.G. & G.J. Pierce. 1998. Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Marine Ecology Progress Series*, 167: 275 – 289.

Brownell, R.L. 2004. Potential competition with fisheries? The case of sperm whales and beaked whales. Investigating the roles of cetaceans in marine ecosystems CIESM Workshop Monographs, 25: 103–106.

Brunetti, N.E. 1981. Distribucion de tallas y biologia reproductive del calamar *Illex argentinus* en el Mar Argentino. *In*: V. Angelescu, ed. Campanas del B/I “Shinkai Maru” 1978 1979. *Contributión de l'Instituto Nacional de Investigación y Desarrollo Pesquero*, 383: 105–119.

Brunetti, N.E. 1988. Contibución al conocimiento biologico pessquero del calamar argentine (Cephalopoda, Ommastrephidae, *Illex argentinus*). *Tesis doctoral. Fac. Cs. Nat. Museo, Universidad Nacional de La Plata*: 135 pp.

Brunetti, N.E. 1990a. Description of Rhynchoteuthion larvae of *Illex argentinus* from summer spawning subpopulation. *Journal of Plankton Research*, 12(5): 1045–1057.

Brunetti, N.E. 1990b. The evolution of the fishery for *Illex argentinus* (Castellanos, 1960) fishery. *Inf. Tec. Investigación Pesquera* (in Spanish), 155: 19 pp.

Brunetti, N.E & J.A. Perez Comas. 1989b. Abundancia, distribution y composicion poblacional del recurso calamar (*Illex argentinus*) en agues uruguayo bonaerenses en mayo, setiembre y noviembre de 1986 y en marzo y mayo de 1987. *Frente Maritimo*, 5(A): 39–59.

Brunetti, N.E. & M.L. Ivanovic. 1992. Distribution and abundance of early life stages of squid (*Illex argentinus*) in the southwest Atlantic. *ICES Journal of Marine Science*, 49: 175–183.

Brunetti, N.E. & M.L. Ivanovic. 2004. *Ommastrephes bartramii*: a potential target for the squid fishery in the Southwest Atlantic. *Revista de Investigacion y Dessarrollo Pesquero*, 16: 51–66.

Brunetti, N.E. & M.L. Ivanovic. 2006. Diet of red squid (*Ommastrephes bartramii*) in the southwest Atlantic. *Revista de Investigacion y Desarrollo Pesquero*, 16: 67–75.

Brunetti, N.E. & G.R. Rossi. 1990. Informe preliminary sobre la campana argentine-sovietica en el B/I “Evrika” (agosto–octubre 1988). *Inf. Tec. INIDEP*, 1: 1–35.

***Brunetti, N.E., M.L. Ivanovic & B. Elena.** 1998a. Calamares omastrefidos (Cephalopoda: Ommastrephidae). *In*: E.E. Boschi, ed. *El Mar argentino. Tomo 2. Los molluscos de interes pesquero. Cultivos y estrategias reproductivas de bivalves y equinoideos*. Mar del Plata: INIDEP Publication: 37–68.

***Brunetti, N.E., M.L. Ivanovic, A. Aubone & L.N. Pascual.** 2006. Reproductive biology of red squid (*Ommastrephes bartramii*) in the southwest Atlantic. *Revista de Investigacion y Desarrollo Pesquero*, 18: 5–19.

***Brunetti, N.E., M.L. Ivanovic & M. Sakai.** 1999. Calamares de importancia commercial en la Argentina. Biologia, distribucion, pesquerias, muestreo biologico. [Squids of commercial value in the waters off Argentina. Biology, distribution, fisheries and biological sampling]. INIDEP (Instituto Nacional de Investigacion y Desarrollo Pesquero) – JICA (Japan International Cooperation Agency) Contribucion, 1121: 45 pp.

Brunetti, N.E., M.L. Ivanovic, M. Sakai & L.N. Pascual. 2002. Two new records of giant squid (*Architeuthis* sp.) from the Patagonian region. *Revista de Investigacion y Desarrollo Pesquero*, 15: 95–110.

***Brunetti, N.E., M.L. Ivanovic, R. Rossi, B. Elena & S. Pineda.** 1998b. Fishery biology and life history of *Illex argentinus*, *In*: T. Okutani, ed. Large Pelagic Squids. Japan Marine Fishery Resources Research Center. Tokyo. 217–231 pp.

***Brunetti, N.E., B. Elena, G.R. Rossi, M. Sakai, S.E. Pineda & M.L. Ivanovic.** 1998c. Description of an *Architeuthis* from Argentine waters. *In* A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. *Cephalopod biodiversity, ecology and evolution. South African Journal of Marine Science*, 20: 355–361.

Bruun, A.F. 1943. The biology of Spirula spirula. *Dana Report* No. 24. Carlsberg Foundation, Copenhagen. 48 pp.

Bruun, A.F. 1945. Cephalopoda. *Zoology Iceland*, 64(4): 1–15. (Spiaggiamenti).

Bruyn, P.J.N. de, M.N. Bester, S. Mecenero, S.P. Kirkman, J.P. Roux & N.T.W. Klages. 2003. Temporal variation of cephalopods in the diet of Cape fur seals in Namibia. *South African Journal of Wildlife Research*, 33(2): 85–96.

Bruyne, de R.H., R.A. Bank, J.P.H.M. Adema & F.A. Perk. (1994). Dutch namelist of the Mollusca from the Netherlands and Belgium: festive edition at the occasion of the 60-year jubilee of the Dutch Malacological Society. Backhuys Publishers: Leiden, The Netherlands. ISBN 90–73348–33–1: 149 pp.

Bublitz, C. 1981. Systematics of the cephalopod family Gonatidae from the southeastern Bering Sea. M.S. Thesis, Univ. Alaska, Fairbanks, 171 p.

***Buresch, KC., G. Gerlach & R.T. Hanlon.** 2006. Multiple genetic stocks of longfin squid *Loligo pealeii* in the NW Atlantic: stocks segregate inshore in summer, but aggregate offshore in winter. *Marine Ecology Progress Series*, 310: 263–270.

Buresch, K.M., R.T. Hanlon, M.R. Maxwell & S. Ring. 2001. Microsatellite DNA markers indicate a high frequency of multiple paternity within individual field-collected egg capsules of the squid *Loligo pealeii*. *Marine Ecology Progress Series*, 210: 161–165.

Buresch, K.C., J.G. Boal, G.T. Nagle, J. Knowles, R. Nobuhara, K. Sweeney & R.T. Hanlon. 2004. Experimental evidence that ovary and oviducal gland extracts influence male agonistic behavior in squids. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 206(1): 1–3.

Buresch, K.C., J.G. Boal, J. Knowles, J. Debose, A. Nichols, A. Erwin, S.D. Painter, G.T. Nagle & R.T. Hanlon. 2003. Contact chemosensory cues in egg bundles elicit male–male agonistic conflicts in the squid *Loligo pealeii*. *Journal of Chemical Ecology,* 29(3): 547–560.

***Burgess, L.A.** 1967. *Loliolus rhomboidalis*, a new species of loliginid squid from the Indian Ocean. *Bulletin of Marine Science*, 17: 319–329.

***Burgess, L.A.** 1982. Four new species of squid (Oegopsida: *Enoploteuthis*) from the central Pacific and a description of adult *Enoploteuthis reticulata*. *US Fish and Wildlife Service Fishery Bulletin*, 80(4): 703–734.

Burgess, L.A. 1991. *Nautilus*: The pearly or chambered nautilus. *The Tropical Fish Hobbyist,* May 1991: 38–51.

***Burgess, L.A.** 1992 [1991]. Squids of the genus *Abralia* (Cephalopoda) from the central equatorial Pacific with a description of *Abralia heminuchalis*, a new species. *Bulletin of Marine Science*, 49(1–2): 113–136. [Date on title page is 1991; actually published in 1992].

***Burgess, L.A.** 1998. A survey of seminal receptacles in the Enoploteuthidae. *In* N.A. Voss, M.V. Vecchione, R.B. Toll & M.J. Sweeney, Eds. Systematics and Biogeography of Cephalopods, Vol. II. *Smithsonian Contributions to Zoology*, 586: 271–276.

Burton H.R. & J. van den Hoff. 2002. Humans and the southern elephant seal Mirounga leonina. *Aust Mammal*, 24: 127–139.

Burukovsky, R.N., G.V. Zuev, Ch.M. Nigmatullin & M.A. Tsymbal. 1977. Methodological principles for development of reproductive system maturity scales for female squids with reference to *Sthenoteuthis pteropus* (Cephalopoda, Ommastrephidae). *Zoologicheskij Zhurnal*, 56(12): 1781–1791 (In Russian with English summary).

Burukovski, R.N., A.V. Gaevskaya, L.N. Domanevski, Ch.M. Nigmatulin & B.G. Panfilov. (1979). Main results of research on squids carried out by the AtlantNIRO in the central-east Atlantic. *ICES Council Meeting, 1979/K:* 2 pp.

Bush, S.L., B.H. Robison & R.L. Caldwell. (2009) Behaving in the dark: locomotor, chromatic, postural, and bioluminescent behaviors of the deep-sea squid *Octopoteuthis deletron* Young 1972. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 216(1): 7–22. 2009.

Bustamante, P., R.P. Cosson, I. Gallien, F. Caurant & P. Miramand. 2002. Cadmium detoxification processes in the digestive gland of cephalopods in relation to accumulated cadmium concentrations. *Marine Environmental Research*, 53(3): 227–24.

Bustamante, P., K. Das, A. Guerra, V. Lahaye, F. Rocha, A.F. Gonzalez & L. Laria. 2006. The giant squid (*Architeuthis*): a very high level predator? Cephalopod International Advisory Council Symposium 2006, Abstract. p. 72.

Butler, J., D. Fuller & M. Yaremko. 1999. Age and growth of market squid (*Loligo opalescens*) off California during 1998. *Reports of California Cooperative Oceanic Fisheries Investigations*, 40: 191–195.

Byrne, R.A., U. Griebel, J.B. Wood & A. Mather. 2003. Squid say it with skin: a graphic model for skin displays in Caribbean Reef Squid (*Sepioteuthis sepioidea*). *Berliner Parabiol. Abh*, 3: 29–35.

*****Caddy, J.F.** 1983. The Cephalopods: factors relevant to their population dynamics and to the assessment and management of the stocks. *In*: J.F. Caddy, ed. Advances in Assessment of World Cephalopod Resources. *FAO Fisheries Technical Paper*, 231: pp 452.

*****Caddy, J.F. & P.G. Rodhouse.** 1998. Do recent trends in cephalopod and groundfish landings indicate widespread ecological change in global fisheries? *Review in Fish Biology and Fisheries*, 8: 431–444.

Cadrin, S.X. & E.M.C. Hatfield. 2002. Relative biomass and production of longfin inshore squid, *Loligo pealeii*. *Bulletin of Marine Science*, 71(2): 1115–1116.

Cadrin, S.X., A.B. Howe, S.J. Correia & T.P. Currier. 1995. Evaluating the effects of two coastal mobile gear fishing closures on finfish abundance off Cape Cod. *North American Journal of Fisheries Management*, 15(2): 300–315.

Cailliet, G.M. & D.L. Vaughan. 1983. A review of the methods and problems of quantitative assessment of *Loligo opalescens*. *Biological Oceanography*, 2(2–4): 379–400.

Cailliet, G.M., K.A. Karpov & D.A. Ambrose. 1979. Pelagic assemblages as determined from purse seine and large midwater trawl catches in Monterey Bay and their affinities with the market squid, *Loligo opalescens*. *Reports of California Cooperative Oceanic Fisheries Investigations*, 20: 21–30.

*****Cairns, S.D.** 1976. Biological results of the University of Miami deep-sea expedition. 118 Cephalopods collected in the Straits of Florida by the R/V Gerda. *Bulletin of Marine Science*, 26(2): 233–272.

Campagna, C., V. Falabella & M. Lewis. 2007. Entanglement of southern elephant seals in squid fishing gear. *Marine mammal Science*, 23(2): 414–418.

Capitoli, R.R. & E.M. Haimovici. 1993. Feeding of the red porgy (*Pagrus pagrus*) in Southern Brazil. *Frente Maritimo*, 14: 81–86.

Capitoli, R.R., A. Bager & M.L. Ruffino. 1994. The benthic demersal trophic relationships in the *Artemesia longinaris* shrimp commercial fishing area, Barra region of the Patos Lagoon, RS, Brazil. *Nauplius*, 2: 53–74.

Cardenas-Lopez, J.L. & N.F. Haard. 2005. Cysteine proteinase activity in jumbo squid (*Dosidicus gigas*) hepatopancreas extracts. *Journal of Food Biochemistry*, 29(2): 171–186.

Cardoso, F., J. Tarazona & C. Paredes. 1998. Biological aspects of the Patagonian squid *Loligo gahi* (Cephalopoda: Loliginidae) in Huarmey, Peru. *Revista. Peruana de biologia*, 5(1): 9–14.

Cargnelli, L.M., S.J. Griesbach, C. McBride, C.A. Zetlin & W.W. Morse. 1999. Essential fish habitat source document: Longfin inshore squid, *Loligo pealeii*, life history and habitat characteristics. *NOAA Technical Memorandum NMFS NE*, 146: [np]

*****Carlini, D.B.** 1998. The phylogeny of Coleoid Cephalopods inferred from molecular evolutionary analysis of the Cytochrome C oxidase 1, muscle actin and cytoplasmic actin genes. Ph.D. Dissertation, the College of William and Mary, 273 pp.

*****Carlini, D.B. & J.E. Graves.** 1999. Phylogenetic analysis of cytochrome C oxidase I sequences to determine higher–level relationships within the coleoid cephalopods. *Bulletin of Marine Science*, 64(1): 57–76.

*****Carlini, D.B., L.K. Kunkle & M. Vecchione.** 2006. A molecular systematic evaluation of the squid genus *Illex* (Cephalopoda: Ommastrephidae) in the North Atlantic Ocean and Mediterranean Sea. *Olecular Phylogenetics and Evolution*, 41: 496–502.

Carlini R., M. Pulcini & M. Wurtz. 1992a. Cephalopods from the stomachs of Risso's Dolphins, *Grampus griseus*, (Cuvier, 1812), stranded along the central Tyrrhenian coast. European Research on Cetaceans. P.G.H. Evans, ed. Proc. of 6th Conf. of European Cetacean Society, Sandefjord, 6: 196–198.

Carlini R., M. Pulcini & M. Wurtz. 1992b. Cephalopods from the stomachs of cuvier's beaked whale (*Ziphius cavirostris* Cuvier, 1823) stranded at Fiumicino, central Tyrrhenian sea. European Research on Cetaceans. P.G.H. Evans, ed. Proc. of 6th Conf. of European Cetacean Society, Sandefjord, 6: 190–191.

Carlini, D.B., K.S. Reece & J.E. Graves. 2000. Actin gene family evolution and the phylogeny of coleoid cephalopods (Mollusca: Cephalopoda). *Molecular Biology and Evolution*, 17(9): 1353–1370.

Carlini, D.B., R.E. Young & M. Vecchione. 2001. A molecular phylogeny of the octopoda (Mollusca: Cephalopoda) evaluated in light of morphological evidence. *Molecular Phylogeny and Evolution*, 21(3): 388–397.

Carpentieri, P., F. Colloca & G. Ardizzone. 2007. Rhythms of feeding activity and food consumption of two Mediterranean burrowing fishes: *Gnathophis mystax* (Delaroche) and *Chlopsis bicolour* Rafinesque. *Marine Ecology*, 28(4): 487–495.

Carrasson, M, C. Stefanescu & J.E. Cartes. 1992 Diets and bathymetric distributions of two bathyal sharks of the Catalan deep sea (western Mediterranean). *Marine Ecology Progress Series*, 82: 21–30.

Carreto, J.I., H.R. Benavides, R.M. Negri & P.D. Glorioso. 1986. Toxic red tide in the Argentine Sea. Photoplankton distribution and survival of the toxic dinoflagellate Gonyaulax excavate in a frontal area. *Journal of Plankton Research*, 8(1): 15–28.

Carvalho, G.R. & K.H. Loney. 1989. Biochemical genetic studies on the Patagonian squid *Loligo gahi* d'Orbigny. 1. Electrophoretic survey of genetic variability. *Journal of Experimental Marine Biology and Ecology*, 126(3): 231–241.

***Carvalho, G.R. & Ch.M. Nigmatullin.** 1998. Stock structure analysis and species identification. *In*: P.G. Rodhouse, E.G., Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 199–232.

Carvalho, G.R. & T.J. Pitcher. 1989. Biochemical genetic studies on the Patagonian squid *Loligo gahi* d'Orbigny. 2. Population structure in Falkland waters using isozymes, morphometrics and life history data. *Journal of Experimental Marine Biology and Ecology*, 126(3): 243–258.

Carvalho, G.R., A. Thompson & A.L. Stoner. 1992. Genetic diversity and population differentiation of the shortfinned squid *Illex argentinus* in the southwest Atlantic. *Journal of Experimental Marine Biology and Ecology*, 158: 105–121.

Casali, P., G. Piccinetti Manfrin & S. Soro. (1998). Distribuzione di cefalopodi in alto e medio Adriatico. *Biologia Marina Mediterranea*, 5: 307–317.

Casas, J.M. & J. Paz. 1994. Diet of Flemish Cap cod with particular reference to predation on redfish: 1988–93. *Science Council Research Document NAFO*, 94/24, 21 pp.

Casas, J.M. & J. Paz. 1996. Recent changes in the feeding of cod (*Gadus morhua*) off the Flemish Cap, Newfoundland 1989–1993. *ICES Journal of Marine Science*, 53(5): 750–756.

Casaux, R, A. Baroni, & A. Carlini. (1997) The diet of the Weddell seal *Leptonychotes weddellii* at Harmony Point, South Shetland Islands. *Polar Biology*, 18: 371–375.

***Castellanos, Z.J.A. de.** 1960. Una nueva especie de calamar Argentino, *Ommastrephes argentinus* sp. nov. (Mollusca, Cephalopoda). *Neotropica*, 6(20): 55–58, 5 figs.

Castellanos, Z.J.A. de. 1967. Catalogo de los moluscos marinos bonaerenses. *Anales, Consejo Superior de Investigaciones Cientificas*, 7: 9–390.

Castellanos, Z.J.A. de & N. Cazzaniga. 1977. Contributions to the knowledge of *Loligo patagonica* Smith, 1881 (Cephalopoda Decapoda). *Geotropica*, 23(70): 122–131.

***Castellanos, Z.J.A. de & N. Cazzaniga.** 1979. Aclaraciòn a cerca de los Loliginidae del Atlantico Sudoccidental. *Geotropica*, 25(73): 59–68.

Castellanos, Z.J.A. de & N.J. Cazzaniga. 1980. Comments on Peruvian Cephalopods. *Neotropica*, 26(75): 23–27.

Castellanos, Z.J.A. de & R. Menni. 1968. Los cefalópodos de la expedición "Walter Herwig". *Com. Inv. Cient. Prov. Bs As*, 6(2): 1–31.

Castellanos, Z.J.A. de & R. Menni. 1969. Nota preliminar sobre distribución de los cefalópodos del Atlántico sudoccidental. *Anales de la Sociedad Cientifica Argentina*, 188 (5–6): 205–226.

Castillo, L.V., S. Kawaguchi & Y. Maita. 1990. Evidence for the presence of heavy metal binding proteins in the squid *Onychoteuthis borealijaponica*. *In* R. Hirano & I. Hanyu, eds. Proceedings of The Second Asian Fisheries Forum, Tokyo, Japan, 17–22 April 1989. 453–456 pp.

Castillo, R., V. Blaskovic, E. Gomez, B. Saravia & S. Albines. 1996. Characteristics of distribution, concentration and biological aspects of coastal resources, Lima Peru Pacific Press SA, 121: 27–51.

Castillo-Valderrama, R. & M. Gutierrez. 2000. Biomasses of the most abundant pelagic species during Spring 1999. RV Jose Olaya Balandra and RV SNP–2 9911–12 cruise, from Punta Aguja to Punta Caballas. Grafica–Tecnica SRI, 157: 7–22.

Castillo-Valderrama, R. & M. Gutierrez. 2001. Biomasses of the eleven most abundant fishery species in Peruvian sea during summer 2000. *Evaluation cruise of pelagic resources*, 159: 23–37.

Castillo-Valderrama, R., M. Gutierrez & S. Peraltilla-N. 1999c. Biomass of the main fishing resources at the end of Autumn 1999. Cruise RV Jose Olaya Balandra and RV Humboldt 9906 from Paita to Punta Infiernillos. *Informe Instituto del Mar del Peru Callao*, 147: 19–34.

Castillo-Valderrama, R., M. Gutierrez, S. Peraltilla-N. & N. Herrera-A. 1999b. Biomass of the main fishery resources during Summer 1999. Cruise R.V. Jose Olaya Balandra 9902–03 from Tumbes to Tacna. *Informe Instituto del Mar del Peru Callao*, 147: 31–45.

Castillo-Valderrama, R., M. Gutierrez, S. Peraltilla & D. Marin. 2001. Distribution of the eleven most abundant Peruvian marine fishing resources during summer 2000. *Evaluation cruise of pelagic resources*, 159: 7–21.

Castillo-Valderrama, R., L. Vasquez, N.S. Peraltilla, E. Tello & A. Aliaga-R. 1999a. Preferential temperature and salinity ranges of the anchovy and of the giant squid during Summer 1999. R/V Jose Olaya Balandra 9902–03 Cruise from Tumbes to Tacna. *Informe Instituto del Mar del Peru Callao*, 147: 47–58.

Castro, J.J. & V. Hernàndez-García. 1995. Ontogenetic changes in mouth structures, foraging behaviour and habitats use of *Scomber japonicus* and *Illex coindetii*. *Scientia Marina*, 59: 347–355.

Catry, P., R.A. Phillips, B. Phalan, J.R.D. Silk & J.P. Croxall. 2004. Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: Integration of movements, activity and feeding events. *Marine Ecology Progress Series*, 280: 261–273.

***Ceriola, L., N. Ungaro & F. Toteda.** 2007. A “Traffic” Light approach for the assessment of the Broadtail shortfin squid *Illex coindetii* Verany, 1839 in the Southern Adriatic Sea (Central Mediterranean). *Reviews in Fish Biology and Fisheries*, 17(2–3): 145–157.

Ceriola, L., P. Accadia, P. Mannini, F. Massa, N. Milone & N. Ungaro. 2008. A bio-economic indicators suite for the appraisal of the demersal trawl fishery in the Southern Adriatic Sea (Central Mediterranean). *Fisheries Research (Amsterdam) [Fisheries Research].*, Vol. 92, no. 2–3, pp. 255–267.

Ceriola, L., C.A. Marano, M. Martino, L. Quaranta, G. Strippoli & N. Ungaro. 2006. Abbondanza e densita’ di alcuni cefalopodi Teuthoidea nell’Adriatico meridionale. *Biologia Marina Mediterranea*, 13(1): 844–847.

Challier, L., G. Pierce & J.-P. Robin. 2006. Spatial and temporal variation in age and growth in juvenile *Loligo forbesi* and relationships with recruitment in the English Channel and Scottish waters. *Journal of Sea Research*, 55(3): 217–229.

Chacko, D., V.D. Samuel & J. Patterson. 2004. Effect of salinity and fly-ash on the embryonic development of the bigfin squid, *Sepioteuthis lessoniana*. *Journal of the Marine Biological Association of India*, 46(2): 162–168.

Chan, E. H. & A.K.B.M. Noor. 1986. Preliminary data on squids (Loliginidae) from the Matahari Expedition. *In*: A.K.M. Mohsin, M.I.H. Mohamed & M.A. Ambak, eds. Ekspedisi Matahari ‘85. A Study on the Offshore Waters of the Malaysian EEZ 3:221–227 pp.

Chancollon, O., C. Pusineri & V. Ridoux. 2006. Food and feeding ecology of northeast Atlantic swordfish (*Xiphias gladius*) off the Bay of Biscay. *ICES Journal of Marine Science*, 63(6): 1075–1085.

***Chantawong, P.** 1994. Squid light luring fishery in Phuket and Phang–nga provinces, Andaman Sea, Thailand. *National Research Council*, Thailand, 93: 184–194.

***Chantawong, P. & C. Suksawat.** 1997. Cephalopod distribution and abundance in the northern part of Phang-Nga Province, Thailand. *In*: J. Hylleberg, ed. Proceedings of the Seventh Workshop of the Tropical Marine Mollusc Programme, TMMP, on Central and West Java, Indonesia conducted at IPB, UNDIP, LIPI, 11–22 November 1996, Part 1, 17(1): 181–191 pp.

Chelli, M. & A. Voliani. 2004. Geographical distribution and abundance of *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in southeastern Ligurian Sea. *Biologia marina mediterranea*, 11(2): 569–572.

Chen, C.S. & T.S. Chiu. 2003. Variations of life history parameters in two geographical groups of the neon flying squid, *Ommastrephes bartramii*, from the North Pacific. *Fisheries Research*, 63 (3): 349–366.

***Chen, C.S., T.S. Chiu & W.B. Haung.** 2007a. The spatial and temporal distribution patterns of the Argentine short–finned squid, *Illex argentinus*, abundances in the southwest Atlantic and the effects of environmental influences. *Zoological Studies*, 46(1): 111–122.

*__Chen, C.S., W.B. Haung & T.S. Chiu.__ 2007b. Different spatiotemporal distribution of Argentine short–finned squid (*Illex argentinus*) in the southwest Atlantic during high-abundance year and its relationship to sea water temperature changes. *Zoological Studies*, 46(3): 362–374.

*__Chen, C.S., G.J. Pierce, J. Wang, J.-P. Robin, J.C. Poulard, J. Pereira, A.F.. Zuur, P.R. Boyle, N. Bailey, D.J. Beare, P. Jereb, S. Ragonese, A. Mannini & L. Orsi-Relini.__ 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: Trends in *Loligo* spp. abundance in the northeast Atlantic and possible environmental influences. *Fisheries Research*, 78(1): 44–54.

Chen, D.S., G. van Dykhuizen, J. Hodge & W.F. Gilly. 1996. Ontogeny of copepod predation in juvenile squid (*Loligo opalescens*). *Biological Bulletin (Woods Hole)*, 190: 69–81.

Chen, P. & J. Guo. 2001. Preliminary study on *Todaropsis eblanae* (Ball) of northern South China Sea. *J. Tropical Oceanography, (Redai Haiyang Xuebao)*, 20(2): 71–74.

Chen, X. 1997. Studies on some biological parameters of *Todarodes pacificus* in the central-southern Japan Sea. J*ournal Fisheries Science China; Zhongguo Shuichan Kexue*, 4(5): 29–32.

Chen, X. 1998. The fishing ground of *Nototodarus sloani* and its catch distribution around New Zealand waters. *Journal Shanghai Fishery University*, 7(2): 93–101.

Chen, X. 1999. Biology of *Nototodarus sloanii* around New Zealand waters. *Journal of Fisheries Science China*, 6(1): 27–32.

Chen, X. & T.S. Chiu. 2003. Variations of life history parameters in two geographical groups of the neon flying squid, *Ommastrephes bartramii*, from the North Pacific. *Fisheries Research Amsterdam*, 63(3): 349–366.

Chen, X. & J. Guo. 2000. A study on stock of *Ornithoteuthis volatilis* in waters of continental slope of northern South China Sea. *Tropic oceanology, Redai–Haiyang Guangzhou*, 19(3): 13–19.

Chen, X. & B. Liu. 2005. Analysis on catch of *Ommastrephes bartramii* in squid jigging fishery and the relationship between fishing ground and SST in the North Pacific Ocean in 2004. *Journal of Zhanjiang Ocean University*, 25(6): 41–45.

Chen, X. & J. Liu. 2007. Morphological analysis on population structure of *Sthenoteuthis oualaniensis* in the northwestern Indian Ocean. *Shanghai Shuichan Daxue Xuebao*, 16(2): 174–179.

Chen, X. & W. Qian. 2006. Study of the resource density distribution of *Symlectoteuthis oualaniensis* in the northwestern Indian Ocean. *Shanghai Shuichan Daxue Xuebao*, 13(3): 218–223.

Chen, X. & F. Shao. 2006. Study on the resource characteristics of *Symlectoteuthis oualaniensis* and their relationships with the sea conditions in the high sea of the northwestern Indian Ocean. *Zhongguo Haiyang Daxue Xuebao*, 36(4): 611–616.

Chen, X. & L. Xu. 2004. Analysis of relationship between fishing ground of *Ommastrephes bartramii* and surface water temperature and its vertical distribution from 150°E to 165°E in the northwestern Pacific. *Transactions of Oceanology and Limnology*, 2: 36–44.

Chen, X. & X. Zhao. 2005. Catch distribution of jumbo flying squid and its relationship with SST in the offshore waters of Chile. *Marine Fisheries*, 27(2): 173–176.

Chen, X. & X. Zhao. 2006a. Preliminary study on the catch distribution of *Dosidicus gigas* and its relationship with sea surface temperature in the offshore waters of Peru. *Journal of Shanghai Fisheries University*, 15(1): 65–70.

Chen, X. & X. Zhao. 2006b. The relationship between the distribution of production of squid *Illex argentinus* and sea surface temperature in the southwest Atlantic Ocean. *Dalian Shuichan Xueyuan Xuebao*, 20(3): 222–228.

Chen, X., J. Liu & Y. Li. 2005a. Trial on the broken strength of tentacles and arms of *Symplectoteuthis oualaniensis* in the northwestern Indian Ocean. *Marine Fisheries*, 27(4): 324–327.

Chen, X., J. Liu. & Q. Su. 2006a Current status and prospects of identification methods on the cephalopod population. *Shanghai Shuichan Daxue Xuebao*, 15(2): 228–233.

*__Chen, X., B. Liu. & Y. Wang.__ 2005b. Study on the distribution of production of *Illex argentinus* and its relationship with sea surface temperature in the southwest Atlantic Ocean in 2000. *Journal of Zhanjiang Ocean University*, 25(1): 29–34.

Chen, X., S. Tian & L. Xu. 2006b. Analysis on changes of surface water temperature in the spawning and feeding ground of *Ommastrephes bartramii* and its relationship with abundance index in the northwestern Pacific Ocean. *Shanghai Shuichan Daxue Xuebao*, 14(2): 168–175.

Chen, X., L. Xu & S. Tian. 2003a. Spatial and temporal analysis of *Ommastrephes bartramii* resources and its fishing ground in North Pacific Ocean. *Journal of fisheries of China/Shuichan Xuebao*, 27(4): 334–342.

Chen, X., W. Qian, L. Xu & S. Tian. 2003b. Comparison among annual positions of fishing grounds for *Ommastrephes bartramii* from 150°E to 165°E in the North Pacific. *Journal of Zhanjiang Ocean University*, 23(3): 26–32.

Chen, X., W. Qian, L. Xu & S. Tian. 2003c. Study on *Ommastrephes bartramii* fishing ground and forecasting model from 150°E to 165°E in the North Pacific Ocean. *Marine Fisheries Research [Haiyang Shuichan Yanjiu]*, 24(4): 1–6.

Cheng, J. & H. Huang. 2003. The relationship between environment characters and *Ommastrephes bartramii* fishing ground in the North Pacific. *Journal of Fishery Sciences of China*, 10(6): 507–512.

Cherel, Y. 2003. New records of the giant squid *Architeuthis dux* in the southern Indian Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 83(6): 1295–1296.

Cherel, Y. & G. Duhamel. 2003. Diet of the squid *Moroteuthis ingens* (Teuthoidea: Onychoteuthidae) in the upper slope waters of the Kerguelen Islands. *Marine Ecology Progress Series*, 250: 197–203.

Cherel, Y. & G. Duhamel. 2004. Antarctic jaws: cephalopod prey of sharks in Kerguelen waters. *Deep Sea Research (Part I, Oceanographic Research Papers)*, 51(1): 17–31.

Cherel, Y. & K.A. Hobson. 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 272(1572): 1601–1607.

Cherel Y. & N. Klages. 1997. A review of the food of albatrosses. *In*: G. Robertson, R. Gales, eds. Albatross biology and conservation. Surrey Beatty & Sons, Chipping Norton, 113–136 pp.

Cherel, Y. & G.L. Kooyman. 1997. Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctic. *Marine Biology*, 130(3): 335–344.

Cherel, Y. & H. Weimerskirch. 1995. Seabirds as indicators of marine resources: Black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters. *Marine Ecology Progress Series*, 1291–3): 295–300.

Cherel, Y. & H. Weimerskirch. 1999. Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new information from seabird predators. *Marine Ecology Progress Series*, 188: 93–104.

Cherel, Y., G. Duhamel & N. Gasco. 2004. Cephalopod fauna of subantarctic islands: New information from predators. *Marine Ecology Progress Series*, 266: 143–156.

Cherel, Y., H. Puetz & K.I. Hobson. 2002. Summer diet of king penguins (*Aptenodytes patagonicus*) at the Falkland Island, southern Atlantic Ocean. *Polar Biology*, 25(12): 898–906.

Cherel, Y., H. Weimerskirch & C. Trouve. 2000. Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Marine Ecology Progress Series*, 207: 183–199.

Cherel, Y., H. Weimerskirch & C. Trouve. 2002. Dietary evidence for spatial foraging segregation in sympatric albatrosses (*Diomedea* spp.) rearing chicks at alles Nuageuses, Kerguelen. *Marine Biology*, 141(6): 1117–1129.

Cherel, Y., R. Sabatie, M. Potier, F. Marsac & F. Menard. 2007. New information from fish diets on the importance of glassy flying squid (*Hyaloteuthis pelagica*) (Teuthoidea: Ommastrephidae) in the epipelagic cephalopod community of the tropical Atlantic Ocean. *Fishery Bulletin Seattle*, 105(1): 147–152.

Chesalin, M.V. 1993. Distribution and biology peculiarities of purpleback squid, *Sthenoteuthis oualaniensis* in the Arabian Sea. *Hydrobiology Journal*, 29(4): 16–27.

Chesalin, M.V. & V.E. Giragosov. 1993. Egg mass and embryonic development of the purpleback flying squid, *Sthenoteuthis oualaniensis*, (giant Arabian form) in the experimental condition. *Okeanologia*, 33(1): 116–120 (In Russian with English abstract).

Chesalin, M.V. & G.V. Zuev. 2002a. Fisheries perspectives of the squid, *Sthenoteuthis oualaniensis*, in the Arabian Sea. *In* B.G. Ivanov & Ch.M. Nigmatullin, eds. VI All-Russian Conference on Commercial Invertebrates (3–6 September 2002, Kaliningrad-Lesnoe). Theses of Reports. Moscow: VNIRO Publication: 174–176. (In Russian)

***Chesalin, M.V. & G.V. Zuev.** 2002b. Pelagic cephalopods of the Arabian Sea with an emphasis on *Sthenoteuthis oualaniensis*. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(1): 209–221.

Chesalin, M.V., G.E. Shulman, A.M. Shchepkina & G.I. Abolmasova. 1992. Dynamics of reserve matter content in the liver of oceanic squids of the genus *Sthenoteuthis* during maturation. *Marine Biology*, 1–2: 84–89.

***Chikuni, S.** 1983. Cephalopod resources in the Indo-Pacific region. *In*: J.F. Caddy, ed. Advances in Assessment of World Cephalopod Resources, *FAO Fisheries Technical Paper*, 231: 264–305.

Choe, S. 1966. On the eggs, rearing, habits of the fry and growth of some Cephalopods. *Bulletin of Marine Science*, 16: 330–348.

Choi, K.H., S.D. Hwang & J.I. Kim. 1997. Fishing conditions of common squid *Todarodes pacificus* Steenstrup in Korean waters. Spatio-temperal distribution of common squid related to changes in oceanographic conditions. *Journal of the Korean Fisheries Society*, 30(4): 513–522.

Choi, W. & C. Yau. 2006. Reproductive biology of *Uroteuthis (Photololigo) duvaucelii* in Hong Kong waters: or, the mystery of where squid spawn. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: 74 p.

Chojnacki, J. 1972. Length-weight relationship for squids *Illex illecebrosus* (Lesueur) and *Loligo pealei* (Lesueur). *Acta. Ichthyol Piscatoria*, 2(2): 99–103.

Chong, J., C. Oyarzyn, R. Galleguillos, E. Tarifeno, R. Sepulveda & C. Ibanez. 2006. Fishery biology parameters of jumbo squid *Dosidicus gigas* (Orbigny, 1835) (Cephalopoda: Ommastrephidae), in central Chile coast (29°S–40°S) during 1993–1994. *Gayana*, 69(2): 319–328.

Chotiyaputta, C. 1982. Squid fisheries of Thailand. IPFC (Indo Pacific Fishery Commission). Report of the Third Session of the Standing Committee on Resources Research and Development. Sidney, Australia, 28 April – 4 May 1982. *FAO Fisheries Report*, 275: 124–127.

***Chotiyaputta, C.** 1993a. Cephalopod Resources of Thailand. *In*: T. Okutani, R. O'Dor & T. Kubodera, eds. *Recent Advances in Fisheries Biology. Tokai University Press*, *Tokyo*, 71–80 pp.

***Chotiyaputta, C.** 1993b. A survey on diversity and distribution of juvenile squids in the inner and western Gulf of Thailand. *Thai Marine Fisheries Research Bulletin*, 4: 19–36.

Chotiyaputta, C. 1994. Distribution and abundance of juvenile and adult squids in the western Gulf of Thailand. *In*: A. Snidvongs, W. Utoomprukporn & M. Hungspreugs, eds. NRCT JSPS Joint Seminar on Marine Science. Bangkok Thailand Chulalongkorn Univ., 200–207 pp.

***Chotiyaputta, C.** 1997. Distribution, abundance, reproductive biology, age and growth of *Loligo chinensis* and *Loligo duvauceli* in the western Gulf of Thailand. *In*: D.A. Hancock, D.C. Smith, A. Grant & J.P. Beumer, eds. Developing and sustaining world fisheries resources. The state of science and management. Collingwood Australia CSIRO, 614–619 pp.

Chotiyaputta, C. & A. Yamrungreung. 1998. Trap fisheries for squid and their impact on spawning. *In* A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, Eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 285–291.

Chotiyaputta, C., P. Nootmorn & K. Jirapunpipat. 2002. Review of cephalopod fishery production and long term changes in fish communities in the Gulf of Thailand. *In* P.R. Boyle, M.A. Collins & G.J. Pierce,eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(1): 223–238.

Chou, L, A.M. Bright & S. Yeh. 1995. Stomach contents of dolphins (*Delphinus delphis* and *Lissodelphis borealis*) from North Pacific Ocean. *Zoological Studies*, 34(3): 206–210.

Chrachri, A. & R. Williamson. 1993. Electrical coupling between primary hair cells in the statocyst of the squid, *Alloteuthis subulata*. *Neuroscience Letters*, 163(1): 227–231.

Chrachri, A. & R. Williamson. 1998. Synaptic interactions between crista hair cells in the statocyst of the squid *Alloteuthis subulata*. *Journal of Neurophysiology*, 80(2): 656–666.

Chu, E.W. 1984. Sooty shearwaters off California: Diet and energy gain. *In*: D.N. Nettleship, G.A. Sanger & P.F. Springer, eds. *Marine birds: their feeding ecology and commercial fisheries relationships*, 64–71.

Chu, T. 2001. Biological characteristics of oceanic flying squid Sthenoteuthis oualaniensis in the offshore area of Vietnam. *Proceedings of Marine Fisheries Research*, 2: 219–247.

Chu, Y.-J., Y.-E. Ueng & C.-J. Chow. 1992. Comparative study on the characteristics of cephalopod mantle muscle for surimi-based products processing. *Journal of the Fisheries Society of Taiwan*, 19(1): 75–82.

***Chun, C.** 1900. *Aus den Tiefen des Weltmeeres: Schilderungen von der Deutschen Tiefsee-Expedition*. Jena: Gustav Fischer. 549 pp.

Chun, C. 1903a. *Aus den Tiefen des Weltmeeres. Second Edition*, Jena: Gustav Fischer. 592 pp.

***Chun, C.** 1903b. Uber Leuchtorgane und Augen von Tiefsee–Cephalopoden. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 13: 67–91, 14 figs.

***Chun, C.** 1906. System der Cranchien. *Zoologischer Anzeiger*, 31(2):82–86.

***Chun, C.** 1908. Uber Cephalopoden der Deutschen Tiefsee–Expedition. *Zoologischer Anzeiger*, 33(2): 86–89.

***Chun, C.** 1910a. Die Cephalopoden. Oegopsida. *Wissenschaftliche Eregebnisse der Deutschen Tiefsee Expedition auf dem Dampfer “Valdivia” 1898–1899*. 18(1):1–401, 32 figs, 2 text–pls, atlas of 61 pls.

Chun, C. 1910b. *The Cephalopoda, Part I: Oegopsida. Part II: Myopsida and Octopoda. German Deep Sea Expedition 1898–1899*. 18: 436 pp., Atlas of 95 pls (English Translation, 1975).

***Chun, C.** 1913. Cephalopoda. *Report on the scientific results of the “Michael Sars” North Atlantic Deep–sea Expedition 1910*. 3(1): 1–28, 11 figs, 2 pls.

***Chung, W.S. & C.C. Lu.** 2005. The influence of temperature and salinity on the statolith of the oval squid *Sepioteuthis lessoniana* Lesson, 1830 during early developmental stages. *Phuket Marine Biological Center Research Bulletin*, 66: 175–185, 4 figs.

Cincotta, D.E. 1983. The visual system of the squid, *Loligo opalescens*: functional implications of membrane structures. Dissertaton Abstracts International Part B: Science and Engineering 1983. 43(8): 201 pp.

Cinti, A., P.J. Baron & A.L. Rivas. 2004. The effects of environmental factors on the embryonic survival of the Patagonian squid *Loligo gahi*. *Journal of Experimental Marine Biology and Ecology*, 13(2): 225–240.

Clarke, A., P.G. Rodhouse & D.J. Gore. 1994. Biochemical composition in relation to the energetics of growth and sexual maturation in the ommastrephid squid *Illex argentinus*. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 344: 210–212.

Clarke, A., M.R. Clarke, L.J. Holmes & T.D. Waters. 1985. Calorific values and elemental analysis of eleven species of oceanic squids (Mollusca: Cephalopoda). *Journal of Marine Biological Association of the United Kingdom*, 65(4): 983–986.

***Clarke, M.R.** 1962. The identification of cephalopod. “beaks” and the relationship between beak size and total body weight. *Bulletin of the British Museum (Natural History),* to complete.

Clarke, M.R. 1964. Young stages of *Lepidoteuthis grimaldii* (Cephalopoda, Decapoda). *Proceedings of the Malacological Society of London*, 36: 69–78.

***Clarke, M.R.** 1966. A review of the systematics and ecology of oceanic squids. *Advances in Marine Biology*, 4: 91–300.

Clarke, M.R. 1967. A deep sea squid, *Taningia danae* Joubin, 1931. *Symposia of the Zoological Society of London*, 19: 127–143 [141].

Clarke, M.R. 1970. Growth and development of *Spirula spirula*. *Journal of the Marine Biological Association of the United Kingdom*, 50: 53–64.

***Clarke, M.R.** 1978. The cephalopod statolith. An introduction to its form. *Journal of the Marine Biological Association of the United Kingdom*, 58: 701–712.

***Clarke, M.R.** 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Report*, 37: 1–324.

Clarke, M.R. 1983. Cephalopod biomass – estimation from predation. *In* C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Proceedings of the workshop on the biology and resource potential of cephalopods. Memorial National Museum of Victoria*, 44: 95–107.

***Clarke, M.R.** 1986. A *handbook for the identification of cephalopod beaks*. Claredon Press, Oxford. 273 pp.

Clarke, M.R. 1988a. Evolution of buoyancy and locomotion in recent cephalopods. *In*: M.R. Clarke & E.R. Trueman, eds. *The Mollusca. Palaeontology and Neontology of Cephalopods. Academic Press*, London, Vol. 12: 203–213.

*__Clarke, M.R.__ 1988b. Evolution of recent cephalopods. *In*: M.R. Clarke & E.R. Trueman, eds. *The Mollusca. Palaeontology and Neontology of Cephalopods*. *Academic Press*, London, Vol. 12: 331–340.

Clarke. M.R. 1992a. Onychoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. *"Larval" and juvenile cephalopods: a manual for their identification. Smithsonian Contributions to Zoology*, 513: 127–138.

Clarke, M.R. 1992b Lepidoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. *"Larval" and juvenile cephalopods: a manual for their identification. Smithsonian Contributions to Zoology*, 513: 167.

Clarke, M.R. 1992c. Pholidoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. *"Larval" and juvenile cephalopods: a manual for their identification. Smithsonian Contributions to Zoology*, 513: 168–170.

Clarke, M.R. 1992d. Grimalditeuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. *"Larval" and juvenile cephalopods: a manual for their identification. Smithsonian Contributions to Zoology*, 513: 181–182.

*__Clarke, M.R. (ed).__ 1996a. The role of cephalopods in the world's oceans. *Philosophical Transactions of the Royal Society of London B*, 351: 977–1112.

*__Clarke, M.R.__ 1996b. The role of cephalopods in the world's oceans: general conclusion and the future. *Philosophical Transactions of the Royal Society of London B*, 351: 1105–1112.

Clarke, M.R. 1997. Cephalopods in the stomach of a sperm whale stranded between the islands of Terschelling and Ameland, Southern North Sea. *Bulletin de l' Institute Royal des Sciences Naturelles de Belgique*, 67: 53–55.

Clarke M.R. & T.K. Kristensen. 1980. Cephalopod beaks from the stomach of two northern bottlenose whales (*Hyperoodon ampullatus*). *Journal of the Marine Biological Association of the United Kingdom*, 60: 151–156

*__Clarke, M.R. & C.C. Lu.__ 1974. Vertical distribution of cephalopods at 30°N 23°W in the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 54: 969–984.

*__Clarke, M.R. & C.C. Lu.__ 1975. Vertical distribution of cephalopods at 18°N, 25°W in the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 55: 165–182.

Clarke, M.R. & C.C. Lu. 1995. Cephalopoda of Madeiran Waters. *Bolitim do Museu Municipal do Funchal*, Sup. 4: 181–200.

Clarke, M.R. & N. MacLeod. 1976. Cephalopod remains from sperm whales caught off Iceland. *Journal of the Marine Biological Association of the United Kingdom*, 56: 733–749.

Clarke, M.R. & N. MacLeod. 1982. Cephalopod remains from the stomach of sperm whales caught in the Tasman Sea. *Memoirs of the National Museum of Victoria*, 43: 25–42.

Clarke, M.R. & L. Maddock. 1988. Statoliths of fossil coleoid cephalopods. *In*: M.R. Clarke, E.R. Trueman, eds. The Mollusca, Vol. 12 . *Paleontology and Neontology of Cephalopods*, pp. 153–168.

*__Clarke, M.R. & G.E. Maul.__ 1962. A description of the "scaled" squid *Lepidoteuthis grimaldi* Joubin, 1895. *Proceedings of the Zoological Society of London*, 139(1): 97–118.

Clarke, M.R. & N. Merrett. 1972. The significance of squid, whale and other remains from the stomachs of bottom-living deep-sea fish. *Journal of the Marine Biological Association of the United Kingdom*, 52: 599–603.

Clarke, M.R. & P.L. Pascoe. 1985. The stomach contents of a Risso's dolphin (*Grampus griseus*) stranded at Thuriestone, South Devon. *Journal of the Marine Biological Association of United Kingdom*, 65(3): 663–665.

Clarke, M.R. & P.L. Pascoe. 1997. Cephalopod species in the diet of a sperm whale (*Physeter catodon*) stranded at Penzance, Cornwall. *Journal of the Marine Biological Association of the United Kingdom*, 77(4): 1255–1258.

Clarke, M.R. & P.L. Pascoe. 1998. The influence of an electric light on the capture of oceanic cephalopods by a midwater trawl. *Journal of the Marine Biological Association of the United Kingdom*, 78(2): 561–575.

Clarke, M.R. & M.A.C. Roeleveld. 1998. Cephalopods in the diet of sperm whales caught commercially off Durban, South Africa. *In*: A.I.L. Payne, M.R. Lipinski, M.R. Clarke, & M.A.C. Roeleveld, eds. Cephalopod Biodiversity, Ecology and Evolution. *South African Journal of Marine Science*, 20: 41–45.

Clarke, M.R. & C.F.E. Roper. 1998. Cephalopods represented by beaks in the stomach of a sperm whale stranded at Paekakariki, North Island, New Zealand. *South African Journal of Marine Science*, 20: 129–133.

Clarke, M.R. & F. Trillmich. 1980. Cephalopods in the diet of fur seals of the Galapagos Islands. *Journal of Zoology*, 190(2): 211–215.

***Clarke, M.R. & R.E. Young.** 1998. Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. *Journal of the Marine Biological Association of the United Kingdom*, 78(2): 623–641.

***Clarke, M.R., E.J. Denton & J.B. Gilpin-Brown.** 1979. On the use of ammonium for buoyancy in squids. *Journal of the Marine Biological Association of the United Kingdom*, 59: 259–276.

Clarke, M.R., N. MacLeod & O. Paliza. 1976. Cephalopod remains from the stomachs of sperm whales caught off Peru and Chile. *Journal of Zoology*, 180(4): 477–493.

Clarke, M.R., H.R. Martins & P. Pascoe. 1993. The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philosophical Transactions of the Royal Society of London*, B. 339: 67–82.

Clarke, R., O. Paliza & L. Anelio Aguayo. 1988. Sperm whales of the southeast Pacific. Part IV. Fatness, food and feeding. *Investigations on Cetacea*, 21: 53–195.

Clarke, M.R., D.C. Clarke, H.R. Martins & H.M. Silva. 1995. The diet of swordfish (*Xiphias gladius*) in Azorean waters. Arquipélago. *Life and Marine Sciences*, 13A: 53–69.

Clarke, M.R., D.C. Clarke, H.R. Martins & H.M. da Silva. 1996. The diet of the blue shark (*Prionace glauca* L.) in Azorean waters. Arquipélago. *Life and Marine Science*, 14A: 41–56.

Clarke, M.R., J.E. Fitch, T. Kristensen, T. Kubodera & L. Maddock. 1980. Statoliths of one fossil and four living squids (Gonatidae: Cephalopoda). *Journal of the Marine Biological Association of the United Kingdom*, 60: 326–347.

Clausen, A.P. & K. Puetz. 2002. Recent trends in diet composition and productivity of Gentoo, Magellanic and Rockhopper Penguins in the Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 12(1): 51–61.

Clausen, A. & K. Puetz. 2003. Winter diet and foraging range of gentoo penguins (*Pygoscelis papua*) from Kidney Cove, Falkland Islands. *Polar Biology*, 26(1): 32–40.

Coelho, M.L. 1985. Review of the influence of oceanographic factors on cephalopod distribution and life cycles. *In*: Biology and ecology of squids *Illex illecebrosus* and *Loligo pealei* in the northwest Atlantic. *Northwest Atlantic Fisheries Organ.*, Dartmouth, N.S., Canada, 9: 47–57.

Coelho, M.L. 1990. Gametogenesis in the squid *Illex illecebrosus*. *Journal of Cephalopod Biology*, 1(2): 75–99.

Coelho, M.L. 1991. Abundance and recruitment of cephalopods. *Bulletin of Marine Science*, 49(1–2): 661–662.

***Coelho, M.L. & R.K. O'Dor.** 1993. Maturation, spawning patterns and mean size at maturity in the short-finned squid *Illex illecebrosus*. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology. Tokai University Press*, pp. 81–91.

Coelho, M.L., S.S. Lopes & J.P. Andrade. 1995. Estimates of individual fecundity in the squid *Loligo vulgaris* (Cephalopoda: Loliginidae). *Copenhagen Denmark ICES*, 8 pp.

Coelho, M.L., K.A. Stobberup, R.K. O'Dor & E.G. Dawe. 1994. Life history strategies of the squid, *Illex illecebrosus*, in the northwest Atlantic. *Aquatic Living Resources*, 7(4): 233–246.

Coelho, M.L., P. Domingues, E. Balguerias, M. Fernández& J.P. Andrade. 1997. A comparative study of the diet of *Loligo vulgaris* (Lamarck, 1799) (Mollusca: Cephalopoda) from the south coast of Portugal and the Saharan Bank (Central- East Atlantic). *Fisheries Research*, 29: 245–255.

Coelho, M.L., J. Quintela, V. Bettencourt, G. Olavo & H. Villa. 1994. Population structure, maturation and fecundity of the squid *Loligo vulgaris* from southern Portugal. *Fisheries Research*, 21: 87–102.

***Cohen, A.C.** 1976. The systematics and distribution of *Loligo* (Cephalopoda: Myopsida) in the western North Atlantic with description of two new species. *Malacologia*, 15: 229–367.

Colbourne, E., E.G. Dawe, D.G. Parson, E.F. Murphy, W.R. Bowering, E.L. Dalley, J.T. Anderson, J.B. Dempson, D. Orr, D.E. Stansbury & G.P. Ennis (eds). 2002. A preliminary review of environmental-stock relationships for some species of marine organisms in NAFO waters of the Northwest Atlantic. *Science Council Research Document NAFO*, 2/34: 21 pp.

Coleman, N. 1984. Molluscs from the diet of commercially exploited fish off the coast of Victoria, Australia. *Journal of the Malacological Society of Australia*, 6(3–4): 143–154.

Collins, M.A. 1998. A female giant squid (*Architeuthis*) stranded on the Aberdeenshire coast. *Journal of Molluscan Studies*, 64(4): 489–492.

Collins, M.A. & G.J. Pierce. 1996. Size selectivity in the diet of *Loligo forbesi* (Cephalopoda: Loliginidae). *Journal of the Marine Biological Association of the United Kingdom*, 76: 1081–1090.

Collins, M.A., A.A. Allcock & M. Belchier. 2004. Cephalopods of the South Georgia slope. *Journal of the Marine Biological Association of the United Kingdom*, 84(2): 415–419.

Collins, M.A., G.M. Burnell & P.G. Rodhouse. 1995a. Age and growth of the squid *Loligo forbesi* (Cephalopoda: Loliginidae) in Irish waters. *Journal of the Marine Biological Association of the United Kingdom*, 75(3): 605–620.

Collins, M.A., G.M. Burnell & P.G. Rodhouse. 1995b. Reproductive strategies of male and female *Loligo forbesi* (Cephalopoda: Loliginidae). *Journal of the Marine Biological Association of the United Kingdom*, 75(3): 621–634.

Collins, M.A., G.M. Burnell & P.G. Rodhouse. 1995c. Recruitment, maturation, and spawning of *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Irish waters. *ICES Journal of Marine Science*, 52(1): 127–137.

Collins, M.A., G.J. Pierce & P.R. Boyle. 1997. Population indices of reproduction and recruitment in *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish and Irish waters. *Journal of Applied Ecology*, 34: 778 – 786.

Collins, M.A., C. Yau, L. Allcock & M.H. Thurston. 2001. Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 81(1): 105–117.

Collins, M.A., S. De Grave, C. Lordan, G.M. Burnell & P.G. Rodhouse. 1994. Diet of the squid *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Irish waters. *ICES Journal of Marine Science*, 51: 337–344.

Collins, M.A., C. Lordan, S. De Grave, G.M. Burnell & P.G. Rodhouse. 1993. Aspects of the diet of the squid *Loligo forbesi* Steenstrup in Irish waters. *Copenhagen Denmark ICES*, 1993 13 pp.

Collins, M.A., C. Lordan, K. Flannery, D.T.G. Quigley & F.G. Howard. 1997 New records of cephalopods caught in Irish and Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, 77: 561–564.

Collins, M.A., C. Yau, P.R. Boyle, D. Friese & U. Piatkowski. 2002. Distribution of cephalopods from plankton surveys around the British Isles. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. *Bulletin of Marine Science*, 71(1): 239–254.

*__Collins, M.A., P.R. Boyle, G.J. Pierce, L.N. Key, S.E. Hughes & J. Murphy.__ 1999. Resolution of multiple cohorts in the *Loligo forbesi* population from the west of Scotland. *ICES Journal of Marine Science*, 56: 500–509.

Collins, S. 1986. An evaluation of AFZ squid logbook data and samples collected by AFZ observers. *Technical Report, Marine Laboratory, Department of Sea Fisheries, Tasmania*, 14: 24 pp.

Collins, T.F.T. & I. Tsutsui. 2003 Neurotransmitters of mantle and fin muscles in spear squid *Loligo bleekeri*. *Journal of the Marine Biological Association of the United Kingdom*, 83(4): 857–860.

Colloca, F., P. Carpentieri, E. Balestri & G.D. Ardizzone. 2004. A critical habitat for Mediterranean fish resources: shelf-break areas with *Leptometra phalangium* (Echinodermata: Crinoidea). *Marine Biology*, 145: 1129–1142.

Colman, N. 1984. Molluscs from the diets of commercially exploited fish off the coast of Victoria, Australia. *Journal of Malacology Society, Australia*, 6(3–4): 143–154.

Connan, M., P. Mayzaud, M. Boutoute, H. Weimerskirch & Y. Cherel. 2005. Lipid composition of stomach oil in a procellariiform seabird *Puffinus tenuirostris*: implications for food web studies. *Marine Ecology Progress Series*, 290: 277–290.

Cooper J. 1979. Length-mass relationships, water content and energy values for two species of squid, *Loligo reynaudii* and *Todaropsis eblanae*, off the south-western cape. *Fishery Bulletin, South Africa*, 11: 43–45.

Cooper, J., S.R. Henley & N.T.W. Klages. 1992. The diet of the wandering albatross *Diomedea exulans* at sub-Antarctic Marion Island. *Polar Biology*, 12(5): 477–484.

Cordo, H.D. 2006. Structure and abundance of ling spawning stock (*Gepyterus blacodes*) in Argentine waters during the period 1995–2000. *INIDEP informe tecnico*, 60: 17 pp.

Cordova-Murueta, J.H. 2002. Protein digestion in penaeid shrimps. *Cent. De Investigaciones Biologicas del Noroeste*, 35 pp.

Cordova-Murueta, J.H. & F.L. Garcia-Carreno. 2002. Nutritive value of squid and hydrolyzed protein supplement in shrimp feed. *Aquaculture*, 210(1–4): 371–384.

Coria, N., M. Libertelli, R. Casaux & C. Darrieu. 2000. Inter-annual variation in the autumn diet of the Gentoo Penguin at Laurie Island, Antarctica. *Waterbirds*, 23(3): 511–517.

Cornwell C.J., J.B. Messenger & R.T. Hanlon. 1997. Chromatophores and body patterning in the squid *Alloteuthis subulata*. *Journal of the Marine Biological Association of the United Kingdom*, 77: 1243–1246.

Costa, P.A.S. & F.C. Fernandes. 1993a. Reproductive cycle of *Loligo sanpaulensis* (Cephalopoda: Loliginidae) in the Cabo Frio region, Brazil. *Marine Ecology Progress Series*, 101: 91–97.

Costa, P.A.S. & F.C. Fernandes. 1993b. Seasonal and spatial changes of cephalopods caught in the Cabo Frio (Brazil) upwelling ecosystem. *Bulletin of Marine Science*, 52(2): 751–759.

Cottrell, P.E. & A.W. Trites. 2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). *Marine Mammal Science*, 18(2): 525–539.

Craig, S., P.R. Boyle, K.D. Black & J. Overnell. 2002. Closing the lifecycle and developmental plasticity in squid. *Bulletin of Marine Science*, 71(2): 1117.

Creutzberg, F. & G.C.A. Duineveld. 1986. The role of the lesser weever *Trachinus vipera* and the dab *Limanda limanda* in the benthic system of the southern North Sea. *ICES Council Meeting*, 1986/L:4: 10 pp.

Croxall, J.P. & P.A. Prince. 1996. Cephalopods as prey. I. Seabirds. *Philosophical Transactions of the Royal Society of London, Series B*, 351: 1023–1043.

Croxall, J.P., P.A. Prince & K. Reid. 1997. Dietary segregation of krill-eating South Georgia seabirds. *Journal of Zoology*, 242(3): 531–556.

Croxall, J.P., A.J. Hall, H.J. Hill, A.W. North & P.G. Rodhouse. 1995. The food and feeding ecology of the white-chinned petrel *Procellaria aequinoctialis* at South Georgia. *Journal of Zoology*, 1995. 237(1): 133–150.

Cruz-Escalona, V.H., M.S. Peterson, L. Campos-Davila & M. Zetina-Rejon. 2005. Feeding habits and trophic morphology of inshore lizardfish (Synodus foetens) on the central continental shelf off Veracruz, Gulf of Mexico. *Journal of Applied Ichthyology*, 21(6): 525–530.

Csirke, J. 1987. The Patagonian fishery resources and the off shore fisheries in the Southwest Atlantic. *FAO Fisheries Technical Paper*, 286: 75 pp.

Csirke, J. 2005. Southwest Atlantic. Review of the state of world marine fishery resources. *FAO Fisheries Technical Paper*, 457: 65–75.

Cuccu, D., P. Addis, F. Damele & G. Manfrin Piccinetti. 2003. Primo censimento della teutofauna dei mari circondanti la Sardegna. *Biologia Marina Mediterranea*, 10: 795–798.

*****Cuccu, D., P. Jereb, P. Addis, A.A. Pendugiu, A. Sabatini & A. Cau.** 2005. Eccezionali catture di *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) nei mari sardi. *Biologia Marina Mediterranea*, 12(1): 500–503.

Cui, X., W. Fan & X. Shen. 2003. Development of the fishing condition analysis and forecasting sytem of *Ommastrephes bartramii* in the northwest Pacific Ocean. *Journal of Fisheries of China*, 27(6): 600–605.

Cullen, J.M., T.L. Mantague & C. Hall. 1992. Food of little penguins *Eudyptula minor* in Victoria: comparison of three localities between 1985 and 1988. *Emu*, 91: 318–341.

Cunha, M.M. & A. Moreno. 1994. Recent trends in the Portuguese squid fishery. *Fisheries Research*, 21: 231–242.

Cunha, M.M. da, A. Moreno & J.M.F. Pereira. 1995. Spatial and temporal occurrences of *Loligo* spp. in Portuguese waters. *Copenhagen Denmark ICES*, 16 pp.

Cushing, D.H. 1975. Marine ecology and fisheries. *London, Cambridge University Press*, 271 pp.

D'Aniello, A., G. D'Onofrio, M. Pischetola & J.M. Denucé. 1989. Effect of pH, salinity and Ca2+, Mg2+, K+ and SO4 2+ ions on hatching and viability of *Loligo vulgaris* embryo. *Aquaculture Research*, 36(9): 876–881.

D'Aniello, A., M. Pischetola, F. Vanacore, M. de Nicola & M. Denuce. 1990. Effect of mercury, cadmium and copper on the development and viability of *Loligo vulgaris* and *Sepia officinalis* embryos. *Italian Journal of Biochemistry*, 39(2): 130A–132A.

D'Onghia, G., P. Maiorano & P. Panetta. 1996. *Octopoteuthis sicula* (Rueppel, 1844) and *Brachioteuthis riisei* (Steenstrup, 1882) (Cephalopoda: Teuthoidea) from the northwestern Ionian Sea. *Bollettino Malacologico*, 5(8): 137–142.

D'Onghia, G., P. Maiorano & A. Tursi. 1997. Morphometric and biological data on *Ancistrocheirus lesueurii* (Orbigny, 1842) from the middle-eastern Mediterranean Sea. *Scientia Marina, Barcelona*, 61(3): 389–396.

D'Onghia, G., P. Maiorano. P. Panza. & P. Panetta. 1998. Occurrence of *Chtenopteryx sicula* (Verany, 1851) (Mollusca, Cephalopoda) in the north-western Ionian Sea. *Biologia Marina Mediterranea*, 5(1): 690–693.

D'Onghia, G., A. Matarrese, A. Tursi, P. Maiorano & P. Panetta. 1995. Osservazioni sulla teutofauna epi e mesobatiale nel Mediterraneo orientale (Mar Ionio e Mar Egeo). *Biologia Marina Mediterranea*, 2(2): 199–204.

Dai, Q.S., Z.B. Lu, M.J. Hong, F.S. Xiao & J.F. Zhu. 2004. Fauna composition of necton and fishery resources in the southern waters of Taiwan Strait. *Journal of Fishery Sciences of China/Zhongguo Shuichan Kexue*, 11(4): 360–366.

***Dall, W.H.** 1871. Descriptions of sixty new forms of mollusks from the West Coast of North America and the North Pacific Ocean, with notes on others already described. *American Journal of Conchology*, 7(2): 93–160, 4 pls.

Dalpadado, P., B. Ellertsen, B. Melle & H.R. Skjoldal. 1998. Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the Nordic seas. *Sarsia*, 83(2): 103–116.

Daly H.I., G.J. Pierce, M.B. Santos, J. Royer, S.K. Cho, G. Stowasser & J.P. Robin. 2001. Cephalopod consumption by trawl caught fish in Scottish and English Channelwaters. *Fisheries Research*, 52: 51–64.

Danakusumah, E. 1999. Studies on the biology and culture of the neritic squid *Sepioteuthis lessoniana* Lesson, 1830. Effects of stocking density on survival rate. *In*: J. Hylleberg, ed. *Proceedings of the 9th Workshop of the Tropical Marine Mollusc Programme, TMMP, Indonesia, 19–29–August 1998*, Part 1 19(1): 223–226.

Daneri, G.A., A. Carlini & P.G.K. Rodhouse. 2000. Cephalopod diet of the southern elephant seal, *Mirounga leonina*, at King George Island, South Shetland Islands. *Antarctic Science*, 12(1): 16–19.

Dauphin, Y. 2006. Structure and composition of the septal nacreous layer of *Nautilus macromphalus* L. (Mollusca, Cephalopoda). *Zoology*, 109(2): 85–95.

Davis, R.W., N. Jaquet, D. Gendron, U. Markaida, G. Bazzino & W. Gilly. 2007. Diving behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. *Marine Ecology Progress Series*, 333: 291–302.

Dawe, E.G. 1988. Length-weight relationships for short-finned squid in Newfoundland and the effect of diet on condition and growth. *Transactions of the American Fishery Society*, 117(6): 591–599.

Dawe, E.G. 1999. Migration patterns of short-finned squid and fishery effects inferred from research survey and fishery data. *Science Council Research Document NAFO*, 99/49, 11 pp.

Dawe, E.G. & P.C. Beck. 1985. Distribution and size of juvenile short-finned squid (*Illex illecebrosus*) (Mollusca: Cephalopoda) south of Newfoundland during winter. *In*: K.M. Mangold. & S.v. Bjoletsky, eds. *Biology and Distribution of Early Juvenile Cephalopods*, 35(3–4): 139–147.

Dawe, E.G. & P.C. Beck. 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. *ICES*, 1992, 10 pp.

Dawe, E.G. & P.C. Beck. 1997. Population structure, growth, and sexual maturation of short-finned squid (*Illex illecebrosus*) at Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(1): 137–146.

Dawe, E.G. & J.K.T. Brodziak. 1998. Trophic relationships, ecosystem variability, and recruitment. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 125–156.

***Dawe, E.G. & L.C. Hendrickson.** 1998. A review of the biology, population dynamics and exploitation of short-finned squid in northwest Atlantic Ocean, in relation to assessment and management of the resource. *Science Council Research Document NAFO*, 98/59: 33 pp.

***Dawe, E.G. & W.G. Warren.** 1993. Recruitment of short-finned squid in the northwest Atlantic Ocean and some environmental relationships. *Journal of Cephalopod Biology*, 2(2): 1–21.

Dawe, E.G., P.C. Beck & J. Drew. 1999. The fishery for short-finned squid (*Illex ellecebrosus*) in NAFO Subareas 3 and 4 in 1998. *Science Council Research Document NAFO*, 99/50: 13 pp.

*__Dawe, E.G., P.C. Beck & J. Drew.__ 2001. An update of the fishery for short-finned squid (*Illex illecebrosus*) in the Newfoundland area during 2000 with descriptions of some biological characteristics. *Science Council Research Document NAFO*, 01/57: 8 pp.

Dawe, E.G., W.R. Bowering & J.B. Joy. 1999. Predominance of squid (*Gonatus* spp.) in the diet of Greenland halibut (*Reinhardtius hippoglossoides*) on the deep slope of the northeast Newfoundland continental shelf. *University of Bergen Norway Department of Fisheries and Marine Biology*, 6 pp.

Dawe, E.G., E.B. Colbourne & K.F. Drinkwater. 1998a. Environmental effects on short-finned squid recruitment to Canadian fishing areas. *Science Council Research Document NAFO*, 98/54: 14 pp.

Dawe, E.G., E.B. Colbourne & K.F. Drinkwater. 1998b. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). *Council Meeting of the International Council for the Exploration of the Sea*, Sept. 1998.

Dawe, E.G., E.L. Dalley & W.W. Lidster. 1994. Fish prey spectrum of short-finned squid (*Illex illecebrosus*) at Newfoundland. *In*: J.S. Campbell, P. Schwinghamer & P.E.K. Symons, eds. *Selected Proceedings of the Symposium on the Biology and Ecology of Northwest Atlantic cod*, 54(1): 200–208.

Dawe, E.G., L.C. Hendrickson & M.A. Showell. 2000. An update to commercial catch and survey indices for short-finned squid (*Illex illecbrosus*) in the northwest Atlantic for 1999. *Science Council Research Document NAFO*, 00/37: 7 pp.

*__Dawe, E.G., G.W. Marshall & M.C. Mercer.__ 1992. Analysis of length, sex and maturity data for short-finned squid (*Illex illecebrosus*) from samples collected at Newfoundland, Canada, 1965–1988. *Canadian Technical Report of Fishery and Aquatic Science*, 1860: 57 pp.

Dawe, E.G., P.C. Beck, J.J. Drew & A.L. Pardy. 2004. Biological characteristics of squid (*Illex illecebrosus*) in the Newfoundland area (NAFO Subarea 3) during 2001–2003. *Science Council Research Document NAFO*, 0 4/52, 10 pp.

Dawe, E.G., P.C. Beck, H.J. Drew & G.H. Winters. 1981. Long distance migration of a short-finned squid, *Illex illecebrosus*. *Journal of North Atlantic Fisheries Science*, 2: 75–76.

Dawe, E.G., J.C. Shears, N.E. Balch & R.K. O'Dor. 1990. Occurrence, size, and sexual maturity of long-finned squid (*Loligo pealei*) at Nova Scotia and Newfoundland, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 1830–1835.

*__Dawe, E.G., L.C. Hendrickson, E.B. Colbourne, K.F. Drinkwater & M.A. Showell.__ 2007. Ocean climate effects on the relative abundance of short-finned (*Illex illecebrosus*) and long-finned (*Loligo pealeii*) squid in the northwest Atlantic Ocean. *Fisheries Oceanography*, 16(4): 303–316.

*__Dawe, E.G., L.C. Hendrickson, E.B. Colbourne, M.A. Showell, D.D. Jones & D.A. Methven.__ 2001. Squids as potential indicators species of environmental or ecosystem change in the Northwest Atlantic Ocean. *ICES Council Meeting/K:07 16 pp.*

Dawe, E.G., L.C. Hendrickson, E.B. Colbourne, M.A. Showell, K.F. Drinkwater, D.D. Jones & D.A. Methven. 2002. Environmental regulation of the relative abundance of two squid species in the Northwest Atlantic Ocean, *Illex ellecebrosus* and *Loligo pealei*. *Science Council Research Document NAFO*, 2/40: 16 pp.

Dayaratne, P. 1993. Exploitation of small pelagic fish resources by the purse seiners in the southwest coast of Sri Lanka. *Journal of the Marine Biological Association of India*, 35(1–2): 39–45.

de Gurjao, L.M., F.N. de-Andrade, A. Manuel, R.A. de-Santos & P. Cascon. 2004. *Revista Biociencias Taubate*, 10(1–2): 40–45.

de Heij, A. & R.P. Baayen. 1999. Seasonal distribution of the cephalopod *Alloteuthis subulata* in the central and southern North Sea. *Basteria*, 63(4/6): 129.

de Heij, A. & R.P. Baayen. 2006. seasonal distribution of cephalopod species living in the central and southern North Sea. *Basteria*, 69(4–6): 91–119).

de la Cruz-Gonzalez, F.J., E.A. Aragon-Noriega, J.I. Urciaga-Garcia, C.A. Salinas-Zavala, M.A. Cisneros-Mata & L.F. Beltran-Morales. 2007. Socioeconomic analysis of the shrimp and giant squid fisheries in the Northeastern of Mexico. *Interciencia*, 32(3): 144–150.

de Oliveira Santos, M.C., S. Rosso, R.A. Dos Santos, S.H.B. Lucato & M. Bassoi. 2002. Insights on small cetacean feeding habits in southeastern Brazil. *Aquatic Mammals*, 28, no. 1, pp. 38–45.

Deagle, B.E., S.N. Jarman, D. Pemberton & N.J. Gales. 2005. Genetic screening for prey in the gut contents from a giant squid (*Architeuthis* sp.). *Journal of Heredity*, 96(4): 417–423.

***Debose, J.L. & G.A. Nevitt.** 2006. Seasonal aggregations of Roper's inshore squid associated with coral spawning. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 57: 1014–1015.

***Degner E.** 1925. Cephalopoda. *Report on the Danish Oceanographical Expeditions 1908 to 1910 to the Mediterranean and Adjacent Seas*, 2(9): 1–94, 52 figs.

***DeKay, J.E.** 1843. Zoology of New York or the New York Fauna. Part V. Mollusca. Albany NY. *Carroll and Cook*, 271 pp., 40 pls.

***Dell, R.K.** 1951. A new species of squid, *Histioteuthis cookiana* from New Zealand waters. *Zoology Publications from Victoria University College*, 14: 1–6.

***Dell, R.K.** 1959. Some additional New Zealand cephalopods from Cook Straight. *Zoology Publications from Victoria University of Wellington*, 25: 1–12, 8 figs.

Dell, R.K. 1970. A specimen of the giant squid *Architeuthis* from New Zealand. *Records of the Dominion Museum*, 7(4): 25–36.

Demarcq, H. & V. Faure. 2000. Coastal upwelling and associated retention indices derived from satellite SST. Application to Octopus vulgaris recruitment. *Oceanologica Acta*, 23: 391–408.

Demir, M. 1952. The invertebrate Benthos of the Littoral of the Sea of Marmara closer to the Bosphorus. *Hidrobiol. Mecm. Istambul Ser. A*, 2: 615 pp.

Denis, V. & J.P. Robin. (dir.) 2000. Spatio-temporal pattern in cephalopod resources exploited by the French Atlantic Fishery . Empirical models of abundance based on environmental parameters. *Caen France Universite de Caen Basse Normandie, IBBA*, 2000: 293 pp.

Derby, C.D., C.E. Kicklighter, P.M. Johnson & X. Zhang. 2007. Chimical composition of inks of diverse marine mollusks suggests convergent chemical defenses. *Journal of Chimical Ecology*, 33(5): 1105–1113.

Desportes, G. & R. Mouritsen. 1988. Diet of the pilot whale, *Globicephala* melas, around the Faroe islands. *ICES Council Meeting,* 1988/N: 12.

Desportes, G. & R. Mouritsen. 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. *Report of the International Whaling Commission*, (special issue 14): 305–324.

Diaz Uribe, J.G., A. Hernandez Herrera, E. Morales Bojorquez, S. Martinez Aguilar, M.C. Suarez Highera & A. Hernandez Lopez. 2006. Histological validation of the gonadal maturation stages of female jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. *Ciencias Marinas*, 32(1A): 23–31.

Dickson, J., S.A. Morley & T. Mulvey. 2004. New data on *Martialia hyadesi* feeding in the Scotia Sea during winter; with emphasis on seasonal and annual variability. *Journal of the Marine Biological Association of the United Kingdom*, 84(4): 785–788.

Didenko, V.D. 1991a. Biological resources of cephalopods in the pelagic zone of the Okhotsk Sea during the winter season of 1990/91. *In: Rational Use of Bioresrouces of the Pacific Ocean. Communication of the All USSR Conference.* Abstract. 89–90. [In Russian].

Didenko, V.D. 1991b. Biological resources of cephalopods in the western Bering Sea during the autumn season of 1990. *In: Rational Use of Bioresources of the Pacific Ocean. Communications of the All USSR Conference.* Abstract 90–92. [In Russian].

***Diekmann, R. & Piatkowski, U.** 2002a. Early life stages of cephalopods in the Sargasso Sea: Distribution and diversity relative to hydrographic conditions. *Marine Biology*, 141(1): 123–130.

***Diekmann, R. & U. Piatkowski.** 2002b. Species composition and distribution of paralarval cephalopods in the subtropical North Atlantic Ocean with an emphasis on seamounts. *Bulletin of Marine Science*, 71(2): 1118.

Diekmann, R. & U. Piatkowski. 2004. Species composition and distribution patterns of early life stages of cephalopods at Great Meteor Seamount (subtropical North-east Atlantic). *Archive of Fishery and Marine Research*, 51(1–3): 115–131.

***Dillane, E., P. Galvin, J. Coughlan, M. Lipinski & T.F. Cross.** 2005. Genetic variation in the lesser flying squid *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in east Atlantic and Mediterranean waters. *Marine Ecology Progress Series*, 292: 225–232.

Dillane, E., P. Galvin, J. Coughlan, G.P. Rodhouse & F.T. Cross. (2000). Polymorphic variable number of tandem repeat (VNTR) loci in the ommastrephid squid, *Illex coindetii* and *Todaropsis eblanae*. *Molecular Ecology*, 9: 1002–1004.

***Dilly, P.N.** 1972. *Taonius megalops*, a squid that rolls up into a ball. *Nature, London*, 237(5355): 403–404.

Dilly, P.N. 1976. The structure of some cephalopod statoliths. *Cell Tissue Research*, 175(2): 147–16.

Dilly, P.N. & P.J. Herring. 1974. The ocular light organ of *Bathothauma lyromma* (Mollusca: Cephalopoda). *Journal of Zoology*, 172(1): 81–120.

Dilly, P.N. & M. Nixon. 1976a. Growth and development of *Taonious megalops* (Mollusca, Cephalopoda, and some phases of its life cycle. *Journal of Zoology*, 179(1): 19–83.

Dilly, P.N. & M. Nixon. 1976b. The dermal tubercles of *Cranchia scabra* Mollusca, Cephalopoda); surface structure and development. *Journal of Zoology, London*, 179(3): 291–295.

Dilly, P.N., M. Nixon & J.Z. Young. 1977. *Mastigoteuthis* the whip-lash squid. *Journal of Zoology, London*, 181: 527–559.

Dimarco, F.P. & R.T. Hanlon. 1997. Agonistic behavior in the squid *Loligo plei* Loliginidae, Teuthoidea): Fighting tactics and the effects of size and resource value. *Ethology*, 103(2): 89–108.

Dimmlich, W.F. & F.E. Hoedt. 1998. Age and growth of the myopsid squid *Loliolus noctiluca* in Western Port, Victoria, determined from statolith microstructure analysis. *Journal of the Marine Biological Association of the United Kingdom,* 78: 577–586.

Dohmoto, N., K.C. Wang, T. Mori, I. Kimura, T. Koriyama & H. Abe. 2001. Development of a new type fish sauce using the soy sauce fermentation method. *Bulletin of the Japanese Society of Scientific Fisheries*, 67(6): 1103–1109.

Dolar, M.L.L., W.A. Walker, G.L. Kooyman & W.F. Perrin. 2003. Comparative feeding ecology of spinner dolphins (*Stenella longirostris*) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu Sea. *Marine Mammal Science*, 19(1): 1–19.

Dolganova, N. & A. Lazhentsev. 2006. Feeding of mass nekton species in the epipelagic waters of the northwestern Japan Sea. *PICES XV. Book of Abstracts*, 137 p.

Dollfus, R.Ph. 1958. Copépodes, Isopodes et Helminthes parasites de Céphalopodes de la Méditerranée et de l'Atlantique européen. *In*: Faune Marine des Pyrénées Orientales, 61–72 pp.

Domaschenz, P. & Y. Zunic. 2006. Management of the southern suid jig fishery. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 58.

***Dong, Zh.** 1978. On the geographical distribution of cephalopods in Chinese waters. *Oceanol. Limnol. Sinica*, 9: 108–116 [in Chinese with English abstract].

Dong, Zh. 1988. Cephalopod larvae from the central equator waters of the Pacific. *Tropical Oceanology. Redai–Haiyang*, 7(3): 80–83.

Dong, Zh. 1996. On the present status and exploratory problems of resource of *Todarodes pacificus* in the Yellow Sea. *Marine Science Haiyang, Kexue*, 6: 34–38.

Dong, Zh., Y. Zheng & S. Zhu. 1988. Cephalopod larvae from the southern East China Sea. J*ournal of Fisheries, China Shuichan–Xuebao*, 12(1): 51–55.

Dong, Zh., J. Guo, R. Lue & Y. Li. 1981. Cephalopod larvae from the northern South China Sea. *Oceanology et Limnologia Sinica*, 12(5): 457–462.

D'Onghia, G., A. Matarrese, A. Tursi & P. Maiorano. 1996. Cephalopod collected by bottom trawling in the North Aegean Sea (Eastern Mediterranean). *Oebalia*, 22: 33–46.

Dorfer, K.A., M.J. Roberts & D. Baird. 2000. The influence of water turbidity and surface waves on squid catches. 10th Southern African Marine Science Symposium, SAMSS 2000: Land, Sea and People in the new Millennium, Abstracts, 1 p.

***Dorneles, P.R., J. Lailson-Brito, R.A. dos Santos, P.A. Silva da Costa, O. Malm, A.F. Azevedo & J.P. Machado Torres.** 2007. Cephalopods and cetaceans as indicators of offshore bioavailablility of cadmium off Central South Brazil Bight. *Environmental Pollution*, 148(1): 352–359.

Dragovich, A. & J.A. Kelly. 1967. Occurrence of the squid, *Lolliguncula brevis*, in some coastal waters of western Florida. *Bulletin of Marine Science*, 17: 840–844.

Drapeau, L., L. Pecquerie, P. Freon & L.J. Shannon. 2004. Quantification and representation of potential spatial interactions in the southern Benguela ecosystem. *African Journal of Marine Science*, 26: 141–159.

*****Drew, G.A.** 1911. Sexual activities of the squid *Loligo pealii* (Les.). I. Copulation, egg-laying and fertilization. *Journal of Morphology*, 22: 327–360.

*****Drew, G.A.** 1919. Sexual activities of the squid *Loligo pealii* (Les.). II. The spermatophore. *Journal of Morphology*, 32: 379–432.

Dudnik, Yu.I., A.M. Orlov, S.T. Kim & S.N. Tarasyuk. 1995. Fishery resources of the continental slope off northern Kurils. *Rybn. Khoz.*, 1: 24–28.

Duffy, C.A.J. 1997. Further records of the goblin shark, *Mitsukurina owstoni* (Lamniformes: Mitsukurinidae), from New Zealand. N.Z. *Journal of Zoology*, 24(2): 167–171.

Dunning, M.C. 1982. Squid and cuttlefish resources of Australian waters. IPFC (Indo-Pacific Fishery Commission) Report of the Third Session of the Standing Committee on Resources Research and Development. Sidney, Australia, 28 April– 4 May 1982. *FAO Fisheries Report*, 175: 103–108.

*****Dunning, M.C.** 1988a. Distribution and comparative life history studies of deepwater squid of the family Ommastrephidae in the Australasian waters. Doctoral Thesis, University of Queensland, Brisbane, Queensland, Australia.

*****Dunning, M.C.** 1988b. T*odarodes pacific pusillus* new subspecies (Cephalopoda, Ommastrephidae) from northern Australian waters. *Memoirs of the Museum of Victoria*, 49: 149–157.

*****Dunning, M.C.** 1988c. First records of *Nototodarus hawaiiensis* (Berry, 1912) (Cephalopoda, Ommastrephidae) from northern Australia with a reconsideration of the identity of *N. sloani philippinensis* Voss 1962. *Memoirs of the Museum of Victoria*, 49(1): 159–168.

Dunning, M.C. 1993. Summer populations of *Ommastrephes bartramii* (Lesueur, 1821) and *Todarodes filippovae* Adam, 1975 (Cephalopoda; Ommastrephidae) from the Tasman Sea. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology. Tokai Univerity Press, Tokyo:* 97–118.

*****Dunning, M.C.** 1998a. An overview of the fisheries biology and resource potential of *Ommastrephes bartramii* (Cephalopoda; Ommastrephidae) in the Southern Hemisphere. *In*: T. Okutani, ed. *Contributed Papers of the International Symposium on Large Pelagic Squids*. Tokyo: JAMARC Publication: 65–76.

*****Dunning, M.C.** 1998b. A review of the systematics, distribution, and biology of the arrow squid genera *Ommastrephes* Orbigny, 1835, *Sthenoteuthis* Verrill, 1880, and *Ornithoteuthis* Okada, 1927 (Cephalopoda: Ommastrephidae). *In*: N.A. Voss, M. Vecchione, R.B. Toll & M.J. Sweeney, eds. Systematics and Biogeography of Cephalopods, Vol. 2. *Smithsonian Contributions to Zoology*, 586: 425–433.

*****Dunning, M.C.** 1998c. Zoogeography of arrow squids (Cephalopoda: Ommastrephidae) in the Coral and Tasman Seas, southwestern Pacific *In:* N.A. Voss, M. Vecchione, R.B. Toll & M.J. Sweeney, eds. Systematics and Biogeography of Cephalopods, Vol. 2, *Smithsonian Contributions to Zoology*, 586: 435–453.

*****Dunning, M.C.** 1998d. Loliginidae. *In*: K.E. Carpenter & V.H. Niem, eds. The living marine resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks. *FAO Species Identification Guide for Fishery Purposes*. Rome, FAO. pp. 764–780.

*****Dunning, M.C.** 1998e. Enoploteuthidae. *In*: K.E. Carpenter & V.H. Niem eds. The living marine resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks. *FAO Species Identification Guide for Fishery Purposes*. Rome, FAO. pp. 781–783.

*****Dunning, M.C.** 1998f. Ommastrephidae. *In*: K.E. Carpenter & V.H. Niem eds. The living marine resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks. *FAO Species Identification Guide for Fishery Purposes*. Rome, FAO. pp. 788–796.

*****Dunning, M.C.** 1998g. Mastigoteuthidae. *In*: K.E. Carpenter & V.H. Niem eds. The living marine resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks. *FAO Species Identification Guide for Fishery Purposes*. Rome, FAO. pp. 799.

*****Dunning, M.C. & S.B. Brandt.** 1985. Distribution and life history of deep-water squid of commercial interest from Australia. *Australian Journal of Marine and Freshwater Research*, 36: 343–359.

*Dunning, M.C. & E.C. Förch.** 1998. A review of the systematics, distribution and biology of arrow squids of the genus *Nototodarus* Pfeffer, 1912 (Cephalopoda: Ommastrephidae). *In*: N.A. Voss, M. Vecchione, R.B. Toll & M.J. Sweeney, eds. Systematics and Biogeography of Cephalopods, Vol. 2. *Smithsonian Contributions to Zoology*, 586: 393–404.

*Dunning, M.C. & C.C. Lu.** 1998. Order Teuthoidea. *In*: P.L. Beesley, G.J.B. Ross, & A. Wells, eds. *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5.* CSIRO Publishing: Melbourne, Part A xvi: 515–542.

*Dunning, M.C. & J.H. Wormuth.** 1998. The Ommastrephid squid Genus Todarodes: a review of systematics, distribution, and biology (Cephalopoda: Teuthoidea), *In*: N.A. Voss, M.Vecchione, R.B. Toll & M.J. Sweeney, eds. Systematics and Biogeography of Cephalopods, Vol. 2, *Smithsonian Contributions to Zoology*, 586: 385–391.

*Dunning, M.C., M.R. Clarke & C.C. Lu.** 1993. Cephalopods in the diet of oceanic sharks caught off eastern Australia. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*: 119–131.

Dunning, M., S. McKinnon, C.C. Lu & J. Yeatman. 1994. Demersal cephalopods of the Gulf of Carpentaria, Australia. *Australian Journal of Marine and Freshwater Resources*, 45: 351–374.

Durholtz, M.D. & M.R. Lipinski. 2000. Influence of temperature on the microstructure of statoliths of the thumbstall squid *Lolliguncula brevis*. *Marine Biology*, 136(6): 1029–1037.

Durholtz, M.D., R.H. Kretsinger & M.R. Lipinski. 1999. Unique proteins from the statoliths of *Lolliguncula brevis* (Cephalopoda: Loliginidae). *Comparative Biochemistry and Physiology*, B, 123B(4): 381–388.

Durholtz, M.D., M.R. Lipinski & J.G. Field. 2002. Laboratory validation of periodicity of incrementation in statoliths of the South African chokka squid *Loligo vulgaris reynaudii* (d'Orbigny, 1845): a re-evaluation. *Journal of Experimental Marine Biology and Ecology*, 279(1–2): 41–59.

Durholtz, M.D., M.R. Lipinski, W.J. Przybylowicz & J. Mesjasz-Przybylowicz. 1997. Nuclear microprobe mapping of statoliths of chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845. *The Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 193(2): 125–140.

Dürr J. & J.A. González. (2002) Feeding habits of *Beryx splendens* and *Beryx decadactylus* (Berycidae) off the Canary Islands. *Fisheries Research*, 54: 363–374.

Durward, R.D., E. Vessey, R.K. O'Dor & T. Amaratunga. 1979. Maturation index and fecundity for female squid, *Illex illecebrosus* (Le Sueur, 1821). *ICNAF, Research Bulletin*, 14: 67–72.

Easton, D.J. 1989. An overview of the New Zealand squid catching sector. *The First World Cephalopods Conference, Lisbon, Portugal*, pp. 95–102.

Ebert, D.A., L.J.V. Compagno & P.C. Cowley. 1992. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. *In* A.I.L. Payne, ed. Benguela trophic functioning. *South Africa*, 12: 601–609.

*Ehrenberg, C.G.** 1831. Animalia invertebrata exclusis insects. Volume 4, unpaginated [126 pages]. *In*: C.G. Ehrenberg, 1828–1845. Symbolae Physicae, seu Icones et descriptiones Corporum Nauralium novorum aut minus cognitorum... P.C. Hemprich et C.G. Ehrenberg... *Pars Zoologica*. 4 volumes, unpaginated. Berolini.

Ehrhardt, N.M. 1991. Potential impact of a seasonal migratory jumbo squid (*Dosidicus gigas*) stock on a Gulf of California sardine (*Sardinops sagax caerulea*) population. *Bulletin of Marine Science*, 49(1): 325–332.

Ehrhardt, N.M., P.S. Jacquemin, F. Garcia, G. Gonzales, J.M. Lopez, J. Ortiz & A. Solis. 1983. Summary of the fishery and biology of the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. *In* C.F.E. Roper, C.C. Lu & F.G. Hochberg, edrs. *Proceedings of the workshop on the biology and resource potential of cephalopods. Memorial National Museum Victoria*. 44: 305–311.

*Ehrhardt, N.M., A. Solis, J. Pierre, J. Ortiz, P. Ulloa, G. Gonzalez & F. Garcia.** 1986. Biological analysis and stock assessment of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico during 1980. *Ciencias Pesqueras*, 5: 63–76.

Elizarov, A.A. 1996. Fishery biology of the squid *Berryteuthis magister* and slope fish communities in the western Bering Sea. Scientific results of the VNIRO expedition in 1993–1995 under the joint Russian–Japanese research program on *B. magister* in the Bering Sea. *VNIRO Russia*. 164 pp.

Elliott, W. & M. Samame. 2001. Structure of demersal system during the autumn evaluation RV Jose Olaya Balandra cruise 2004–05. Informe. *Instituto del Mar del Peru*, 160: 79–97.

Ellis, R. 1997. The models of *Architeuthis*. *Curator*, 40(1): 30–55.

Ellis, R. 1998. The Search for the Giant Squid. *The Lyons Press*, 322 pp.

Elorduy Garay, J.F. & J. Caraveo Patino. 1994. Feeding habits of the ocean whitefish, *Caulolatilus princeps* Jenyns 1842 (Pisces: Branchiostegidae), in La Paz, B.C.S. *Mexico. Ciencias Marinas*, 20(2): 199–218.

Emery, A.M., L.R. Noble & P.R. Boyle. 2002. Squid family values: Multiple paternity of *Loligo forbesi* egg strings examined. *Bulletin of Marine Science*, 71(2): 1119.

Emery, A.M., I.J. Wilson, S. Craig, P.R. Boyle & L.R. Noble. 2001. Assignment of paternity groups without access to parental genotypes: multiple mating and developmental plasticity in squid. *Molecular Ecology*, 10(5): 1265–1278.

Emery, A.M., P.W. Shaw, E.C. Greatorex, P.R. Boyle & L.R. Noble. 2000. New microsatellite markers for assessment of paternity in the squid *Loligo forbesi* (Mollusca: Cephalopoda). *Molecular Ecology*, 9(1): 110–112.

Emmett, R.L. & R.D. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. *In*: J.H. Helle, Y. Ishida, D. Noakes & V. Radchenko, eds. Recent changes in ocean production of Pacific salmon. *NPAFC Bulletin*, 2: 11–20.

Emslie, S.I. & J.I. McDaniel. 2002. Adelie penguin diet and climate change during the middle to late holocene in northern Marguerite Bay, Antarctic Peninsula. *Polar Biology*, 25(3): 222–229.

Emslie, S.D. & E.J. Woehler. 2005. A 9000 year record of Adelie penguin occupation and diet in the Windmill Islands, East Antarctica. *Antarctic Science*, 17(1): 57–66.

***Engeser, T. & K. Bandel.** 1988. Phylogenetic classification of coleoid cephalopods. *In*: J. Wiedman & J. Kullman, eds. Cephalopods Present and Past. *Schweizerbartsche Stuttgart*, pp. 105–115.

Eno, N.C. 1994. The morphometrics of cephalopod gills. *Journal of the Marine Biological Association of the United Kingdom*, 74(3): 687–706.

Erikstad, K.E. 1989–90. Winter diets of four seabird species in the Barents Sea after a crash in the capelin stock. *Polar Biology*, 10: 619–627.

Estrella, C., R. Guevara-Carrasco, W. Avila, J. Palacios & A. Medina. 2000. Statistic report on hydrobiological resources of artisanal fishery, by species, arts, ports, coves and months during the second semester of 1999. *Informe Instituto del Mar del Peru Callao*, 151: 194 pp.

Estrella, C., J. Palacios, W. Avila, A. Medina & R. Guevara-Carrasco. 2000. Statistical report on the hydrobiological rsources of the marine artisanal fishery by species, gear, month and landing place during the first semester of 2000. *Informe Instituto del Mar del Peru*, 158: 157 pp.

Evans, D.H. & P.G. Wares. 1972. Food habits of striped marlin and sailfish off Mexico and southern California. *Research Report of U.S. Fish and Wildlife Service*, 76: 1–10.

Evans, K. 1986. Arrow squid behaviour and vulnerability to netting techniques. *Technical Report, Marine Laboratory, Department of Sea Fisheries, Tasmania*, 12: 23 pp.

Evans, K. & M.A. Hindell. 2004. The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters. *ICES Journal of Marine Science*, 61: 1313–1329.

Fagundez, S.B. & G. Robaina. 1992. Effects of temperature, salinity and photoperiod on the embryonic development of the squid *Sepioteuthis sepioidea* (Blainville, 1823). *Memorias de la Sociedad de Ciencias Naturales La Salle*, (52)137: 93–103.

Falandysz, J. 1990. Mercury content of squid Loligo opalescens. *Food Chemistry., 38(3): 171–177.*

Falandysz, J. 1992. Macroelements content of common Pacific squid (*Loligo opalescens*). *Z. Lebensm. Unters. Forsch.*, 195(5): 423–425.

***Falcon, L.I., M. Vecchione & C.F.E. Roper.** 2000. Paralarval gonatid squids (Cephalopoda: Oegopsida) from the mid-North Atlantic Ocean. *Proceedings of the Biological Society of Washington*, 113(2): 532–541.

Falk, K. & J. Durinck. 1993. The winter diet of thick-billed murres, *Uria lomvia*, in western Greenland, 1988–1989. *Canada Journal of Zoology*, 71(2): 264–272.

Falk, K., J.K. Jensen & K. Kampp. 1992. Winter diet of Atlantic puffins (*Fratercula arctica*) in the northeast Atlantic. *Colonial Waterbirds*. 15(2): 230–235.

FAO. 2005, Review of the state of world marine fishery resources. *FAO Fisheries Technical Paper*, 457: 235 pp.

*__FAO__. 2009.

Fernandez, F. & J.A. Vazquez. 1995. The jumbo flying squid *Dosidicus gigas* (Orbigny, 1835) in Chile: Analysis of an ephemeral fishery. *Estudios Oceanologicos, Facultad de Recursos del Mar, Universidad de Antofagasta*, 14: 17–21.

*__Ferussac, A.E. de.__ 1823 [in 1822–1831]. Dictionnaire classique d'Histoire Naturelle, par Messieurs Audouin. I–XVII: 1822–1831. Paris, Rey et Gravier.

*__Ferussac, A.E. de.__ 1834. Notice sur deux nouvelles especes des Cephalopodes appartenant aux genres Calmaret et Cranchie. *L'Institut, Journal General des Societes et Travaux Scientifiques de la France et de l'Etranger*, 2(77):355. [also published twice in 1835].

*__Férussac, A.E. de & A. d'Orbigny.__ [1834] 1835–1848. Histoire naturelle générale et particulière des Céphalopodes Acétabuliferes vivants et Fossiles, lvi & 361pp; Atlas of 144 Plates. Paris: J. B. Balliere.

Field, I.C., C.J.A. Bradshaw, J. Hoff, H.R. Burton & M.A. Hindell. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology*, 150(6): 1441–1452.

*__Field, J.C., K. Baltz, A.J. Phillips & W.A. Walker.__ 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. *Reports of California Cooperative Oceanic Fisheries Investigations*, 48: 131.

Fields, G.W. 1950. A preliminary report on the fishery and on the biology of the squid *Loligo opalescens*. *California Department of Fish and Game*, 36: 367–377.

*__Fields, G.W.__ 1965. The structure, development, food relations, reproduction, and life history of the squid *Loligo opalescens* Berry. *Department of Fish and Game, State of California*, 2: 108.

Fields, W.G. & V.A. Gauley. 1971. Preliminary description of an unusual gonatid squid (Cephalopoda: Oegopsida) from the North Pacific. *Journal of Fisheries Research Board Canada*, 28(11): 1796–1801.

*__Filippova, J.A.__ 1968a. A new species of the genus *Cycloteuthis* (Cephalopoda: Oegopsida). *Malacological Review., 1: 119–124.*

*__Filippova, J.A.__ 1968b. New data on the cephalopoda of the Indian Ocean. *Proceedings of Symposium on Mollusca (India)*. Part I: 257–264.

Filippova, J.A. 1970. Distribution of Cephalopoda species abundant in the epipelagic waters of the Indian Ocean. *Trudy molod. Uchen*, (4): 42–52.

*__Filippova, J.A.__ 1972. New data on the squids (Cephalopoda: Oegopsida) from the Scotia Sea (Antarctic). *Malacologia*, 11(2): 391– 406.

*__Filippova, J.A.__ 1992 [1991]. Morpho-ecological aspects of the study of Antarctic squids. *Bulletin of Marine Science*, 49(1–2): 662 p.

*__Filippova, J.A.__ 2002a. Review of Soviet/Russian studies on squids in the Antarctic Ocean. *In* P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(1): 255–267.

*__Filippova, J.A.__ 2002b. The peculiarities of morphogenesis of the Antarctic squid *Alluroteuthis antarcticus* Odhner, 1923 (Neoteuthidae; Oegopsida).

*__Filippova, J.A. & E.A. Pakhomov.__ 1994. Young squid in the plankton of Prydz Bay, Antarctica. *Antarctic Science*, 6(2): 171–173.

*__Filippova, Y.A. & V.L. Yukhov.__ 1982. New data on the genus *Alluroteuthis* Odner, 1923 (Cephalopoda: Oegopsida). Antarktoka. *Doklady Komissii*, 21: 157–168.

Filippova, J.A., D.O. Alekseyev, V.A. Bizikov & D.N. Khromov. 1997. Commercial and mass cephalopods of the world ocean. A Manual for Identification. *VNIRO Publishing, Moscow.* 272 pp. (in Russian).

Finger, J.M. & J.D. Smith. 1987. Molecular association of Cu, Zn, Cd and sup (210)Ps in the digestive gland of the squid *Nototodarus gouldi*. *Marine Biology*, 95(1): 87–91.

Finke, E., H.O. Portner, P.G. Lee & D.M. Webber. 1996. Squid (*Lolliguncula brevis*) life in shallow waters: oxygen limitation of metabolism and swimming performance. *Journal of Experimental Biology*, 199: 911–921.

*****Fischer, H.** 1896. Note préliminaire sur le *Pterygioteuthis giardi*, céphalopode nouveau recueilli dans le cours de l'Expédition scientifique du Talisman (1883). *Journal de Conchyliologie*, 43(4):205–211, 1 plate. [date of publication for 43(4) = 1/IX/96].

*****Fischer, H. & L. Joubin.** 1907. Expéditions scientifiques du Travailleur et du Talisman. *Céphalopodes*, 8: 313–353.

Fiscus, C.H. 1982. Predation by marine mammals on squids of the eastern North Pacific Ocean and the Bering Sea. *Marine Fisheries Review*, 44(2):1–10.

Fiscus, C.H. & L.L. Jones. 1999. A note on cephalopods from the stomachs of Dall's porpoises (*Phocoenoides dalli*) from the Northwestern Pacific and Bering Sea, 1978–1982. *Journal of Cetacean Resource Management*, 1(1): 101–107.

Fiscus, C.H. & H. Kajimura. 1981. Food of the Pacific White-sided dolphin, *Lagenorhynchus obliquidens*, Dall's Porpoise, Phocoenoides dalli , and Northern Fur Seal, Callorhinus ursinus off California and Washington. *Fishery Bulletin*, 78(4): 951–959.

Fiscus, C.H. & R.W. Mercer. 1982. Squids taken in surface gillnets in the North Pacific Ocean by the Pacific Salmon Investigations Program, 1955–72. *NOAA Technical Memo Seattle, WA. USA NOAA NMFS*, 35 pp.

Fiscus, C.H. & K. Niggol. 1965. Observations of cetaceans – off California, Oregon and Washington. *U.S. Fish Wildlife Service, Species Scientific Report on Fishery*, 198, 27 p.

Fiscus, C.H. & D.W. Rice. 1974. Giant squids, *Architeuthis* sp., from stomachs of sperm whales captured off California. *California Fish and Game*, 60(2): 91–93.

Fiscus, C.H., D.W. Rice & A.A. Wolman. 1989. Cephalopods from the stomachs of sperm whales taken off California. *NOAA Technical Report*, 21 pp.

Fitch, J.E. & R.L. Brownell. 1971. Food habits of the franciscana *Pontoporia blainvillei* (Cetacea Platanistidae) from South America. *Bulletin of Marine Science*, 21(2): 626–636.

Flamigni, C. & O. Giovanardi. 1984. Biological data, collected during the Pipeta expeditions on the squid *Loligo vulgaris* Lam. in the Adriatic. *FAO Fisheries Report, 290.*

Flinn, R.D., A.W. Trites, E.J. Greg & R.I. Perry. 2002. Diets of fin, sei and sperm whales in British Columbia: An analysis of commercial whaling records, 1963–1967. *Marine Mammal Science*, 18(3): 663–679.

Flores, E.E.C. 1983a. Laboratory observations on the visual attack of the squid, *Todarodes pacificus*. *Memoirs of National Museum Victoria*, 44: 205–212.

Flores, E.E.C. 1983b. Visual discrimination testing in the squid *Todarodes pacificus*: experimental evidence for lack of color vision. *Memoirs of National Museum Victoria*, 44: 213–227.

Folkow, L.P. & A.S. Blix. 1999. Diving behaviour of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian seas. *Polar Biology*, 22(1): 61–74.

Fonseca, P. & A. Campos. 2002. First records of trawl cod–end selectivity for cephalopods in Portuguese waters (ICES Division IXA). *Bulletin of Marine Science*, 71(2): 1119–1120.

Fonseca, P., A. Campos & A. Garcia. 2002. Bottom trawl cod end selectivity for cephalopods in Portuguese continental waters. *Fisheries Research, Amsterdam*, 59(1–2): 263–271.

Fonseca, V.S.S. & M.V. Petry. 2007. Evidence of food items used by *Fulmarus glacialoides* (Smith 1840) (Procellariiformes: Procellariidae) in Southern Brazil. *Polar Biology*, 30(3): 317–320.

Fonseca, V.S.S., M.V. Petry & A.H. Jost. 2001. Diet of the Magellanic Penguin on the Coast of Rio Grande do Sul, Brazil. *Waterbirds*, 24(2): 290–293.

Foote, K.G., R.T. Hanlon, P.J. Iampietro & R.G. Kvitek. 2004. Acoustic mapping of squid egg clusters and their bottom habitat in Monterey Bay, California. *Journal of the Acoustical Society of America*, 116(4, pt. 2): 2487.

Foote, K.G., R.T. Hanlon, P.J. Iampietro & R.G. Kvitek. 2006. Acoustic detection and quantification of benthic egg beds of the squid *Loligo opalescens* in Monterey Bay, California. *Journal of the Acoustical Society of America*, 119(2): 844–856.

Foote, K.G., G. Kenneth, P.J. Iampietro & M. Young. 2006. Comparing repeated sidescan sonar measurements of benthic squid egg beds in Monterey Bay, CA. *Journal of the Acoustical Society of America*, 120(5, pt. 2): 3060 p.

Foote, K.G., R.T. Hanlon, A.E. Henry, A. Hochstaedter, R. Kvitek, D. Sullivan & Y. Yogozawa. 2003. Acoustic detectability of squid egg beds. *Journal of the Acoustical Society of America*, 114(4, pt. 2): 2374.

***Förch, E.C.** 1986. Rhynchoteuthion larvae from New Zealand coastal waters (Cephalopoda: Ommastrephidae). *Vie Milieu*, 36(3): 177–183.

***Förch, E.C.** 1998. The marine fauna of New Zealand: Cephalopoda: Oegopsida: Architeuthidae (Giant Squid). *NIWA Biodiversity Memoir*, 110: 1–113.

Förch, E.C. & Y. Uozumi. 1990. Discovery of a specimen of *Lycoteuthis lorigera* (Steenstrup, 1875) (Cephalopoda: Teuthoidea) from New Zealand and additional notes on its morphology. *New Zealand Journal of Marine and Freshwater Research*, 24(2): 251–258.

Forsythe, J.W. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in fishery biology. Tokai University Press*, *Tokyo*, pp. 133–143.

Forsythe, J.W. 2002. Clinical variation in the growth rate versus temperature relationship of the reef squid, *Sepioteuthis lessoniana*, from Japan, Okinawa and Thailand. *Bulletin of Marine Science*, 71(2): 1120.

Forsythe, J.W. & R.T. Hanlon. 1989. Growth of the Eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). *Aquaculture and Fisheries Management*, 20: 1– 14.

Forsythe, J.W. & W.F. Van Heukelem. 1987. Growth. *In*: Cephalopod Life Cycles. Vol. 2. Comparative Reviews (ed. P.R. Boyle). *Academic Press* London, pp. 135–156.

***Forsythe, J., N. Kangas & R.T. Hanlon.** 2004. Does the California market squid (*Loligo opalescens*) spawn naturally during the day or at night? A note on the successful use of ROVs to obtain basic fisheries biology data. *Fishery Bulletin*, 102: 389–392.

Forsythe, J.W., L.S. Walsh, P.E. Turk & P.G. Lee. 2001. Impact of temperature on juvenile growth and age at first egg-laying of the Pacific reef squid *Sepioteuthis lessoniana* reared in captivity. *Marine Biology*, 138(1): 103–112.

Foyle, T.P. & R.K. O'Dor. 1988. Predatory strategies of squid (*Illex illecebrosus*) attacking small and large fish. *Marine Behavioral Physiology*, 13(2): 155–168.

Francis, M.P., R.J. Hurst, B.H. McArdle, N.W. Bagley & O.F.S.O. Anderson. 2002. New Zealand demersal fish assemblages. *Environmental Biology of Fishes*, 65(2): 215–234.

Frandsen, R.P. & K. Wieland. 2004. Cephalopods in Greenland waters. *Teknisk Rapport Pingortitaleriffik*, 57: 1–19.

Fridriksson, A. 1943. Remarks on the age and growth of the squid. *Greinar*, 2: 170–174.

Fu, E., M. Wang, Q. Yu, Y. Li & Y. Chen. 1999. Analysis of fishing ground of *Nototodarus sloani* in New Zealand. *Journal of Dalian Fisheries College*, 14(2): 50–54.

Fu, X.Y., C.H. Xue, B.C. Miao, J.N. Liang, Z.J. Li & F.X. Cui. 2006. Purification and characterization of Trimethylamine-N-Oxide Demethylase from jumbo squid (*Dosidicus gigas*). *Journal of Agricultural and Food Chemistry*, 54(3): 968–972.

Fujino, T., K. Miyashita, Y. Hiroki, T. Shimura, S. Masuda & T. Goto. 2007. Regime shift of mesopelagic fish – long-term biomass index change of Maurolicus japonicus in the Japan/East Sea. *The Changing North Pacific: Previous Patterns, Future Projections and Ecosystem Impacts*, p. 166.

***Fujita, K. & J. Hattori.** 1976. Stomach content analysis of longnose lancetfish, *Alepisourus ferox*, in the eastern Indian Ocean and the Coral Sea. *Japanese Journal of Ichthyology*, 23(3): 133–42.

Furness, R.W. 1994. An estimate of the quantity of squid consumed by seabirds in the eastern North Atlantic and adjoining seas. *Fisheries Research*, 21: 165–178.

***Furtado, A.** 1887. Sur une nouvelle espèce de céphalopode appartement an genre Ommatostrephes. *Memorias da Academia Real das Sciencas de Lisboa*, 6(2): 3–16, 2 pl.

Furukawa, I. & Y. Sakurai. 2006. Temperature dependent growth of *Loligo bleekeri statoliths* through hatching. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: 74 p.

Fuwa, S., M. Ishizaki, H. Hashiguchi & T. Imai. 1999. Fishing gear characteristics on jig for oval squid *Sepioteuthis lessoniana. Fisheries engineering (Japan) Suisan Kogaku Japan*, 35(3): 283–291.

Fuwa, S., M. Ishizaki, N. Okada, S. Ikawa & T. Imai. 1996. Physical characteristics of jig for oval squid *Sepioteuthis lessoniana. Fisheries engineering (Japan) Suisan Kogaku*, 32(3): 229–238.

Fuwa, S., M. Ishizaki, Y. Shin'-Yashiki, S. Miyamoto & T. Imai. 1996. Towing performance of jig for oval squid *Sepioteuthis lessoniana. Fisheries Engineering (Japan) Suisan Kogaku Japan*, 33(2): 97–103.

Gaard, E. 1987. An investigation of the squid *Loligo forbesi* Steenstrup on Faroe Bank. International Council for the Exploration of the Sea (CM Papers and Reports) K: 18.

***Gabb, W.M.** 1862. Description of two new species of Cephalopods in the Museum of the California Academy of Natural Sciences. *Proceedings of the California Academy of Natural Sciences*, 2:170–172.

***Gabb, W.M.** 1868. Description of a new species of cephalopod from the South Pacific. *American Journal of Conchology*, 4(1):23–24, 1 pl.

Gabb, W.M. 1869. Description of a new species of Sepioteuthis from the West Indies. *American Journal of Conchology*, 4(4): 193–194.

Gaevskaya, A.V. & C.M. Nigmatullin. 1976. Biotic relationships of *Ommastrephes bartramii* in the North and South Atlantic. *Zoologicheskij Zhurnal*, 55 (12): 1800–1810 (In Russian with English abstract).

Gaevskaya, A.V. & Ch.M. Nigmatullin. 1981. Some ecological aspects of host-parasite links of the squid, *Sthenoteuthis pteropus* (Steenstrup, 1855), in the tropical Atlantic. *Biologicheskie Nauki*, 1: 52–57 (In Russian).

Gaevskaya, A.V. & O.A. Shukhgalter. 1992. Ontogenic peculiarities of formation of helminth fauna in squids of the Ommastrephidae family. *Ehkologiya Morya*, 40: 65–71.

Gaffney, P.M. 2000. Molecular tools for understanding population structure in Antarctic species. *Antarctic Science*, 12(3): 288–296.

Gales, R. & D. Pemberton. 1990, Seasonal and local variation in the diet of the little penguin, *Eudyptula minor*, in Tasmania. *Australian Wildlife Research*, 17: 231–259.

Gales, R., D. Pemberton, C.C. Lu & M.R. Clarke. 1993. Cephalopod diet of the Australian fur seal: Variation due to location, season and sample type. *Australian Journal of Marine and Freshwater Research*, 44(5): 657–671.

Gales R., D. Pemberton, C.C Lu & M.R. Clarke. 1994. Cephalopod diet of the Australian fur seal: variation due to location, season and sample type. *Australian Journal of Marine and Freshwater Research*, 44: 657–671.

Galvón-Magana, F., H.J. Nienhui & A.R. Klimely. 1989. Seasonal abundance and feeding habits of sharks in the lower Gulf of California, Mexico. *California Fish and Game*, 75: 74–84.

Gamulin-Brida, H. & V. Ilijanic. 1972. Contribution a la connaissance des céphalopodes de L'Adriatique. *Acta Adriatica*, vol. XIV, 6: 3–12.

Gan, J., X. Jia, Q. Lin, C. Li & W. Cai. 2006. BHC and DDT in the squids in continental shelf of northern South China Sea. *Marine Environmental Science*, 25 (Supp. 1): 20–24.

Gannon, D.P., A.J. Read, J.E. Craddock, K.M. Fristrup & J.R. Nicolas. 1997. Feeding ecology of long-finned pilot whales *Globicephala melas* in the western North Atlantic. *Marine Ecology Progress Series*, 48(1–3): 1–10.

Garcia-Godos, I. 2006. A note on the occurrence of sperm whales (*Physeter macrocephalus*) off Peru, 1995–2002. *Journal of Cetacean Research and Management*, 8(1): 113–119.

Garoia, F., I. Guarniero, A. Ramsak, N. Ungaro, N. Landi, C. Piccinetti, P. Mannini & F. Tinti. 2004. Microsatellite DNA variation reveals high gene flow and panmictic populations in the Adriatic shared stocks of the European squid and cuttlefish (Cephalopoda). *Heredity*, 93: 166–174.

Garren, F., Y. Verin, J.L. Dufour, P. Porche & J.J. Vayne. 2003. Identification sheets for fishes and cephalopods of the Channel and the North Sea. *Boulogn sur Mer, France, Ifremer*, 25 pp.

Garri, R. & M.E. Re. 2002. Morphology of the digestive apparatus of *Enteroctopus megalocyathus* and *Loligo sanpaulensis* (Mollusca, Cephalopoda). *Iheringia, Serie Zoologia*, 92(2): 81–91.

Garthe, S., W.A. Montevecchi, U. Ojowski & I.J. Stenhouse. 2004. Diets of northern fulmar (*Fulmarus glacialis*) chicks in the northwest Atlantic Ocean. *Polar Biology*, 27(5): 277–280.

*Garthwaite, R.L., C.J. Berg, Jr. & J. Harrigan.** 1989. Population genetics of the common squid *Loligo pealei* LeSueur, 1821, from Cape Cod to Cape Hatteras. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*, 177(2): 287–294.

Gauldie, R.W. 1994. Statocyst, statolith, and age estimation of the giant squid, *Architeuthis kirki*. *Veliger*. 37(1): 92–109.

Gavrilov, G.M. & N.F. Pushkareva. 1985. Bioproductivity of the USSR EEZ in the Sea of Japan. *Bioproductivity of the Far Eastern Seas*, 110: 3–12.

Ge, Y. & S. Qiu. 1991 Preliminary consideration on the methods of forecasting the catch of Japanese squid, *Loligo japonica*, in the Yellow Sea and Bohai Sea. *Marine fisheries, Shanghai*, 13(2): 56–60.

Ge, Y., S. Jiang & S. Qiu. 1990. Preliminary analysis on the biological characteristics of squid in the East China Sea and the Yellow Sea. *Marine Fisheries Haiyang-Yuye*, 12(3): 102–106.

Ge, Y., K. Shou, D. Yu & S. Qie. 1988. Preliminary studies on the fishing condition of common squid, *Todarodes pacificus*, in the Yellow Sea. *Marine Fisheries Haiyang-Yuye*, 10(4): 153–157.

Gentiloni, P., S. Agnesi & C. Gargiulo. (2001). Dati sulla distribuzione e biologia del cefalopode *Illex coindetii* (Verany, 1839) nel mar Tirreno centrale. *Biologia Marina Mediterranea*, 8: 715–719.

Georgakarakos, S., J. Haralabus, V.D. Valavanis, C. Arvanitidis & D. Koutsoubas. 2000. Prediction of fishery exploitation stocks of Loliginid and Ommastrephid squids in Greek waters (Eastern Mediterranean) using uni- and multivariate time series analysis techniques. Millennium Cephalopod Conference, CIAC 2000, Aberdeen, 3–7 July 1999 (Abst.).

Georgakarakos, S., J. Haralabous, V. Valavanis, C. Arvanitidis, D. Koutsoubas & A. Kapantagakis. 2002. Loliginid and ommastrephid stock prediction in Greek waters using time series analysis techniques. *Bulletin of Marine Science*, 1:269 – 287.

Georgantelis, D., T. Papavergou, P. Tsoumbaris & V. Katsouyannopoulos. 2001. Determination of trace metals in canned cephalopods. *7th International Conference on Environmental Science and Technology*, Syros, Greece, 3: 109–113.

George, M.J.A. & E.M.C. Hatfield. 1995. First records of mated female *Loligo gahi* (Cephalopoda: Loliginidae) in the Falkland Islands. *Journal of the Marine Biological Association of the United Kingdom*, 75(3): 743–745.

Gestal C., A. Guerra, E. Abollo & S. Pascual. 2000. *Aggregata sagittata* n. sp. (Apicomplexa: Aggregatidae), a coccidian parasite from the European flying squid *Todarodes sagittatus* (Mollusca: Cephalopoda). *Systematic Parasitology*, 47:203–206.

Gestal, C., C.M. Nigmatullin, F.G. Hochberg, A. Guerra & S. Pascual. 2005. *Aggregata andresi* n. sp. (Apicomplexa: Aggregatidae) from the ommastrephid squid *Martialia hyadesi* in the SW Atlantic Ocean and some general remarks on *Aggregata* spp. in cephalopod hosts. *Systematic Parasitology*, 60(1): 65–73.

Ghofar, A. 1994. Cephalopods in the stomach of tuna caught from southern Indonesian water. *In*: A. Snidvongs, W. Utoomprukporn & M. Hungspreugs, eds. NRCT JSPS Joint Seminar on Marine Science. *Bangkok Thailand Chulalongkorn University*, 195–199 pp.

Giardina, B., S.G. Condo & O. Brix. 1992. The interplay of temperature and protons in the modulation of oxygen binding by squid blood. *Biochemisty Journal*, 281(3): 725–728.

*Gibson, D.J.M.** 1995. The New Zealand squid fishery, 1979–93. *New Zealand Fishery Technology Report*, 42: 43 pp.

Gibson, D. & J.B. Jones. 1993. Fed up with parasites? A method for estimating asymptotic growth in fish populations. *Marine Biology*, 117(3): 495–500.

Gilbert, D.L. 1991. The naming of the North American common squid. *Bulletin of Marine Science*, 49(1–2): 662.

Gillespie, A. 1953. An incursion of the flying squid, *Ommastrephes sagittatus* (Lamarck), on the east coast of Scotland. *N West Nat.*, 1(n.s.): 384–387.

*Gilly, W.F., C.A. Elliger, C.A. Salinas, S. Camarilla-Coop, G. Bazzino & M. Beman.** 2006a. Spawning by jumbo squid *Dosidicus gigas* in San Pedro Martir Basin, Gulf of California, Mexico. *Marine Ecology Progress Series*, 313: 125–133.

*Gilly, W.F., U. Markaida, C.H. Baxter, B.A. Block, A. Boustany, L. Zeidberg, K. Reisenbichler, B. Robison, G. Bazzino & C. Salinas.** 2006b. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Marine Ecology Progress Series*, 324: 1–17.

Giordano, D. & P. Carbonara. (1999). Nota sulla distribuzione dei molluschi cefalopodi nel Tirreno centro-meridionale. *Biologia Marina Mediterranea*, 6: 573–575.

***Giordano, D., G. Florio, T. Bottari & S. Greco.** 2001. Occurrence of *Histioteuthis bonnellii* and *Histioteuthis reversa* (Cephalopoda: Histioteuthidae) in the southern Tyrrhenian Sea (Western Mediterranean). *Scientific Council Research Document NAFO*, 01/165: 6 pp.

***Girard, A.** 1890. Nota sobre os Cephalopodes de Portugal. *Jornal de Sciencias Mathematicas, Physicas e Naturaes*, (series 2)1(3): 200–205.

Girsch, S.J., P.J. Herring & F. McCapra. 1976. Structure and preliminary biochemical characterization of the bioluminescent system of *Ommastrephes pteropus* (Steenstrup) (Mollusca: Cephalopoda). *Journal of the Marine Biological Association of the United Kingdom*, 56: 707–722.

Gislen, T. 1944. Physiological and ecological investigations concerning the littoral of the northern Pacific. Sections II–IV. Regional conditions of the Pacific coast of America and their significance for the development of marine life. *Lunds University, Arsskr., N. F., Div. 2*, 40(8): 1–92.

Glass, C.W., B. Sarno, O.M. Henry, G.D. Morris & H.A. Carr. 1999. By-catch reduction in Massachusetts Inshore squid (*Loligo pealeii*) trawl fisheries. *Marine Technology Society Journal*, 33(2): 35–42.

Glass, C.W., B. Sarno, H.O. Milliken, G.D. Morris & H.A. Carr. 1998. Squid (*Loligo pealei*) reactions to towed fishing gears; the role of behaviour in by-catch reduction. *ICES Council Meeting*

Glaubrecht, M., V. Salcedo & A. Mario. 2000. Annotated type catalogue of the Cephalopoda (Mollusca) in the Museum fuer Naturkunde, Humboldt University of Berlin. *Mitteilungen aus dem Museum fuer Naturkunde in Berlin Zoologische Reihe*, 76(2): 269–282.

Glaubrecht, M. & M.A. Salcedo-Vargas. 2004. The Humboldt squid *Dosidicus gigas* (Orbigny, 1835): history of the Berlin specimen, with a reappraisal of other (bathy-) pelagic “gigantic” cephalopods (Mollusca, Ommastrephidae, Architeuthidae). *Mitteilungen der Museum Naturkunde Berlin, Zoology*, 80(1): 53–69.

Glazer, J.P. & D.S. Butterworth. 2006. Some refinements of the assessment of the South African squid resource, *Loligo vulgaris reynaudii*. *Fisheries Research*, 78(1): 14–25.

Gleadall, I.G. & M.A. Salcedo-Vargas. 2004. Catalogue of the cephalopoda specimens in the Zoology Department of Tokyo University Museum. *Interdisciplinary Information Sciences*, 10(2): 113–142.

Glorioso, P.D. 1987. Temperature distribution related to shelf-sea fronts on the Patagonic shelf. *Continental Shelf Research,* 7(1): 27–34.

Glorioso, P.D. & R.A. Flather. 1995. A barotropic model of the currents off SE South America. *Journal of Geophysical Research*, 100: 13427–13440.

***Gmelin, J.F.** 1789. Tomus, I. (VI), Vermes [pp. 3021–3910]. Caroli a Linne, Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Editio Decima Tertia, Aucta, Reformata. Georg. Emanuel. Beer, Lipsiae. [for dates see Hopkins (1908); for editions see Kabat and Petit (1988)].

Go, Y.B. & H.S. Shin. 1988. Species occurrence and food chain of fisheries resources, nekton, on the coast of Pukchon, Cheju Island. 1 Species composition and diversity. *Bulletin Korean Fisheries Society*, 21(3): 131–138.

Goldman, D.A. 1995. A juvenile of the scaled squid *Polidoteuthis adami* Voss, 1956 (Cephalopoda: Oegopsida), from the Florida Keys. *Proceedings of the Biological Society of Washington*, 108(1): 136–146.

Goldman, D.A. & M.F. McGowan. 1991. Distribution and abundance of Ommastrephid squid paralarvae off the Florida Keys in August 1989. *Bulletin of Marine Science*, 49(1–2): 614–622.

Goldsworthy, S.D., M. Lewis, R. Williams, X. He, J.W. Young & J. Van den Hoff. 2002. Diet of Patagonian toothfish (*Dissostichus eleginoides*) around Macquarie Island, South Pacific Ocean. *Marine and Freshwater Research*, 53(1): 49–57.

***Golub, A.N.** 2001. Oceanographic factors influencing squid larval distribution in the Southwest Atlantic. *ICES, Council Meeting/K:12*

Golub, A.N., S.A. Murzov, Yu.A. Aleksandronets, Yu.N. Zheronkin, V.V. Laptikhovsky & Ch.M. Nigmatullin. 2001. Distribution of different life cycle stages of squid, *Sthenoteuthis pteropus* (Cephalopoda: Ommastrephidae), in the tropical Atlantic in March–May, 1986 in connection with water dynamics. *Voprosy rybolovstva (Moscow)*, Supplement 1: 62–65 (In Russian).

Gomez-Guillen, M. & P. Montero. 1997. Improvement of giant squid (*Dosidicus gigas*) muscle gelation by using gelling ingredients. *Food Research and Technology*, 204(5): 379–384.

Gomez-Guillen, M.C., J.L. Hurtado & P. Montero. 2002. Autolysis and protease inhibition effects on dynamic viscoelastic properties during thermal gelation of squid muscle. *Journal of Food Science*, 67(7): 2491–96.

Gomez-Guillen, M.C., O. Martinez-Alvarez & P. Montero. 2003. Functional and thermal gelation properties of squid mantle proteins affected by chilled and frozen storage. *Journal of Food Science*, 68(6): 1962–1967.

Gomez-Guillen, M.C., T. Solas, J. Borderias & P. Montero. 1996a. Effect of heating temperature and sodium chloride concentration on ultrastructure and texture of gels made from giant squid (*Dosidicus gigas*) with addition of starch, iota-carrageenan and egg white. *Zeitschrift Lebensmittel Untersuchung und Forschung*, 202(3): 215–220.

Gomez-Guillen, M.C., T. Solas, J. Borderias & P. Montero. 1996b. Ultrastructural and rheological changes during the gelation of giant squid (*Dosidicus gigas*) muscle. *Zeitschrift Lebensmittel Untersuchung und Forschung*, 202(3): 215–220.

Gomez-Villota, F. 2006. The diet of sperm whales, *Physeter macrocephalus*, stranded in New Zealand: Implications for conservation. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 28.

Goncalves, J.M., F.M. Porteiro, F. Cardigos & H.R. Martins. 1995. The Azorean adult squid Loligo forbesi Cephalopoda: Loliginidae) in captivity: Transport, handling, maintenance, tagging and survival. *Copenhagen Denmark ICES*, 15 pp.

Gong, Y. 2005. Productivity of common squid, *Todarodes pacificus*, in Korean waters and its adjacent regions. *PICES 14th Annual Meeting Book of Abstracts*, p. 115.

Gong, Y., Y.S. Kim & D.H. An. 1993. Abundance of neon flying squid in relations to oceanographic conditions in the North Pacific. *International North Pacific Fisheries Commission Bulletin*, 53: 191–204.

Gong, Y., H.D. Jeong, K.H. Choi, K. Seong & S. Kim. 2006. Fluctuations in the abundance of common squid, *Todarodes pacificus* and environmental conditions in the Far East regions during 52 years. *Journal of Ecology and Field Biology*, 29(1):1–16.

Gonzalez, A. & J. Castaneda. 1997. Biological characteristics of hake and other demersal species in winter 1996. Evaluation cruise of Peruvian hake resource in winter 1996 RV SNP 1 9607 08 Crucero de evaluacion del recurso merluza en invierno de 1996 BIC SNP 1 9607 08, Lima Peru Visual Service SRL, 124: 71–78.

Gonzalez, A.F. & A. Guerra. 1996. Reproductive biology of the short-finned squid *Illex coindetii* (Cephalopoda, Ommastrephidae) of the northeastern Atlantic. *Sarsia*, 81: 107–118.

Gonzalez, A.F. & P.G. Rodhouse. 1998. Fishery biology of the seven star flying squid *Martialia hyadesi* of South Georgia during winter. *Polar Biology*, 19(4): 231–236.

Gonzalez, A.F, R. Castillo & L. Vasquez. 1997a. Other important resources during the stock assessment cruise for peruvian hake, RV Humboldt 9705–06, Callao to Puerto Pizarro. *Informe, Instituto del Mar del Peru*, 128: 104–121.

Gonzalez, A.F., B.G. Castro & A. Guerra. 1996. Age and growth of the short-finned squid *Illes coindetii* in Galician waters (NW Spain) based on statolith analysis. *ICES Journal of Marine Science*, 53, 802–810.

* **Gonzalez, A.F., A. Guerra & F. Rocha.** 2003. New data on the life history and ecology of the deep-sea hooked squid *Taningia danae*. *Sarsia*, 88(4): 297–301.

González, A.F., J. Otero & A. Guerra. 2006. Distribution and growth of common squid paralarvae in the Ria of Vigo (NW Spain). *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 51.

Gonzales A.F., M. Rasero & A. Guerra. 1992a. Evidence for a recent and sudden increase in the abundance of *Illex coindetii* (Cephalopoda: Ommastrephidae) off the Galician coast (NW Spain). *In*: F. Giusti & G. Manganelli, eds. *Abstract of the 11th International Malacological Congress*, Siena, 1992. University of Siena, Siena: 304–306.

Gonzalez, A.F., M. Rasero & A. Guerra. 1992b. *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda, Ommastrephidae): Their present status in Galician fisheries. *ICES 1992 Copenhagen*, 14 pp.

*__Gonzales A.F, M. Rasero & A. Guerra.__ 1994. Preliminary study of Illex coindetii and Todaropsis eblanae (Cephalopoda: Ommastrephidae) in northern Spanish Atlantic waters. *Fisheries Research*, 21: 115–126.

Gonzalez, A.F., E.G. Dawe, P.C. Beck & J.A.A. Perez. 2000. Bias associated with statolith-based methodologies for ageing squid; a comparative study on *Illex illecebrosus* (Cephalopoda: Ommastrephidae). *Journal of Experimental Marine Biology and Ecology*, 244(2): 161–180.

Gonzalez, A.F., A. Guerra, F. Rocha & J. Gracia. 2002. Recent finds of the giant squid *Architeuthis* in northern Spanish waters. *Journal of the Marine Biological Association of the United Kingdom*, 82: 859–861.

Gonzalez, A.F., A. Lopez, A. Guerra & A. Barreiro. 1994. Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. *Fisheries Research*, 21(1–2): 179–191.

*__Gonzalez, A.F., P.N. Trathan, C. Yau & P.G. Rodhouse.__ 1997b. Interactions between oceanography, ecology and fishery biology of the ommastrephic squid *Martialia hyadesi* in the South Atlantic. *Marine Ecology Progress Series*, 152(1–3): 205–215.

González, A.F., A. Pasqual, C. Gestal, E. Abollo & A. Guerra. 2003. What makes a cephalopod a suitable host for parasite? The case of Galician waters. *Fisheries Research*, 60:177–183.

González, A.F., J. Otero, A. Guerra, R. Prego, F.J. Rocha & A.W. Dale. 2005. Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain). *Journal of Plankton Research*, 27(3): 271–277.

Gonzalez, M. & P. Sanchez. 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. *Scientia Marina*, 66(2): 199–208.

Gonzalez, M., M. Fernandez Casado, Ma. Pilar Rodriguez, A. del, Segura & J.J. Martin. 2000. First record of the giant squid *Architeuthis* sp. (Architeuthidae) in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 80(4): 745–746.

*__Goodrich, E.S.__ 1896. Report on a collection of Cephalopoda from the Calcutta Museum. *Transactions of the Linnean Society of London, Series 2, Zoology*, 7(1): 1–24.

Gorbatenko, K.M., V.I. Chuchukalo & G.A. Shevtsov. 1995. Daily ration of two mass squid species in the Bering Sea and Okhotsk seas during the autumn–winter period. *In* B.N. Kotenev, ed. Multiple Investigations of the Bering Sea Ecosystem. Russia IZD. *VNIRO*: 349–357.

Gordoa, A. & E. Macpherson. 1989. Biomass indices and recruitment levels for hake and other commercial species in ICSEAF divisions 1.4 and 1.5 from 1988 surveys. *Collected Scientific Papers, IICSEAF Reclamations Scientific Documents*, 16: 103–118.

Goss, C., D. Middleton & P. Rodhouse. 2001. Investigations of squid stocks using acoustic survey methods. *Fisheries Research (Amsterdam)*, 54(1): 111–121.

Goto, T. 2002. Paralarval distribution of the Ommastrephid squid *Todarodes pacificus* during fall in the southern Sea of Japan, and its implication for locating spawning grounds. *Bulletin of Marine Science*, 71(1): 299–312.

Goto, T. 2005. Examination of different preservatives for *Todarodes pacificus* paralarvae fixed with borax-buffered formalin-seawater solution. *In*: C. Chotiyaputta, E.M.C. Hatfield, C.C., Lu, eds. *Phuket Marine Biological Center Research Bulletin*, 66: 213–219.

Goto, T., H. Iio, S. Inoue & H. Kakoi. 1974. Squid bioluminescence. I. Structure of Watasenia oxyluciferin, a possible light-emitter in the bioluminescence of Watasenia scintillans. *Tetrahedron-Letter*, 26: 2321–2324.

*__Gould, A.A.__ 1852. Mollusca and Shells. United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, 12:1–510, atlas of 52 pls.

Gowland, F.C., P.R. Boyle & B.T.G. Gowland. 2002. Pattern development in hatchling *Loligo forbesi* and its potential for quantification of chromatophore arrangement. *Bulletin of Marine Science*, 71(2): 1067–1071.

Gowland, F.C., P.R. Boyle & L.R. Noble. 2002. Morphological variation provides a method of estimating thermal niche in hatchlings of the squid *Loligo forbesi* (Mollusca: Cephalopoda). *Journal of Zoology*, 258: 505–513.

Gowland, F.C., P.R. Boyle & L.R. Noble. 2003. Asymmetry in the embryonic chromatophore pattern of the squid *Loligo forbesi* (Mollusca: Cephalopoda): a proxy for developmental instability. *Journal of the Marine Biological Association of the United Kingdom*, 83(4): 1101–1105.

Gowland, F.C., N.A. Moltschaniwskyj & M.A. Steer. 2002. Description and quantification of developmental abnormalities in a natural *Sepioteuthis australis* spawning population (Mollusca: Cephalopoda). *Marine Ecology Progress Series*, 243: 133–141.

***Grant, R.G.** 1833. On the structure and characters of *Loligopsis*, and account of a new species (*Lol. guttata*, Grant) from the Indian Seas. *Transactions of the Zoological Society of London*, 1:21–28, 10 figs.

Gray, J.E. 1828. Spicilegia Zoologica; or Original Figures and short systematic Descriptions of new and unfigured Animals. Part I. Treuttel, Wurtz and Co. London, 8 pp., 6 pls.

***Gray, J.E.** 1849. Catalogue of the Mollusca in the Collection of the British Museum. Part I. Cephalopoda Artepedia. London, 164 pp.

Green, K. & H.R. Burton. 1993. Comparison of the stomach contents of southern elephant seals *Mirounga leonina*, at Macquarie Heard Islands. *Marine Mammal Science*, 9: 10–22.

Green, K., K.R. Kerry, T. Disney & M.R. Clarke. 1998. Dietary studies of light-mantled sooty albatrosses *Phoebetria palpebrata* from Macquarie and Heard islands. 1998. *Marine Ornithology*, 26(1–2): 19–26.

***Grieb, T.M.** 1976. A study of spermatogenesis in the spawning population of the squid, *Loligo opalescens* (Cephalopoda, Decapoda). M.A. Thesis, San Francisco State, University (USA), 102 pp.

Grigioni, S., D. Pichon & R. Boucher-Rodini. 2002. Accessory nidamental glands symbiotic associations in sepioids and myopsids. *Bulletin of Marine Science*, 71(2): 1124.

***Grimpe, G.** 1922. Systematische ubersicht der europaischen Cephalopoden. *Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig*, 45: 36–52.

Grimpe, G. 1925. Zur Kenntnis der Cephalopodenfauna der Nordsee. *Wissenschaftliche Meeresuntersuchungen Helgoland*, 16(3): 1–124.

***Grimpe, G.** 1931. Teuthologische Mitteilungen. XIII. Uber die Cephalopoden der Sunda-Expedition Rensch. *Zoologischer Anzeiger*, 95(5/8): 149–174, 14 figs.

***Grimpe, G.** 1932. Studien uber die Cephalopoden des Sudangebietes. I. Zur Kenntnis der gattung *Loliolus* Steentrup, 1856. *Jena, Z. Naturw.*, 67: 469–487.

Grist, E.P.M. & S. Des Clers. 1998. How seasonal temperature variations may influence the structure of annual squid populations. *IMA Journal of Mathematical Applied Medicne and Biology*, 15: 187–209.

Grist, E.P.M. & G.D. Jackson. 2007. How long would it take to become a giant squid? *Reviews in Fish Biology and Fisheries*, 17(2–3): 385–399.

Griswold, C.A. & J. Prezioso. 1981. In situ observations on the reproductive behaviour of the long-finned squid, *Loligo pealei*. *Fishery Bulletin*, 78: 945–947.

Groger, J., U. Piatkowski & H. Heinemann. 2000. Beak length analysis of the Southern Ocean squid *Psychroteuthis glacialis* (Cephalopoda: Psychroteuthidae) and its use for size and biomass estimation. *Polar Biology*, 23(1): 70–74.

Guarniero, I., F. Garoia, R. Di Placido, A. Ramsak, P. Mannini & F. Tinti. 2003. Species-specific microsatellite loci for the European squid (*Loligo vulgaris*). *Molecular Ecology Notes*, 3(2): 312–313.

Gudmundson, C.J., T.K. Zeppelin & R.R Ream. 2006. Application of two methods for determining diet of northern fur seals (*Callorhinus ursinus*). *Fishery Bulletin Seattle*, 104(3): 445–455.

Guerra, A. 1982. Cefalópodos capturados en la campana "Golfo de Cadiz–81". *Resultados de Expediciones Cientificas*, 10: 17–49.

Guerra, A. 1984. Cefalopodos de la ria de Vigo. Resultados preliminares. *Cuadernos da Area de Ciencias Marinas, Seminario de Estudos Galegos*, 1: 333–348.

***Guerra, A.** 1992. Mollusca, Cephalopoda. *In*: Fauna Ibérica. Museo Nacional de Ciencias Naturales. *SIC*. Madrid. 327 pp.

Guerra, A. & B.G. Castro. 1994. Reproductive-somatic relationships in *Loligo gahi* (Cephalopoda: Loliginidae) from the Falkland Islands. *In*: P.G. Rodhouse, U. Piatkowski & C.C. Lu, eds. Southern Ocean cephalopods: life cycle and populations. *Antarctic Science*, 6: 175–178.

***Guerra, A. & F. Rocha.** 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). *Fisheries Research*, 21(1–2): 43–69.

Guerra, A. & F. Rocha. 1997. On a floating egg mass of the diamond shaped squid *Thysanoteuthis rhombus* (Cephalopoda: *Thysanoteuthis*) in the western Mediterranean. *Iberius*, 15(1): 125–130.

Guerra, A., B.G. Castro & M. Nixon. 1991. Preliminary study on the feeding by *Loligo gahi* (Cphalopoda: Loliginidae). *Bulletin of Marine Science*, 49: 309–311.

***Guerra, A., A.F. Gonzalez & F. Rocha.** 2004a. A review of records of giant squid in the northeastern Atlantic and severe injuries in *Architeuthis dux* stranded after acoustic exploration. *ICES Council Meeting Documents*. Copenhagen no. 2004.

Guerra, A., G. Pérez-Gandaras & E. Morales. 1985. Juvenile planktonic cephalopods from NW Africa. *Vie Milieu*, 35(3/4): 169–170.

Guerra, A., P. Sanchez & F. Rocha. 1994. The Spanish fishery for *Loligo*: recent trends. *Fisheries Research*, 21(1–2): 217–230.

Guerra, A., F. Simon & A.F. González. 1993.Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the northeastern Atlantic Ocean. *In*: T. Okutani, R.K. O´Dor & T. Kubodera, eds. Recent Advances in Cephalopod Fisheries Biology. *Tokai University Press, Tokyo*, pp. 159–164.

***Guerra, A., A.F. Gonzáles, E.G. Dawe & F. Rocha.** 2004b. Records of giant squid in the northeastern Atlantic, and two records of males *Architeuthis* sp. off the Iberian Peninsula. *Journal of the Marine Biological Association of the United Kingdom*, 84(2): 427–431.

Guerra, A., F. Rocha, F. Casas & M.T. Fernandez. 1992. *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda, Loliginidae): Their present status in Galician fisheries. *Copenhagen Denmark ICES*, 1992. 20 pp.

***Guerra, A., F. Rocha, A.F. Gonzalez & L.F. Buckle.** 2001. Embryonic stages of the Patagonian squid *Loligo gahi* (Mollusca: Cephalopoda). *The Veliger*, 44: 109–115.

Guerra, A., R. Villanueva, K.N. Nesis & J. Bedoya. 1998. Redescription of the deep-sea cirrate octopod Cirroteuthis magna Hoyle, 1885, and considerations on the genus *Cirroteuthis* (Mollusca: Cephalopoda). *Bulletin of Marine Science*, 63(1): 51–81.

***Guerra, A, S.G. Gonzalez, F. Rocha, J. Gracia & M. Vecchione.** 2004c. Calamares gigantes varados: victimas de exploraciones acusticas. *Investigacion y Ciencia*, July: 35–37.

Guerra, A., A.F. Gonzalez, F.J.Rocha, R. Sagarminaga & A. Canadas. 2002a. Plantonic egg masses of the diamond-shaped squid *Thysanoteuthis rhombus* in the eastern Atlantic and the Mediterranean Sea. *Journal of Plankton Research*, 24(4): 333–338.

***Guerra, A., A.F. Gonzalez, F.J. Rocha, M. Segonzac & J. Gracia.** 2002b. Observations from submersibles of rare, long-arm bathypelagic squids. *Sarsia*, 87(2): 189–192.

Guescini, A. & G. Manfrin. 1986. Recovery of uncommon cephalopods in the Adriatic Sea: *Abralia veranyi* (Ruppel, 1844) and *Ommastrephes caroli* (Furtado, 1887). *Nova Thalassia*, 8(3): 519–521.

Guo, J. & P. Che. 2000. A study on exploitation of cephalopoda stock in South China Sea. *Tropical Oceanology*, 19: 51–58.

Gutsal, D.K. 1991. New information on the vertical distribution of the squid *Sthenoteuthis oualaniensis*. *Marine Biology*, 4: 94–98.

Ha, B.S. 1982. Studies on the lipid of aquatic products (Part 4). On the flesh lipid composition of cephalopods. *Bulletin of the Korean Fisheries Society*, 15(1): 59–73.

Hacker-Sinclair, E. 1992. Stomach contents of four short-finned pilot whales (*Globicephala macrorhynchus*) from the Southern California Bight. *Marine Mammal Science*, 8(1): 76–81.

Haefner, P. 1964. Morphometry of the common Atlantic squid *Loligo pealei* and the brief squid *Lolliguncula brevis*, in Delaware Bay. *Chesapeake Science*, 5: 138–144.

Hai, V.D. 2005. Impacts of light power on fish and squid retina. *Proceedings of National Workshop on Fishing, processing and fisheries logistics*. pp. 185–198.

Haimovici, M. & J.A.A. Perez. 1990. Distribution and sexual maturation of the Argentinian squid, *Illex argentinus* off southern Brazil. *Scientia Marina Barcelona*, 54: 179–185.

Haimovici, M. & J.A.A. Perez. 1991. Cephalopods fished in four bottom-trawl surveys on the external shelf and slope off southern Brazil. *Atlantica*, 13(1): 189–200.

Haimovici, M. & J.A.A. Perez. 1992 [1991]. Coastal cephalopod fauna of Southern Brazil. *Bulletin of Marine Science*, 49(1–2): 221–230.

Haimovici, E.M., A.S. Martins & E.R.L. Teixeira. 1993. Distribution, food and observations of the reproduction of the Argentine hake (*Merluccius hubbsi*) in Southern Brazil. *Frente Maritimo*, 14: 33–40.

Haimovici, M., U. Piatkowski & R. Aguiar dos Santos. 2002. Cephalopod paralarvae around tropical seamounts and oceanic islands off the northeastern coast of Brazil. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(1): 313–330.

Haimovici, M., E.A.G. Vidal & J.A.A. Perez. 1995. Larvae of *Illex argentinus* from five surveys on continental shelf of southern Brazil. *ICES Marine Science Symposium*, 199: 414–424.

Haimovici, M., N.E. Brunetti, P.G. Rodhouse, J. Csirke & R.H. Leta. 1998. *Illex argentinus*. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 27–58.

Hall, K.C., A.J. Fowler & M.C. Geddes. 2007. Evidence for multiple year classes of the giant Australian cuttle *Sepia apama* in northern Spencer Gulf, South Australia. *Reviews in Fish Biology and Fisheries*, 17(2–3): 367–384.

Hamabe, M. 1962. Embryological studies on the common squid, *Ommastrephes sloani pacificus* Steenstrup, in the southwestern waters of the Sea of Japan. *Bulletin of Japan Sea Regional Fisheries Research Laboratory*, 10: 1–45.

Hamabe, M. 1965. Embryological and ecological studies on the common squid in the Sea of Japan. 189 pp. Published by author.

Hamabe, M. & T. Shimizu. 1966. Ecological studies on the common squid, *Todarodes pacificus* Steenstrup, mainly in the southwestern waters of the Japan Sea. *Bulletin of Japan Sea Regional Fisheries Research Laboratory*, 16: 13–55.

Hamabe, M., R. Saito & T. Kawakami. 1974. A trial to inference of locating fishing grounds for New Zealand *Nototodarus sloani sloani* (Gray) from the information concerning propagation of Japanese *Todarodes pacificus* Steenstrup. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 80: 1–10.

Hamabe, M., T. Sato & T. Kawakami. 1974. A preliminary note on the ecology of copulation of the ommastrephid squid *Illex illecebrosus* (Lesueur) in the northwest Atlantic. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 78: 97–102.

Hamano, T., K.-I. Hayashi, K. Kubota, H. Matsushita & K. Tabuchi. 1996. Population structure and feeding behavior of the stomatopod crustacean *Kempina mikado* (Kemp & Chopra, 1921) in the East China Sea. *Fishery Science*, 62(3): 397–399

Han, S., M. Dong, D. Tang & D. Qiu. 1999. Analysis of the nutrient components of squid. *Oceanologia et lemnologia sinica Qingdao*, 17(2): 64–68.

Haneda, Y. 1986. On a new type of luminous fishes and squids ingested luminescence. *In*: T. Uyeno, R. Arai, T. Taniuchi & K. Matsuura, eds. Proceeding of the second international conference on Indo-Pacific Fishes. *Indo-Pacific Fish Biology Tokyo*, pp. 838–839.

Haneda, Y. & F.I. Tsusil. 1971. Descriptions of some luminous squids from the water of northern New Guinea collected by the R/V Tagula. *Science Report Yokosuka City Museum*, 18: 29–33.

Hanlon, R.T. 1982. The functional organization of chromatophores and iridescent cells in the body patterning of *Loligo plei* (Cephalopoda: Myopsida). *Malacologia*, 23(1): 89–120.

Hanlon, R.T. 1988. Behavioral and body patterning characters useful in taxonomy and field identification of cephalopods. *In*: R.T. Hanlon, ed. AMU International Symposium on Life History, Systematics and Zoogeography of Cephalopods. *Malacologia*, Vol. 29(1): 247–264.

Hanlon, R.T. 1996. Evolutionary games that squids play: Fighting, courting, sneaking, and mating behaviors used for sexual selection in *Loligo pealei*. *Biological Bulletin*, 191(2): 309–310.

Hanlon, R.T. 1998. Mating systems and sexual selection in the squid *Loligo*: How might commercial fishing on spawning squids affect them? *Reports of California Cooperative Oceanic Fisheries Investigations*, 39: 92–100.

Hanlon, R.T. 2006. Key behavioral attributes of squid and cuttlefish spawning aggregations that warrant consideration for conservation and fisheries management. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 60.

***Hanlon, R.T & J.B. Messenger.** 1996. Cephalopod behaviour. *Cambridge University Press, UK*, 232 pp.

Hanlon, R.T., R.F. Hixon & W.H. Hulet. 1983. Survival, growth, and behavior of the loliginid squids *Loligo plei*, *Loligo pealei*, and *Lolliguncula brevis* (Mollusca: Cephalopoda) in closed sea water systems. *The Biological Bulletin of the Marine Biological Laboratory, Woods Hole*, 165(3): 637–685.

Hanlon, R.T., N. Kangas & J.W. Forsythe. 2004. Egg-capsule deposition and how behavioral interactions influence spawning rate in the squid *Loligo opalescens* in Monterey Bay, California. *Marine Biology*, 145: 923–930.

Hanlon, R.T., M.R. Maxwell & N. Shashar. 1997. Behavioral dynamics that would lead to multiple paternity within egg capsules of the squid *Loligo pealei*. *Biological Bulletin*, 193(2): 212–214.

Hanlon, R.T., M.J. Smale & W.H.H. Sauer. 1994. An ethogram of body patterning behavior in the squid *Loligo vulgaris reynaudii* on spawning grounds in South Africa. *The Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 187(3): 363–372.

Hanlon, R.T., M.J. Smale & W.H.H. Sauer. 2002. The mating system of the squid *Loligo vulgaris reynaudii* (Cephalopoda, Mollusca) off South Africa: Fighting, guarding, sneaking, mating and egg laying behaviour. *Bulletin of Marine Science*, 71(1): 331–345.

Hanlon, R.T., P.E. Turk & P.G. Lee. 1991. Squid and cuttlefish mariculture: an updated perspective. *Journal of Cephalopod Biology*, 2: 31–40.

Hanlon, R.T., R.F. Hixon, W.H. Hulet & W.T. Yang. 1979. Rearing experiments in the California market squid *Loligo opalescens* Berry, 1911. *Veliger*, 21(4): 428–431.

Hanlon, R.T., P.E. Turk, P.G. Lee & W.T. Yang. 1987. Laboratory rearing of the squid *Loligo pealei* to the juvenile stage: growth comparisons with fishery data. *Fishery Bulletin*, 85: 163–167.

Hanlon, R.T., R.F. Hixon, P.E. Turk, P.G. Lee & W.T. Yang. 1985. Behavior, feeding and growth of young *Loligo forbesi* (Cephalopoda: Myopsida) reared in the laboratory. *In*: K.M. Mangold & S.V. Boletzky, eds. Biology and distribution of early juvenile cephalopods. *Vie et Milieu*, 35(3–4): 247–248.

Hanlon, R.T., M.R. Maxwell, N. Shashar, E.R. Loew & K.L. Boyle. 1999. An ethogram of body patterning behavior in the biomedically and commercially valuable squid *Loligo pealei* off Cape Cod, Massachusetts. *Biological Bulletin*, 197(1): 49–62.

Hanlon, R.T., W.T. Yang, P.E. Turk, P.G. Lee & R.F. Hixon. 1989. Laboratory culture and estimated life span of Eastern Atlantic squid, *Loligo forbesi* Steenstrup, 1856 (Mollusca: Cephalopoda). *Aquaculture and Fishery Management*, 20: 15–33.

Hanlon, R.T., M.R. Maxwell, K.M. Buresch, S. Ring, N. Shashar & R.B. Sussman. 2002. Demonstration of multiple paternity within individual egg capsules of *Loligo pealeii*: Genetic and behavioral evidence from field and laboratory studies. *Bulletin of Marine Science*, 71(2): 1125–1126.

Hanlon R.T., S.v. Boletzky, T. Okutani, G. Perez-Gandaras, P. Sanchez, C. Sousda-Reis & M. Vecchione. 1992. Suborder Myposida Orbigny, 1845. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. Larval and Juvenile Cephalopods: A Manual for their identification. *Smithsonian Contribution to Zoology*, 513: 37–53.

Hanni, K.D., D.J. Long, R.E. Jones, P. Pyle & L.E. Morgan. 1997. Sightings and strandings of Guadalupe fur seals in central and northern California, 1988–1995. *Journal of Mammal*, 78(2): 684–690.

Harada, Y. & S. Hayashi. 1994. Horizontal and vertical distribution of young Japanese common squid, *Todarodes pacificus* in Toyama Bay and its adjacent waters of the Sea of Japan. *Bulletin Toyama Prefecutal Fisheries Experiment Station*, 5: 1–12.

Harcourt, R.G., C.J.A. Bradshaw, K. Dickson & L.S. Davis. 2002. Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series*, 227: 11–24.

Hardwick, J.E. & J.D. Spratt. 1979. Indices of the availability of market squid, *Loligo opalescens*, to the Monterey Bay fishery. *Reports of California Cooperative Oceanic Fisheries Investigations*, 20: 35–39.

Harman, R.F. & R.E. Young. 1985. The larvae of ommastrephid squids (Cephalopoda: Teuthoidea) from Hawaiian waters. *Vie Milieu*, 35(3/4): 211–222.

Harman, R.F., R.E. Young, S.B. Reid, K.M. Mangold, T. Suzuki & R.F. Hixon. 1989. Evidence for multiple spawning in the tropical oceanic squid, *Sthenoteuthis oualaniensis* (Teuthoidea: Ommmastrephidae). *Marine Biology*, 101(4): 513–519.

Harrison, C.S., T.S. Hida & M.P. Seki. 1983. Hawaiian seabird ecology. *Wildlife Monographs*, 85: 1–71.

Harting, P. 1860. Description de quelques fragments de deux cèphalopodes gigantesques. *Verhandelingen der Koninklijke Akademie van Wetenschappen, Amsterdam*, 9(1)[1861]: 16 pages, 3 plates. [Published as separate, 1860].

Hasan, A.K., R. Riad & M. Atta. 1994. Trophic relations of *Sepia officinalis* and *Loligo vulgaris* (Mollusca: Cephalopoda) in Alexandria waters. *Bulletin of the National Institute of Oceanography and Fisheries (Egypt)*, 20(1): 161–173.

Hastie, L.C. 1996. Estimation of trawl codend selectivity for squid (*Loligo forbesi*), based on Scottish research vessel survey data. *ICES Journal of Marine Science*, 53: 741– 744.

***Hastie, L.C., J.B. Joy & G.J. Pierce.** 1994. Reproductive biology of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Scottish coastal waters. *Journal of the Marine Biological Association of the United Kingdom*, 74: 367–382.

***Hastie, L.C., G.J. Pierce, J. Wang, I. Bruno, A. Moreno, U. Piatkowski & J.P. Robin.** 2009. Cephalopods in the north-eastern Atlantic: species, biogeography, ecology, exploitation and conservation. *Oceanography and marine biology: an annual review*, 47: 111–190.

Hatanaka, H. 1986. Growth and life span of short-finned squid *Illex argentinus* in the waters off Argentina. *Bulletin of Japan Sea Regional Fisheries Research Laboratory*, 52: 11–17.

Hatanaka, H. 1988. Feeding migration of short-finned squid *Illex argentinus* in the waters off Argentina. *Nippon Suisan Gakkaishi*, 54(8): 1343–1349.

Hatanaka, H., R.K. O'Dor & C.F.E. Roper. 1993. III. Population structure session. *In* T. Okutani, R.K. O'Dor & T. Kubodera, eds. Recent advances in cephalopod fisheries biology. Contributed papers to 1991 CIAC International Symposium and Proceedings of the Workshop on Age, Growth, and Population Structure. *Tokai University Press*, 752 pp.

***Hatanaka, H., S. Kawahara, Y. Uozumi & S. Kasahara.** 1985. Comparison of life cycles of five ommastrephid squids fished by Japan: *Todarodes pacificus*, *Illex illecebrosus*, *Illex argentinus*, *Nototodarus sloani sloani* and *Nototodarus sloani gouldi*. *Northwest Atlantic Fisheries Organization, Dartmouth*, 9: 59–68.

Hatanaka, H., T. Sato, J. Augustyn, A. Payne & R. Leslie. 1983. Report on the Japan/South Africa joint trawling survey on the Agulhas Bank in November/December 1980. *Japan Marine Fishery Resource Research Center*, 73 pp, 13 ref.

Hatate, H., H. Amagoi & J. Takahashi. 1999. Proteolytic activity in crude enzyme extracts from livers of squids and cuttlefish. *Journal National Fishery University Japan*, 47(3): 121–127.

Hatfield, E.M.C. 1991. Post-recruit growth of the patagonian squid *Loligo gahi* (d'Orbigny). *Bulletin of Marine Science*, 49: 349–361.

Hatfield, E.M.C. 1996. Towards resolving multiple recruitment into loginid fisheries: *Loligo gahi* in the Falkland Islands fishery. *ICES Journal of Marine Science*, 53(3): 565–575.

Hatfield, E.M.C. 1998. Seasonal temperature change affects the growth of the squid *Loligo gahi* (Chephalopoda: Loliginidae): 1. The length-at-age relationship. *Copenhagen Denmark ICES*, 23 pp.

Hatfield, E.M.C. 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: Loliginidae). *Fisheries Research Amsterdam*, 47(1): 27–40.

***Hatfield, E.M.C. & S.X. Cadrin.** 2002. Geographic and temporal patterns in size and maturity of the longfin inshore squid (*Loligo pealeii*) off the northeastern United States. *Fishery Bulletin*, 100: 200–213.

Hatfield, E.M.C. & S. des Clers. 1998. Fisheries management and research for *Loligo gahi* in the Falkland Islands. *Report of California Cooperative Oceanic Fisheries Investigations*, 39: 81–91.

***Hatfield, E.M.C. & P.G. Rodhouse.** 1991. Biology and fishery of the Patagonian squid *Loligo gahi* (d'Orbigny, 1835): A review of current knowledge. *Journal of Cephalopod Biology*, 2: 41–49.

Hatfield, E.M.C. & P.G. Rodhouse. 1994. Distribution and abundance of juvenile *Loligo gahi* in Falkland Island waters. *Marine Biology., 121(2): 267–272.*

Hatfield, E.M.C., P.G. Rodhouse & D.L. Barber. 1992. Production of soma and gonad in maturing female *Illex argentinus* (Mollusca: Cephalopoda). *Journal of the Marine Biological Association of the United Kingdom*, 72: 281–291.

Hatfield, E.M.C., P.G. Rodhouse & J. Porebski. 1990. Demography and distribution of the Patagonian squid (*Loligo gahi* d'Orbigny) during the austral winter. *Journal du Conseil, Counseil International pour l'Exploration de la Mer*, 46(3): 306–312.

Hatfield, E.M.C., P.G. Rodhouse & P.N. Trathan. 1991. Recruitment of seasonal broods of the Patagonian squid (*Loligo gahi* d'Orbigny) into the commercial fishery around the Falkland Islands: 1985 to 1990. *Copenhagen Denmark ICES*, 16 pp.

***Hatfield, E.M.C., R.T. Hanlon, J.W.. Forsythe & E.P.M. Grist.** 2001. Laboratory testing of a growth hypothesis for juvenile squid *Loligo pealeii* (Cephalopoda: Loliginidae). *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 845–857.

Haug, T. & T. Holthe. 1984. First record of the squid *Histioteuthis bonnellii* (Ferussac, 1835) from Norway. *Fauna Blindern*, 37(1): 22–25.

Haug, T., K.T. Nilssen & L. Lindblom. 2004. Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. *Polar Research*, 23(1): 35–42.

Hauksson, E. & V. Bogason. 1995a. Food of harp seals (*Phoca groenlandica* Erxleben, 1777), in Icelandic waters, in the period of 1990–1994. *ICES Council Meeting*, 1995/N:14.

Hauksson, E. & V. Bogason. 1995b. Occurrences of bearded seals (*Erignathus barbatus* Erxleben, 1777) and ringed seal (*Phoca hispida* Schreber, 1775) in Icelandic waters, in the period 1990–1994, with notes on their food. *ICES Copenhagen*, 7 pp.

Hayashi, K. 1996. Composition and distribution of lipids in different tissues of the arrow squid *Loligo bleekeri*. *Fishery Science*, 62(1): 84–87.

Hayashi, K. & K. Kawasaki. 1990. Diacyl glyceryl ethers in the flesh and liver of gonatid squid *Gonatopsis makko*. *Bulletin Japanese Society of Science and Fisheries*, 56(8): 1345.

Hayashi, K. & S. Yamamoto. 1987. Distribution of diacyl glyceryl ethers in the different tissues and stomach contents of gonatid squid *Berryteuthis magister*. *Bulletin of the Japanese Society of Fisheries*, 53(6): 1057–1063.

Hayashi, K., H. Kishimura & Y. Sakurai. 1990. Level and composition of diacyl glyceryl ethers in the different tissues and stomach contents of giant squid *Moroteuthis robusta*. *Japanese Society of Science and Fisheries*, 56(10): 1635–1639.

Hayashi, K., K. Uchiyama, S. Kasahara & T. Minami. 1987. Vertical distribution of eggs of the squid, *Watasenia scintillans* and some species of fishes in Toyama Bay, the Japan Sea. *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, 37: 163–174.

Hayashi, S. 1960. Development of the squid, *Ommastrephes sloani pacificus* (Steenstrup). *Bulletin Fac. Fish., Nagasaki University*, 9: 43–47.

Hayashi, S. 1987. Vertical distribution of eggs of the squid, *Watasenia scintillans* and some species of fishes in Toyama Bay, the Japan Sea. *Bulletin of Japan Sea Regional Fisheries Research Laboratory*, 37: 163–174.

Hayashi, S. 1989a. Occurrence of diacyl glyceryl ethers in liver lipids of gonatid squid *Gonatopsis borealis*. *Bulletin of Japanese Society of Fishery Oceanography*, 55(8): 1383–1387.

Hayashi, S. 1989b. Wax esters in the stomach content lipids of gonatid squid *Gonatopsis borealis*. *Bulletin of Japanese Society of Fishery Oceanography*, 55(8): 1463.

Hayashi, S. 1989c. Spawning behavior and embryonic development of the firefly squid, *Watasenia scintillans*. *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 1: 1–14.

***Hayashi, S.** 1991. Seasonal changes in distribution of eggs and paralarvae of Cephalopoda in Toyama Bay, the Japan Sea. *Bulletin of the Japanese Society of Fishery Oceanography*, 55(4): 315–322.

Hayashi, S. 1993. Growth and maturation of the firefly squid, *Watasenia scintillans* (Berry), in Toyama Bay and adjacent waters of the Sea of Japan. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 173–178.

Hayashi, S. 1994. Survival of the firefly squid, *Watasenia scintillans* in the rearing at different salinity levels. *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 5: 21–25.

***Hayashi, S.** 1995a. Spawning time of the day of firefly squid, *Watasenia scintillans*, assumed from set net catch. *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 6: 17–23.

*__Hayashi, S.__ 1995b. Fishery biological studies of the firefly squid, *Watasenia scintillans* (Berry), in Toyama Bay. *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 7: 1–128.

Hayashi, S. 1997. Effect of salinity on the hatching of firefly squid, *Watasenia scintillans* (Short Paper). *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 9: 45–48.

Hayashi, S. 2003. Recent trend in Oval Squid, *Sepioteuthis lessoniana*, Fishery in Toyama Bay. *Bulletin of Toyama Prefectural Fisheries Experiment Station*, 14: 11–28.

Hayashi, S. & K. Hirakawa. 1997. Diet composition of the firefly squid, *Watasenia scintillans*, from Toyama Bay, southern Japan Sea. *Bulletin of the Japan Sea National Fisheries Research Institute*, 47: 57–66.

Hayase, S., A.K.M. Mohsin & M.Z.M. Said. 1988. Length composition aspect for some demersal species. *In*: A.K.M. Mohsin, M.I.H. Mohamed & M. A. Ambak, eds. Ekspedisi Matahari ‘87. A Study on the Offshore Waters of the Malaysian EEZ, 8: 135–143.

Hayward, P., A. Nelson-Smith & C. Shields. 1999. Gids van kust en strand: flora en fauna [Coast and beach guide: flora and fauna]. Tirion: Baarn, Netherlands. ISBN 90–5210–327–5. 352, ill. pp.

Hedd, A. & R. Gales. 2001. The diet of shy albatrosses (*Thalassarche cauta*) at Albatross Island, Tasmania. *Journal of Zoology*, 253(1): 69–90.

*__Hemphill, H.__ 1892. Note on a Californian *Loligo*. *Zoe*, 3: 51.

*__Hendrix, J.P. Jr., W.H. Hulet & M.J. Greenberg.__ 1981. Salinity tolerance and the responses to hypoosmotic stress of the bay squid *Lolliguncula brevis*, a euryhaline cephalopod mollusc. *Comparative Biochemistry and Physiology*, 69A: 641–648.

Hendrickson, L.C. 1999. Fishery effects on spawner escapement in the northwest Atlantic *Illex illecebrosus* stock. *Science Council Research Document NAFO*, 99/66, 8 pp.

Hendrickson, L.C. 2004. Population biology of northern shortfin squid (*Illex illecebrosus*) in the Northwest Atlantic Ocean and initial documentation of a spawning area. *ICES Journal of Marine Science*, 61(2): 252–266.

Hendrickson, L.C. 2006. Distribution of northern shortfin squid (*Illex illecebrosus*) in Subarea 3 based on multi-species bottom trawl surveys conducted during 1995–2005. *Science Council Research Document NAFO*, 06/45, 5 pp.

Hendrickson, L.C. & D.R. Hart. 2006. An age-based cohort model for estimating the spawning mortality of semelparous cephalopods with an application to per-recruit calculations for the northern shortfin squid, *Illex illecebrosus*. *Fisheries Research*, 78(1): 4–13.

Hendrickson, L.C. & E.M. Holmes. 2004. Essential fish habitat source document: Northern shortfin squid *Illex illecebrosus*, life history and habitat characteristics. *NOAA Techinical Memorandum NMFS NE*, no. 191.

Hendrickson, L.C. & M.A. Showell 2006. Assessment of northern shortfin squid (*Illex illecebrosus*) in Subareas 3 and 4 for 2005. *Science Council Research Document NAFO*, 06/46, 16 pp.

Hendrickson, L.C., E.G. Dawe & M.A. Showell. 2001. Assessment of subarea 3 and 4 northern shortfin squid (*Illex illecebrosus*) for 2000. *Science Council Research Document NAFO*, 01/61, 13 pp.

Hendrickson, L.C., E.G. Dawe & M.A. Showell. 2002. Assessment of northern shortfin squid (*Illex illecebrosus*) in Subareas 3 and 4 for 2001. *Science Council Research Document NAFO*, 2/56, 17 pp.

Hendrickson, L.C., E.G. Dawe & M.A. Showell. 2003. Interim monitoring report for the assessment of northern shortfin squid (*Illex illecebrosus*) in Subareas 3 and 4 during 2002. *Science Council Research Document NAFO*, 3/48, 13 pp.

Hendrickson, L.C., E.G. Dawe & M.A. Showell. 2004. Assessment of northern shortfin squid (*Illex illecebrosus*) in Subareas 3 and 4 for 2003. *Science Council Research Document NAFO*, 4/38, 18 pp.

Hendrickson, L.C., E.G. Dawe & M.A. Showell. 2005. Interim monitoring report for the assessment of northern shortfin squid (*Illex illecebrosus*) in Subareas 3 and 4 during 2004. *Science Council Research Document NAFO*, 05/45, 9 pp.

Henry, A.E., J.D. McDaniel & C.D. Chan. 2005. Size differences, by sex, of adult market squid (*Loligo opalescens*) at harvest in distinct temperature areas near the Channel Islands. *Proceedings of the Sixth California Islands Symposium, Ventura, California*, December 1–3, 2003, 453–460.

Henry, K., V. Denis & J.P. Robin. 1998. Ommastrephid squids exploited by French trawlers: Preliminary analysis of stock structure based on Southern Brittany landings. *ICES 1998 Copenhagen*, 10 pp.

Heppel, D. 1992. A re-evaluation of the records of *Sthenoteuthis pteropus* (Steenstrup, 1855) (Cephalopoda: Ommastrephidae) from the British Isles. *Journal of Conchology*, 34: 125–138.

***Herke, S.W. & D.W. Foltz.** 2002. Phylogeography of two squid (*Loligo pealei* and *Loligo plei*) in the Gulf of Mexico and northwestern Atlantic Ocean. *Marine Biology*, 140: 103–115.

Hernandez-Andres, A., C. Gomez-Guillen, P. Montero & M. Perez-Mateos. 2005. Partial characterization of protease activity in squid (*Todaropsis eblanae*) mantle: modification by high-pressure treatment. *Journal of Food Science*, 70(4): 239–245.

Hernandez-Garcia, V. 1991. Distribution of flying squids (*Cephalopoda teuthoidea*) in the CECAF area (Preliminary results). *ICES 1991 Copenhagen*, 10 pp.

Hernandez-Garcia, V. 1992. Preliminary notes about feeding of three species of flying squids (Cephalopoda, Ommastrephidae) in the northwest Africa (CECAF area). *ICES 1992 Copenhagen*, 13 pp.

Hernandez-Garcia, V. 1995. The diet of the swordfish, *Xiphias gladius* Linnaeus, 1758, in the central eastern Atlantic, with emphasis on the role of cephalopods. *Fishery Bulletin*, 93: 403–411.

Hernandez-Garcia, V. 1995. Cephalopods from the CECAF area: Fishery and ecology role. *Copenhagen Denmark ICES*, 8 pp.

Hernández-Garcia, V. 2002a. Contents of the digestive tract of a false killer whale (*Pseudorca crassidens*) stranded in Gran Canaria (Canary Islands, central east Atlantic). *In* P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(1): 367–369.

***Hernàndez-García, V.** 2002b. Reproductive biology of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) off northwest Africa (4°N, 35°N). *Bulletin of Marine Science*, 71(1): 347–366.

Hernandez-García, V. & C. Bas. 1993. Size evolution analysis of exploited cephalopods on the Saharan coast (CECAF, Division 34.1.3) between 1967–70 and 1989–90. *Boletino del Instituto Espanol de Oceanografia*, 9(1): 215–225.

Hernandez-Garcia, V. & J.J. Castro. 1995. Reproductive biology of the subfamily Illicinae, *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae Steenstrup, 1857) off Northwest Africa. *ICES Copenhagen*, 10 pp.

Hernandez-Garcia, V. & B. Castro. 1996. On the cephalopod fishery off the southwest of Gran Canaria (Canary Island, Spain). *Copenhagen Denmark ICES*, 10 pp.

Hernandez-Garcia, V. & J.J. Castro. 1998. Morphological variability in *Illex coindetii* (Cephalapoda: Ommastrephidae) along the Northwest coast of Africa. *Journal of the Marine Biological Association of the United Kingdom*, 78: 1259–1268.

Hernández-García V. & V. Martín. 1994. Stomach contents of two short–finned pilot whale (*Globicephala macrorhynchus* Gray, 1846) (Cetacea, Delphinidae) off theCanary Islands: A preliminary note. *ICES Council Meeting*, /N:16.

***Hernandez-Garcia, V., U. Piatkowski & M.R. Clarke.** 1998. Development of the darkening of *Todarodes sagittatus* beaks and its relation to growth and reproduction. *South African Journal of Marine Science*, 20: 363–373.

***Hernandez-Herrera, A, E. Morales-Bojorquez, M.A. Cisneros-Mata, M.O. Nevarez-Marinez & G.I. Rivera-Parra.** 1998. Management strategy for the giant squid (*Dosidicus gigas*) fishery in the Gulf of California, Mexico. *Reports of California Cooperative Oceanic Fisheries Investigations*, 39: 212–218.

Herrera, A. 2001a. Review of stock assessment and fishery biology of *Dosidicus gigas* in the Gulf of California, Mexico. *Fisheries Research*, 54(1): 83–94.

Herring, P.J., P.N. Dilly & C. Cope. 1985. The photophore morphology of *Selenoteuthis scintillans* Voss and other lycoteuthids (Cephalopoda: Lycoteuthidae). *Journal of Zoology*, 206(4): 567–589.

***Herring, P.J., P.N. Dilly & C. Cope.** 1992a. Different types of photophores in the oceanic squids *Octopoteuthis* and *Taningia* (Cephalopoda: Octopoteuthidae). *Journal of Zoology*, 227: 479–491.

***Herring, P.J., E.A. Widder & S.H.D. Haddock.** 1992b. Correlation of bioluminescence emissions with ventral photophores in the mesopelagic squid *Abralia veranyi* (Cephalopoda: Enoploteuthidae). *Marine Biology*, 112(2): 293–298.

***Herring, P.J., P.N. Dilly & C. Cope.** 2002. The photophores of the squid family Cranchiidae (Cephalopoda: Oegopsida). *Journal of Zoology*, 258(1): 73–90.

Herrmann, M., H. Gonschior & U. Piatkowski. 2001. Hydrographic changes push European common squid *Alloteuthis subulata* into Kiel Bay, western Baltic Sea. *ICES Council Meeting*, 2001/K:13.

Herzenstein, S. 1885. Materialen zur Fauna der Murmankuste und des Weissen Meeres. *Trudy imp. S. peterb. Obshch. Estest.*, 16: 38–814.

Hess, S.C. 1987. Comparative morphology, variability, and systematic applications of cephalopod spermatophores (Teuthoidea and Vampyromorpha). University of Miami, Florida (Ph.D. dissertation. 597 pp.).

***Hibberd, T. & G.T. Pecl.** 2007. Effects of commercial fishing on the population structure of spawning southern calamary (*Sepioteuthis australis*). *Reviews in Fish Biology and Fisheries*, 17(2–3): 207–221.

***Hidaka, K. & T. Kubodera.** 2000. Squids of the genus Abralia (Cephalopoda: Enoploteuthidae) from the western tropical Pacific with a description of Abralia omiae, a new species. *Bulletin of Marine Science*, 66(2): 417–443.

***Hilgendorf, F.** 1880. Einen riesigen Dintenfisch aus Japan, *Megateuthis martensii* g.n., sp.n. Sitzungsbericht Gesellschaft naturforschender Freunde, Berlin, 4: 65–67.

Hill, S. & D.J. Agnew. 2002. Optimal harvest strategies for single–cohort squid populations. In Boyle, P.R., M.A. Collins & G.J. Pierce: Editors, Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(1): 371–381.

***Hixon, R.F.** 1980a. Growth, reproductive biology, distribution and abundance of three species of Loliginid squid (Myopsida, Cephalopoda) in the Northwest Gulf of Mexico. *Ph.D. Thesis, University of Miami, Coral Gables, Florida*, 233 pp.

Hixon, R.F. 1980b. Potential commercial squid resources of the Gulf of Mexico – an updated review. *In* M. Flandorfer & L. Skuplen, eds. *Proceedings of a workshop for potential fishery resources of the northern Gulf of Mexico*, 54–73.

***Hixon, R.F.** 1983. Loligo opalescens. *In*: P.R. Boyle, ed. Cephalopod Life Cycles. Vol I . Species Accounts. *Academic Press, London (UK)*, 95–114.

Hixon, R.F. & M.R. Villoch. 1984. Daily growth rings in the statoliths of young laboratory cultured squids (*Loligo opalescens*). *American Malacological Bulletin*, 2: 93.

Hixon, R.F., R.T. Hanlon & W.H. Hulet. 1981a. Growth, fecundity and estimated life span of three loliginid squid species in the northwestern Gulf of Mexico. *Journal of Shellfish Research*, 1(1): 116.

Hixon, R.F., R.T. Hanlon & W.H. Hulet. 1981b. Growth and maximal size of the long–finned squid Loligo pealei in the northwestern Gulf of Mexico. *Journal of Shellfish Research*, 1(2): 181–185.

Hjort, J. & J.T. Ruud. 1929. Whaling and fishing in the North Atlantic. *ICES, Rapports et Procès-Verbaux des Réunions,* 56(1): 1–123.

Ho, J.D., N.A. Moltschaniwskyj & G. Carter. 2004. The effect of variability in growth on somatic condition and reproductive status in the southern calamary *Sepioteuthis australis*. *Marine and Freshwater Research*, 55(4): 423–428.

Ho, J.S. & I.H. Kim. 2001. New species of *Doridicola* (Copepoda, Rhynchomolgidae) from Thailand, with a cladistic analysis of the genus. *Journal of Crustacean Biology*, 21(1): 78–89.

Hochachka, P.W., T.W. Moon, T. Mustafa & K.B. Storey. 1975. Metabolic source of power for mantle muscle of a fast swimming squid. *Comparative Biochemistry and Physiology,* B52(1): 151–158.

***Hochberg, F.G.** 1983. The parasites of cephalopods: a review. *In* C.F.E. Roper, C.C. Lu & F.G. Hochberg: Editors. Proceedings of the workshop on the biology and resource potential of cephalopods. *Memoirs of the National Museum of Victoria*, 44: 108–146.

Hochberg, F.G. 2003. New taxa of Cephalopoda described by Kir Nesis. *Ruthenica*, 13(1): 9–11.

***Hochberg, F.G.** 2006. *Gonatopsis octopedatus* Sasaki, 1920. Version 31 May 2006. http://tolweb.org/Gonatopsis_octopedatus/26879/2006.05.31 in The Tree of Life Web Project, http://tolweb.org/

Hochberg, F.G. & M. Nixon. 1992. Vampyromorpha. *In* M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky:, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 211–212.

Hochberg, F.G., M. Nixon & R.B. Toll. 1992. Octopoda. *In* M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 213–219.

Hoeger, U., T.P. Mommsen, R. O'Dor & D. Webber. 1987. Oxygen uptake and nitrogen excretion in two cephalopods, octopus and squid. *Comparative Biolchemisty and Physiology*, 87A(1): 63–67.

***Holme, N.A.** 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom*, 54: 481–503.

Hong, J.P. & J.H. Lee. 1995. Fluctuations of catches in set nets around Kyeongbuk Province. *Bulletin Korean Society of Fish Technology*, 31(2).

Honma, Y., T. Kitami & R. Mizusawa. 1983. Record of cephalopoda in the waters adjacent to Niigata and Sado Island in the Japan Sea, based partially on the pelagic squids stranded ashore. *Bulletin of Biogeography of Society of Japan*, 38: 23–29 (in Japanese).

Hooker, S.K., S.J. Iverson, P. Ostrom & S.C. Smith. 2001. Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. *Canadian Journal of Zoology; Review of Canadian Zoology*, 79(8): 1442–1454.

Hornborg S. 2005 The Swedish cephalopod fauna. Species composition and patterns of abundance. Master Thesis, University Göteborg.

Hotta, H. 1973. Identification of squids and cuttle fish in the adjacent waters of Japan, using the characteristics of beaks. *Seikai Regional Fisheries Research Laboratory*, 294: 133–147.

Hovde, S.C., O.T. Albert & E.M. Nilssen. 2002. Spatial, seasonal and ontogenetic variation in diet of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). *ICES Journal of Marine Science*, 59(2): 421–437.

Hoving, H.J.T., J.G.E. Gittenberger & J.J. Videler. 2006a. A male giant squid *Architeuthis* spec. (Cephalopoda, Architeuthidae) from the Fladen Ground in the northern North Sea. *Basteria*, 70: 153–160.

***Hoving, H.J.T., M.R. Lipinski & J.J. Videler.** 2006b. Reproductive system and the spermatophoric reaction of the mesopelagic squid *Octopoteuthis sicula* (Ruppell 1844) (Cephalopoda: Octopoteuthidae) from southern African waters. *African Journal of Marine Science*, 30(3): 603–612.

***Hoving, H.J.T., M.R. Lipinski & J.J. Videler.** 2008. Reproductive system and the spermatophoric reaction of the mesopelagic squid *Octopoteuthis sicula* (Ruppell 1844) (Cephalopoda: Octopoteuthidae) from southern African waters. *African Journal of Marine Science*, 30(3): 603–612.

***Hoving, H.J.T., M.R. Lipinski, M.A.C. Roeleveld & M.D.Y. Durholtz.** 2007. Growth and mating of southern African *Lycoteuthis lorigera* (Steenstrup, 1875) (Cephalopoda; Lycoteuthidae). *Reviews in Fish Biology and Fisheries*, 17(2–3): 259–270.

***Hoving, H.J.T., M.A.C. Roeleveld, M.R. Lipinski & Y. Melo.** 2004. Reproductive system of the giant squid *Architeuthis* in South African waters. *Journal of Zoology*, 264(2): 153–169.

***Hoving, H.J.T., M.A.C. Roeleveld, M.R. Lipinski & J.J. Videler.** 2006c. Nidamental glands in males of the oceanic squid *Ancistrocheirus lesueurii* (Cephalopoda: Ancistrocheiridae) – sex change or intersexuality? *Journal of Zoology London*, 269(3): 341–348.

Hoving, H.J.T., J.D. Venter, D.E. Worst & M.R. Lipinski. 2005. Adaptation of an immunodot assay for multiple prey identification of squid paralarvae in field trials. *Journal of the Marine Biological Association of the United Kingdom*, 85(6): 1499–1501.

Howard, F.G., M.A. Ngoile & J. Mason. 1987. *Loligo forbesi*: Its present status in Scottish fisheries. *Copenhagen Denmark ICES*, 9 pp.

Howell, S.B. 1867. Description of two new species of cephalopods. *American Journal of Conchology*, 3(2):239–241, 2 pls. [Published September, 1867].

***Hoyle, W.E.** 1885a. Diagnoses of new species of Cephalopoda collected during the Cruise H.M.S. 'Challenger'. Part II. The Decapoda. *Annals and Magazine of Natural History*, series 5, 16: 181–203.

***Hoyle, W.E.** 1885b. Narrative of the Challenger Expedition. Report on the Scientific results of the voyage of the H.M.S. Challenger during the years 1873–76, *Narrative*, 1(1): 269–274, 4 figs.

***Hoyle, W.E.** 1886. Report on the Cephalopods collected by H.M.S. Challenger during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger 1873–1876. *Zoology*, 16(44): 1–245.

***Hoyle, W.E.** 1904. Reports on the Cephalopoda. *Bulletin of the Museum of Comparative Zoology at Harvard College, in Cambridge*, 43(1):1–72, 12 pls.

*__Hoyle, W.E.__ 1910. A list of the generic names of Dibranchiate Cephalopoda with their type species. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 32: 407–413.

Hsieh, H.J., Y.L. Shen, W.S. Tsai, U. Chin-Shin & J. Ming-Shu. 2005. Preliminary investigation on the efficiency of the simply-equipped attracting device. *Penghu Marine Biology Research Center, TFRI, Taiwan*.

Huang, H., Y. Sheng & J. Cheng. 2003. Study on the biological characteristics of *Ommastrephes bartramii* in the North Pacific. *Marine Fisheries*, 25(3): 126–135.

Huang, M. 2004. Study on feeding habits and nutrient level of four cephalopod species from Taiwan Strait and its adjacent areas. *Journal of Oceanography in Taiwan Strait/Taiwan Haixia*, 23(3): 331–339.

Hume, F., M.A. Hindell, D. Pemberton & R. Gales. 2004. Spatial and temporal variation in the diet of a high trophic level predator, the Australian fur seal (*Arctocephalus pusillus doriferus*). *Marine Biology*, 144(3): 407–415.

Hunsicker, M.E & T.E. Essington. 2006. Size-structured patterns of piscivory of the longfin inshore squid (*Loligo pealeii*) in the mid-Atlantic continental shelf ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(4): 754–765.

*__Hunt, J.C.__ 1996. The behavior and ecology of midwater cephalopods from Monterey Bay: submersible and laboratory observations. *Ph.D. dissertation. University of California, Los Angeles*.

Hunt, J.C. & B.A. Seibel. 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): Ontogenetic changes in habitat, behaviour and physiology. *Marine Biology*, 136(3): 543–552.

Hunt, J.C., L.D. Zeidberg, W.M. Hamner & B.H. Robison. 2000. The behaviour of *Loligo opalescens* (Mollusca: Cephalopoda) as observed by a remote operated vehicle (ROV). *Journal of the Marine Biological Association of the United Kingdom*, 80: 873–883.

Hurley, A.C. 1976. Feeding behavior, food consumption, growth and respiration of the squid *Loligo opalescens* raised in the laboratory. *Fishery Bulletin*, 74(1): 176–182.

Hurley, A.C. 1977. Mating behavior of the squid *Loligo opalescens*. *Marine Behavior and Physiology*, 4(3): 195–203.

Hurley, A.C. 1978. School structure of the squid *Loligo opalescens*. *Fishery Bulletin*, 76(2): 433–442.

Ibanez, C.M. & L. Cubillos. 2007. Seasonal variation in the length structure and reproductive condition of the jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) off central-south Chile. *Scientia Marina (Barcelona)*, 71(1): 123–128.

Ibanez, C.M., C. Gonzalez & L. Cubillos. 2004. Diet of the swordfish *Xiphias gladius* Linnaeus, 1758 in oceanic waters off central Chile in winter 2003. *Investigiones Marinas*, 32(2): 113–120.

ICES Living Resources Committee. 2006. Report of the working group on Cephalopod fisheries and life history (WGCEPH). *International Council for the Exploration of the Sea*, C.M. G14:1–59.

Ichihashi, H., H. Kohno, K. Kannan, A. Tsumura & S.I. Yamasaki. 2001. Multielemental analysis of purpleback flying squid using high resolution inductively coupled plasma–mass spectrometry. *Environmental Science and Technology*, 35(15): 3103–3108.

Ichii, T. 2003. Red flying squid. *In*: State of International Fishery Resources. *Fisheries Research Agency*, 304–308 (In Japanese).

Ichii, T., K. Mahapatra, H. Okamura & Y. Oka. 2006. Stock assessment of the autumn cohort of neon flying squid (*Ommastrephes bartramii*) in the North Pacific based on past large-scale high seas driftnet fishery data. *Fisheries Research (Amsterdam)*, 78(2–3): 286–297.

Ichii, T., K. Mahapatra, M. Sakai & D. Inagake. 2006. Life cycle characteristics of the neon flying squid associated with oceanographic regime in the North Pacific. Cephalopod International Advisory Council Symposium 2006, Abstract.

Ichii, T., K. Mahapatra, M. Sakai, D. Inagake & Y. Okada. 2004. Differing body size between the autumn and the winter-spring cohorts of neon flying squid (*Ommastrephes bartramii*) related to the oceanographic regime in the North Pacific: a hypothesis. *Fisheries Oceanography*, 13(5): 295–309.

Ichii, T., K. Mahapatra, T. Watanabe, A. Yatsu, D. Inagake & Y. Okada. 2002. Occurrence of jumbo flying squid *Dosidicus gigas* aggregations associated with countercurrent ridge off the Costa Rica Dome during 1997 El Niño and 1999 La Niña. *Marine Ecology Progress Series*, 231: 151–166.

Ignell, S. 1991. The fisheries for neon flying squid (*Ommastrephes bartramii*) in the central North Pacific Ocean. *NOAA Technical Report*, 105: 97–111.

Ikeda, Y., Y. Sakurai & K. Shimazaki. 1991a. Development of female reproductive organs during sexual maturation in the Japanese common squid *Todarodes pacificus*. *Nippon Suisan Gakkaishi*, 57: 2243–2247 (in Japanese with English abstract).

Ikeda, Y., Y. Sakurai & K. Shimazaki. 1991b. Development of male reproductive organs during sexual maturation in the Japanese common squid *Todarodes pacificus*. *Nippon Suisan Gakkaishi*, 57: 2237–2241 (in Japanese with English abstract).

Ikeda, Y., Y. Sakurai & K. Shimazaki. 1993a. Maturation process of the Japanese common squid, *Todarodes pacificus* in captivity. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo*, 181–189 pp.

Ikeda, Y., Y. Sakurai & K. Shimazaki. 1993b. Fertilization capacity of squid (*Todarodes pacificus*) spermatozoa collected from various sperm storage sites, with special reference to the role of gelatinous substance from oviducal gland in fertilization and embryonic development. *Invertebrate Reproduction and Development*, 23: 39–44.

Ikeda, Y., N. Arai, H. Kidokoro & W. Sakamoto. 2003. Strontium: Calcium ratios in statoliths of Japanese common squid *Todarodes pacificus* (Cephalopoda: Ommastrephidae) as indicators of migratory behavior. *Marine Ecology Progress Series*, 251: 169–179.

Ikeda, Y., S. Onaka, H. Kidokoro & W. Sakamoto. 2003. Notes on an unusual catch of the juvenile diamond-shaped squid *Thysanoteuthis rhombus* in Pacific waters off southern Hokkaido. *Fisheries Science*, 69(3): 660–662.

Ikeda, Y., Y. Ueta, I. Sakurazawa & G. Matsumoto. 2004. Transport of the oval squid *Sepioteuthis lessoniana* Ferussac, 1831 *In*: Lesson 1830–1831 (Cephalopoda: Loliginidae) for up to 24 hours and subsequent transfer to an aquarium. *Fisheries Science*, 70(1): 21–27.

Ikeda, Y., Y. Wada, N. Arai & W. Sakamoto. 1999. Note on size variation of body and statoliths in the oval squid *Sepioteuthis lessoniana* hatchlings. *Journal of the Marine Biological Association of the United Kingdom*, 79(4): 757–759.

Ikeda, Y., A. Yatsu, N. Arai& W. Sakamoto. 2002. Concentration of statolith trace elements in the jumbo flying squid during El Niño and non–El Niño years in the eastern Pacific. *Journal of the Marine Biological Association of the United Kingdom*, 82(5): 863–866.

***Ikeda, Y., I. Sakurazawa, K. Ito, Y. Sakurai & G. Matsumoto.** 2005. Rearing of squid hatchlings, *Heterololigo bleekeri* (Keferstein 1866) up to 2 months in a closed seawater system. *Aquaculture Research*, 36(4): 409–412.

Ikeda, Y., I. Sakurazawa, K. Ohkawa, H. Yamada, M. Ichikawa, Y. Sakurai & G. Matsumoto. 2002. Initial trials on squid rearing, maintenance and experimentation at the Brain Science Institute of Riken. *Bulletin of Marine Science*, 71(2): 1128–1129.

Ikehara, K. 1968. Ecological aspect of the eggs and larvae of a few species of fish and squids, based on the materials taken by means of two kind plankton nets. *Bulletin of the Japan Sea National Fisheries Research Institute, Niigata*, 20: 71–82.

Ikehara, K., S. Kasahara, I. Okachi, T. Shimizu & M. Hamabe. 1977. Contributions of biological information useful for development of inshore squid fishery in the Japan Sea. 1. Ecological and maturity process in *Loligo edulis budo* Wakiya et Ishikawa fished in the waters around the Oki Islets in the western Japan Sea. *Bulletin of the Japan Sea National Fisheries Research Institute Niigata*, 28: 29–49.

Ilyinsky, E.N. 1991. Distribution of squids in the Okhotsk Sea pelagial in summer. *Oceanology*, 31(1): 151–154.

Imber, M.J. 1975. Lycoteuthid squids as prey of petrels in New Zealand seas. *New Zealand Journal of Marine and Freshwater Research*, 9(4): 483–492.

Imber, M.J. 1976. Comparison of prey of the black Procellaria petrels of New Zealand. *New Zealand Journal of Marine Freshwater Research*, 10: 119–130.

Imber, M.J. 1978. The squid families Cranchiidae and Gonatidae (Cephalopoda: Teuthoidea) in the New Zealand region. *New Zealand Journal of Zoology*, 5(3): 445–484.

Imber, M.J. 1992. Cephalopods eaten by wandering albatrosses (*Diomedea exulans* L.) breeding at six circumpolar localities. *Journal of the Royal Society of New Zealand*, 22(4): 243–263.

Imber, M.J. 1996. The food of Cook's petrel *Pterodroma cookii* during its breeding season on Little Barrier Island, New Zealand. *Emu*, 96(3): 189–194.

International Code of Zoological Nomenclature. 1995. Opinion 1973. *Chtenopteryx* Appellöf, 1890 (Mollusca, Cephalopoda): confirmed as the correct original spelling. *Bullletin of Zoological Nomenclature*, 52(1): 96–97.

***International Commission on Zoological Nomenclature.** (1999). International Code of Zoological Nomenclature, Fourth Edition. International Trust for Zoological Nomenclature, 1999, http://www.iczn.org/iczn/index.jsp.

Inoue, S., H. Kakoi & T. Goto. 1976. Squid bioluminescence 3. Isolation and structure of *Watasenia luciferin*. *Tetrahedron Letter*, 34: 2971–2974.

Inoue, S., S. Suguira, H. Kakoi, K. Hasizume, T. Goto & H. Iio. 1975. Squid bioluminiscence. 2. Isolation from *Watasenia scintillans* and synthesis of 2-(p-Hydroxybenzyl)-6-(p-Hydroxyphenyl) 3,7-dihydroimidazo(1,2-a) pyrazin-3 one. *Chemical Society of Japan*, 2: 141–144.

IREPA. 2002. Osservatorio economico sulle strutture produttive della pesca marittima in Italia [Economic observatory on the marine fishery productive structures in Italy]. Franco Angeli s.r.l., Milano, Italy, 312 pp.

Ish, T., E.J. Dick, P.V. Switzer & M. Mangel. 2004. Environment, krill and squid in the Monterey Bay: from fisheries to life histories and back again. *Deep Sea Research (Part II, Topical Studies in Oceanography)*, 51(6–9): 849–862.

Ishida, Y., T. Azumaya & M. Fukuwaka. 1999. Summer distribution of fishes and squids caught by surface gillnets in the western North Pacific Ocean. *Bulletin of National Fisheries Research Institute*, 63: 1–18.

Ishii, M. & M. Murata. 1976. Some information on the fishery and ecology of the squid, *Doryteuthis bleekeri*, Keferstein, in the coastal water of the Shiribeshi District in Hokkaido. *Bulletin of the Hokkaido Regional Fisheries Laboratory*, 41: 31–48.

***Ishikawa, C.** 1914. Uber eine neue art von *Enoploteuthis*, *Enoploteuthis chunii* (spec. nov.), aus Uwodu, Japanisches Meer. *Journal of the College of Agriculture, Imperial University of Tokyo*, 4(7):401–413, 2 pls.

***Ishikawa, C.** 1926. *Loligo yokoyae*, a new species of Myopsid Cephalopoda. *Proceedings of the Imperial Academy*, 2(1): 30–32.

***Ishikawa, C. & Y. Wakiya.** 1914. On a new species of *Moroteuthis* from the Bay of Sagami, *M. lonnbergii*. *Journal of the College of Agriculture, Imperial University of Tokyo*, 4(7):445–460, 2 pls.

***Ishikawa, M.** 1924. On the phylogenetic position of the cephalopod genera of Japan based on the structure of statocysts. *Journal of the College of Agriculture, Imperial University of Tokyo*, 7(3):165–210, 6 pls.

***Ishikawa, M.** 1929. On a new species of a luminous squid from the Sea of Japan. *Proceedings of the Imperial Academy of Japan*, 5(1):51–54, 1 fig.

Ishino, M., K. Iwasaki, K. Otsuka & K. Kihara. 1983. Demersal fish community in relation to the abiotic environmental conditions in the waters off Argentina. *Journal of the Tokyo University of Fisheries*, 70(1–2): 37–58.

Isoda, Y. & T. Azumaya. 1998. Response of fish population to the time-varying reproductive rate. *Bulletin of Fisheries Sciences. Hokkaido University*, 49(1): 1–14.

Isoda, Y., J.R. Bower & S. Hasegawa. 2005. Assessing environmental effects on recruitment of Japanese common squid (*Todarodes pacificus*) in the Japan Sea using a biomass dynamics model. *Bulletin of Fisheries Sciences, Hokkaido University*, 56(1); 19–31.

***Issel, R.** 1908. Diagnosi preliminari di un nuovo genre e di due nouve specie di Cefalopodi appartenenti alla fam. Cranchiidae raccolti dalla R. Nave "Liguria." *Monitore Zoologico Italiano*, 19(4):102–104.

Ito, K. 1998. Migration of *Loligo bleekeri* Keferstein in the coastal waters around Aomori Prefecture. *Bulletin of the Japanese Society of Fisheries Oceanography*, 62(4): 369–377.

***Ito, K.** 2002. Present Status Fisheries of *Loligo bleekeri* (Cephalopoda Loliginidae) in Japan. *Bulletin of the Aomori Prefecture Fishery Experimental Station*, 2: 1–10.

Ito, K. & Y. Sakurai. 2001. Effect of low temperature on embryonic development of *Loligo bleekeri* (Cephalopode:Loliginidae). *Bulletin of the Aomori Prefectural Fisheries Experiment Station.*, 1: 1–8.

Ito, K. & Y. Sakurai. 2006. Interannual catch fluctuations of *Loligo bleekeri* in northern Japan related to changing environmental conditions in coastal waters. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 78.

Ito, K., T. Yanagimoto, Y. Iwata, H. Munehara & Y. Sakurai. 2006. Genetic population structure of the spear squid *Loligo bleekeri* based on mitochondrial DNA. *Nippon Suisan Gakkaishi*, 72(5): 905–910.

Ivanov, B.G. (ed). 1986. Stock abundance and exploitation of squid in the World Ocean. *Moskva, USSR VNIRO*, 184 pp.

Ivanovic, M.L. & N.E. Brunetti. 1994. Food and feeding of *Illex argentinus*. *Antarctic Science*, 6(2): 185–193.

Ivanovic, M.L. & N.E. Brunetti. 2004. Diet of red squid (*Ommastrephes bartramii*) in the Southwest Atlantic. *Revista de invertigacion y desarrollo pesquero*, 16: 67–75.

Ivanovic, M.L., N.E. Brunetti, B. Elena & G.R. Rossi. 1998. A contribution to the biology of the ommastrephid squid *Martialia hyadesi* (Rochebrune and Mabille, 1889) from the southwest Atlantic. *South African Journal of Marine Science*, 20: 73–79.

Iverson, S.J., K.J. Frost & S.L.C. Lang. 2002. Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: Factors contributing to among and with species variability. *Marine Ecology Progress Series*, 241: 161–181.

Iwata, Y. & Y. Sakurai. 2007. Threshold dimorphism in ejaculate characteristics in the squid *Loligo bleekeri*. *Marine Ecology Progress Series*, 345: 141–146.

Iwata, Y., H. Munehara & Y. Sakurai. 2003. Characterization of microsatellite markers in the squid, *Loligo bleekeri* (Cephalopoda: Loliginidae). *Molecular Ecology Notes*, 3(3): 392–393.

Iwata, Y., H. Munehara & Y. Sakurai. 2005. Dependence of paternity rates on alternative reproductive behaviors in the squid *Loligo bleekeri*. *Marine Ecology Progress Series*, 298: 219–228.

*** Izuka, T., S. Segawa & T. Okutani.** 1996a. Biochemical study of the population heterogeneity and distribution of the oval squid *Sepioteuthis lessoniana* complex in southwestern Japan. *American Malacological Bulletin*, 12(1–2): 129–135.

*** Izuka, T., S. Segawa & T. Okutani.** 1996b. Identification of three species in oval squid, *Sepioteuthis lessoniana*, complex by chromatophore arrangements on the funnel. *Venus, Japanese Journal of Malacology*, 55: 139–142.

*** Izuka, T., S. Segawa, T. Okutani & K. Numachi.** 1994. Evidence of the existence of three species of the Oval Squid *Sepioteuthis lessoniana* complex in Ishigaki Island, Okinawa, Southwestern Japan, by isozyme analyses. *Venus, Japanese Journal of Malacology*, 3: 217–228.

Jackson, G.D. 1989. Age and growth of the tropical nearshore loliginid squid *Sepioteuthis lessoniana* determined from statolith growth-ring analysis. *Fishery Bulletin*, 88: 113–118.

Jackson, G.D. 1990. The use of tetracycline staining techniques to determine statolith growth ring periodicity in the tropical loliginid squids *Loliolus noctiluca* and *Loligo chinensis*. *Veliger*, 33: 389–393.

Jackson, G.D. 1991. What statoliths are telling us about tropical squid growth. *Bulletin of Marine Science*, 49(1–2): 663–664.

*** Jackson, G.D.** 1993. Seasonal variation in reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small tropical sepioid *Idiosepius pygmaeus*. *Fishery Bulletin*, 91: 260–270.

*** Jackson, G.D.** 1994a. Statolith age estimates of the loliginid squid *Loligo opalescens* (Mollusca: Cephalopoda): corroboration with culture data. *Bulletin of Marine Science*, 54(2): 554–557.

Jackson, G.D. 1994b. Application and future potential of statolith increment analysis in squid and sepioids. *Canadian Journal of Fisheries and Aquatic Science*, 51: 2612–2625.

Jackson, G.D. 1995a. Seasonal influences on statolith growth in the tropical nearshore squid *Loligo chinensis* (Cephalopoda: Loliginidae) off Townsville, North Queensland. *Fishery Bulletin*, 93: 749–752.

Jackson, G.D. 1995b. The use of beaks as tools for biomass estimation in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biology*, 15(1): 9–14.

Jackson, G.D. 1997. Age, growth and maturation of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biology*, 17(3): 268–274.

Jackson, G.D. 1998. Research into the life history of *Loligo opalescens*: where to from here? *Reports of California Cooperative Oceanic Fisheries Investigations*, 39: 101–107.

Jackson, G.D. 2001. Confirmation of winter spawning of *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in the Chatham Rise of New Zealand. *Polar Biology*, 24: 97–100.

Jackson, G.D. 2004. Advances in defining the life histories of myopsid squid. *Marine and Freshwater Research*, 55: 357–365.

Jackson, G.D. & J.H. Choat. 1992. Growth in tropical cephalopods: An analysis based on statolith microstructure. *Canadian Journal of Fisheries and Aquatic Science*, 49(2): 218–228.

***Jackson, G.D. & M.L. Domeier.** 2003. The effects of an extraordinary El Nino/La Nina event on the size and growth of the squid *Loligo opalescens* off Southern California. *Marine Biology*, 142: 925–935.

***Jackson, G.D. & J.W. Forsythe.** 2002. Statolith age validation and growth of *Loligo plei* (Cephalopoda: Loliginidae) in the north-west Gulf of Mexico during spring/summer. *Journal of the Marine Biological Association of the United Kingdom*, 82: 677–678.

Jackson, G.D. & C.H. Jackson. 2004. Mating and spermatophore placement in the onychoteuthis squid *Moroteuthis ingens*. *Journal of the Marine Biological Association of the United Kingdom*, 84(4): 783–784.

Jackson, G.D. & C.C. Lu. 1994. Statolith microstructure of seven species of Antarctic squid captured in Prydz Bay, Antarctica. *Antarctic Science*, 6 (2): 195–200.

Jackson, G.D. & B.L. McGrath-Steer. 2004. Arrow squid in southern Australian waters: supplying management needs through biological investigations. *IASOS*, Hobart, 156 pp.

Jackson, G.D. & J.F. McKinnon. 1996. Beak length analysis of arrow squid *Nototodarus sloanii* (Cephalopoda: Ommastrephidae) in southern New Zealand waters. *Polar Biology*, 16(3): 227–230.

Jackson, G.D. & P.V. Mladenov. 1994. Terminal spawning in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae). *Journal of Zoology*, 234(2): 189–201.

Jackson, G.D. & N.A. Moltschaniwskyj. 2001a. Temporal variation in growth rates and reproductive parameters in the small near–shore tropical squid *Loliolus noctiluca*; is cooler better? *Marine Ecology Progress Series*, 218: 167–177.

Jackson, G.D. & N.A. Moltschaniwskyj. 2001b. The influence of ration level on growth and statolith increment width of the tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae): an experimental approach. *Marine Biology*, 138(4): 819–825.

Jackson, G.D. & N.A. Moltschaniwskyj. 2002. Spatial and temporal variation in growth rates and maturity in the Indo–Pacific squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae). *Marine Biology*, 140: 747–754.

Jackson, G.D. & R.K. O'Dor. 2001. Time, space and the eco-physiology of squid growth, life in the fast lane. *Vie et Milieu*, 51 (4): 205–215.

Jackson, G.D. & S. O'Shea. 2003. Unique hooks in the male scaled squid *Lepidoteuthis grimaldi*. *Journal of the Marine Biological Association of the United Kingdom*, 83(4): 1099–1100.

Jackson, G.D. & G. Pecl. 2003. The dynamics of the summer-spawning population of the loliginid squid *Sepioteuthis australis* in Tasmania, Australia – a conveyor belt of recruits. *ICES Journal of Marine Science*, 60(2): 290–296.

Jackson, G.D. & V.A. Wadley. 1998. Age, growth, and reproduction of the tropical squid *Nototodarus hawaiiensis* (Cephalopoda: Ommastrephidae) off the North West Slope of Australia. *Fishery Bulletin*, 96(4): 779–787.

Jackson, G.D., N.G. Buxton & M.J.A. George. 2000a. Diet of the southern opah *Lampris immaculatus* on the Patagonian Shelf; the significance of the squid *Moroteuthis ingens* and anthropogenic plastic. *Marine Ecology Progress Series*, 206: 261–271.

***Jackson, G.D., J. Finn & S. Nicol.** 2002. Planktonic cephalopods collected off East Antarctica during the 'BROKE' survey. *Deep Sea Research Part I, Oceanographic Research Papers*, 49(6): 1049–1054.

Jackson, G.D., C.C. Lu & M. Dunning. 1991. Growth rings within the statolith microstructure of the giant squid *Architeuthis*. *Veliger*, 34(4): 331–334.

Jackson, G.D., R.K. O'Dor & Y. Andrade. 2005. First tests of hybrid acoustic/archival tags on squid and cuttlefish. *Marine and Freshwater Research*, 56(4): 425–430.

Jackson, G.D., A.G.P. Shaw & C. Lalas. 2000b. Distribution and biomass of two squid species off southern New Zealand, *Nototodarus sloanii* and *Moroteuthis ingens*. *Polar Biology*, 23: 699–705.

Jackson, G.D., S. Worterspoon & B.L. McGrath-Steer. 2005. Temporal population dynamics in arrow squid *Nototodarus gouldi* in southern Australian waters. *Marine Biology*, 146(5): 975–983.

***Jackson, G.D., S. Wotherspoon & C.H. Jackson.** 2007a. Temporal life history plasticity of the Southern Ocean squid *Todarodes filippovae* from waters off Tasmania, Australia. *Marine Biology*, 150(4): 575–584.

*__Jackson, G.D., J.W. Forsythe, R.F. Hixon & R.T. Hanlon.__ 1997. Age, growth, and maturation of *Lolliguncula brevis* (Cephalapoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length-frequency versus statolith age analysis. *Canadian Journal of Fishery and Aquatic Science*, 54(12): 2907–2919.

Jackson, G.D., B. McGrath-Steer, S. Wotherspoon & A.J. Hobday. 2003. Variation in age, growth and maturity in the Australian arrow squid *Nototodarus gouldi* over time and space – what is the pattern? *Marine Ecology Progress Series,* 264: 57–71.

Jackson, G.D., J.M. Semmens, K.L.. Phillips & C.H. Jackson. 2004. Reproduction in the deepwater squid *Moroteuthis ingens*, what does it cost? *Marine Biology – Berlin*, 145(5): 905–916.

Jackson, G.D., J.F. McKinnon, C. Lalas, R. Ardern & N.G. Buxton. 1998. Food spectrum of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biology*, 20(1): 56–65.

Jackson, G.D., P. Bustamante, Y. Cherel, E.A. Fulton, E.P.M. Grist, C.H. Jackson, P.D. Nichols, H. Pethybridge, K. Phillips, R.D. Ward & J.C. Xavier. 2007b. Applying new tools to cephalopod trophic dynamics and ecology: perspectives from the Southern Ocean Cephalopod Workshop, February 2–3, 2006. *Reviews in Fish Biology and Fisheries*, 17(2–3): 77–78.

Jaeckel, S. 1937 Tintenfische in der westlichen Ostsee. *Archiv für Molluskenkunde*, 69(4): 129–136.

Jakobsdottir, K.B. 2001. Biological aspects of two deep-water squalid sharks: *Centroscyllium fabricii* (Reinhardt, 1825) and *Etmopterus princeps* (Collett, 1904) in Icelandic waters. *Fisheries Research*, 51: 247–265.

James, G.D. & J.C. Stahl. 2000. Diet of southern Buller's albatross (*Diomedea bulleri bulleri*) and the importance of fishery discards during chick rearing. *New Zealand Journal of Marine and Freshwater Research*, 34(3): 435–454.

Jantzen, T.M. & J.N. Havenhand. 2002. Preliminary field observations of mating and spawning in the squid *Sepioteuthis australis*. *Bulletin of Marine Science*, 71(2): 1073–1080.

Jantzen, T.M. & J.N. Havenhand. 2003a. Reproductive behavior in the squid *Sepioteuthis australis* from South Australia: ethogram of reproductive body patterns. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 204(3): 290–304.

Jantzen, T.M. & J.N. Havenhand. 2003b. Reproductive behavior in the squid *Sepioteuthis australis* from South Australia: interactions on the spawning grounds. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 204(3): 305–317.

Januma, S., K. Miyajima & T. Abe. 2003. Development and comparative test of squid liver artificial bait for tuna longline. *Fisheries Science*, 69(2): 288–292.

Jaquet, N. 1996. How spatial and temporal scales influence understanding of sperm whale distribution: A review. *Mammalian Reviews*, 26(1): 51–65.

Jaquet, N. & D. Gendron. 2002. Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. *Marine Biology*, 141(3): 591–601.

Jaquet, N., D. Gendron & A. Coakes. 2003. Sperm whales in the Gulf of California: Residency, movements, behavior, and the possible influence of variation in food supply. *Marine Mammal Science*, 19(3): 545–562.

Jarre, A., M.D. Clarke & D. Pauly. 1991. Re-examination of growth estimates in oceanic squids: the case of *Kondakovia longimana* (Onychoteuthidae). *ICES Journal of Marine Science*, 48(2): 195–200.

Jarvis, E., K. Schiff, L. Sabin & M.J. Allen. 2007. Chlorinated hydrocarbons in pelagic forage fishes and squid of the southern California Bight. *Environmental Toxicology and Chemistry*, 26(11): 2290–2298.

Jayan, K., L. Jose, M.R. Raghunath & K. Devadasan. 1998. Tamarind fruit shell inhibits autolysis in mackerel and squid muscle. *In*: M.S. Hameed & B.M. Kurup, eds. Technological advancements in fisheries. *Proceedings of the National Symposium on Technological Advancements in Fisheries and its Impact on Rural Development held at Cochin by School of Industrial Fisheries, Cochin University of Science and Technology during December 5 to 7, 1995 Cochin India (CUSAT)*, 342–345

*__Jefferts, K.__ 1983. Zoogeography and systematics of cephalopods of the northeastern Pacific Ocean. Ph.D. thesis, Oregon State University, 291 p.

*__Jefferts, K.__ 1985. *Gonatus ursabrunae* and *Gonatus oregonensi*s, two new species of squids from the northeastern Pacific Ocean (Cephalopoda: Oegopsida: Gonatidae). *Veliger*, 28(2): 159–174.

Jefferts, K. 1992. Ctenopterygidae. *In* M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 125–126.

Jefferts, K., J. Burczynski & W.G. Pearcy. 1987. Acoustical assessment of squid (*Loligo opalescens*) off the Central Oregon coast. *Canadian Journal of Fishery and Aquatic Science*, 44(6): 1261–1267.

⋆**Jefferts, K. & C.F.E. Roper.** 1992. Cycloteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 161–163.

Jereb, P. & S. Agnesi. 2005. Review of cephalopod culture and capture fisheries: the Italian situation. *CEPHSTOCK, Final Report, Deliverable* D07.3–4, Annex 6.

Jereb, P. & S. Agnesi. 2009. Current state of knowledge on exploited cephalopods in the Italian waters. *Bollettino Malacologico*, 45: 11–116.

Jereb, P. & S. Ragonese. 1986. Un esemplare di *Loligo forbesi* (Steenstrup, 1856) di notevoli dimensioni proveniente dalla pesca locale di Mazara del Vallo (Canale di Sicilia). [A large size specimen of *Loligo forbesi* (Steenstrup, 1856) from the local fishery of Mazara del Vallo (Sicilian Channel)]. *Nova Thalassia*, 8 Suppl. 3: 675–676.

Jereb, P. & S. Ragonese. 1990. Sui cefalopodi di scarso o nullo interesse commerciale nel Canale di Sicilia. *Oebalia, Supplemento*, Vol. XVI–2: 689–692.

Jereb, P. & S. Ragonese. 1992 [1991]. The association of the squid *Illex coindetii* (Cephalopoda) with target species trawled in the Sicilian Channel. *Bulletin of Marine Science*, 49: 664.

Jereb, P. & S. Ragonese. 1994. The Mediterranean teuthofauna: Towards a biogeographical coverage by regional census. II: Strait of Sicily. *Bollettino Malacologico*, 30(5–9): 161–172.

Jereb, P. & S. Ragonese. 1995a. Nidamental glands and maturity stages in *Illex coindetii* (Mollusca: Cephalopoda) of the Strait of Sicily (Central Mediterranean. *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 34: 247.

⋆**Jereb, P. & S. Ragonese.** 1995b. An outline of the biology of the squid *Illex coindetii* in the Sicilian Channel (Central Mediterranean). *Journal of the Marine Biological Association of the United Kingdom* ,75: 373–390.

⋆**Jereb, P. & C.F.E. Roper (eds).** 2005. Cephalopods of the World. An annotated and illustrated catalogue of cephalopod species known to date. Volume 1. Chambered nautiluses and sepioids(Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). *FAO Species Catalogue for Fishery Purposes*, 4(1): 262 p., 9 colour pls.

⋆**Jereb, P. & C.F.E. Roper.** 2006. Cephalopods of the Indian Ocean. A review. Part I. Inshore squids (Loliginidae) collected during the International Indian Ocean Expedition. *Proceedings of the Biological Society of Washington*, 119(1): 91–136.

Jereb, P., S. Ragonese & F. Bertolino. 1996. *Chiroteuthis veranii* in the Strait of Sicily. *Biologia Marina Mediterrean*, 3(1): 637–638.

⋆**Jereb, P., S. Ragonese & S. von Boletzky (eds).** 1991. Squid age determination using statoliths. Proceedings of the International Workshop held in the Istituto di Technologia dell Pesca e del Pascato. *NTR.–ITPP Special Publications*, No. 1: 128 pp.

Jereb, P., D. Massi, G. Norrito & F. Fiorentino. 2001. Preliminary observations of environmental effects on spatial distribution and abundance of *Eledone cirrhosa* and *Illex coindetii* in the Strait of Sicily (Central Mediterranean Sea). *ICES Council Meeting*, 2001/K:34.

Jereb, P., S. Ragonese, A.I. Arkhipkin, A. Bonanno, M. Gioiello, U. Morara & M. Bascone. 1996. Sicilian Channel squid stocks: *Loligo forbesi* Steenstrup, 1856. *Research Project*, MED 93/010 – EU DGXIV. *Final Report*, 223 pp., 6 App.

Jerez, B., M.I. Roldan & C. Pla. 1998. Biochemical genetics in the Argentinean squid, *Illex argentinus*. *Scientia Marina., 62(1–2): 141–149.*

Jivaluk, J. 2000. Distribution of planktonic malacostraca and cephalopod paralarvae in the South China Sea, Area 3: Western Philippines. *Proceedings of the third Technical Seminar on Marine Fishery Resources Survey in the South China Sea, Area 3: Western Philippines*, 41: 177–196.

⋆**Jivaluk, J.** 2001. Composition, abundance and distribution of zooplankton in the South China Sea, area 4: Vietnamese waters. *Special Paper Southeast Asian Fisheries Development Center*, 44: 77–93.

*⁎**Jivaluk, J., J. Nabhitabhata, A. Nateewathana & P. Watprasit.** 2005. Description of Thai type of bigfin reef squid, *Sepioteuthis lessoniana*, hatchling with note on comparison to Japanese types. *Phuket Marine Biological Center Research Bulletin*, 66: 117–126, 5 figs.

Johnsen, S., E.A. Widder & C.D. Mobley. 2004. Propagation and perception of bioluminescence: factors affecting counterillumination as a cryptic strategy. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 207(1): 1–16.

Johnson, F.E.W. 1986. A multidisciplinary investigation of the hemocytogenic nature of the white bodies of the ommastrephid *Illex illecebrosus* (Lesueur, 1821) (Cephalopoda: Coleoidea). *Dissertation Abstracts International Part B: Science and Engineering*, 46(11).

Johnson, F.E.W. 1987. The vasculature of the white bodies in the ommastrephid squid *Illex illecebrosus* (Lesueur, 1821): A proposed route for the dissemination of newly formed hemocytes. *Canadian Journal of Zoology*, 65(7): 1607–1620.

Jones, M.R.L. 2007. Historic trawl data and recent information infers temporal change in the occurrence of squid in the diet of orange rouphy (*Hoplostethus atlanticus* Collett) in New Zealand. *Reviews in Fish Biology and Fisheries*, 17(2–3): 493–499.

Jonsson, E. 1980. Biological studies on squid, *Todarodes sagittatus* in Icelandic waters during the autumn 1979 with notes on its distribution and migration. *Hafrannsoknarstofnun Fjolrit*, 7: 1–14 (In Icelandic, English summary).

Jonsson, E. 1998. Study of European flying squid, *Todarodes sagittarius* (Lamarck), occurring in deep waters south of Iceland. *ICES Copenhagen*, 1998, 13 pp.

⁎**Jorgensen, E.** 2007. Identification, distribution, and relative abundance of paralarval gonatid squids (Cephalopoda: Oegopsida: Gonatidae) from the Gulf of Alaska, 2001–2003. *Journal of Molluscan Studies*, 73: 155–165.

Joseph, J., P.A. Perigreen & M.R. Nair. 1985. Effect of raw material quality on the shelf-life of frozen squid (*Loligo duvaucelii*) mantles. *Proceedings of the meeting of the Commission C2 and D3 Aptitude a la conservation des poissons et produits de la mer refrigeres, Aberdeen*, 103–109 pp.

⁎**Jothinayagam, J.T.** 1987. Cephalopoda of the Madras Coast. Zoological Survey of India. *Technical Monograph*, 15: 1–85, 29 figs, 3 pls.

⁎**Joubin, L.** 1894. Céphalopodes d'Amboine. *Revue Suisse de Zoologie et Annales du Musée d'Historie Naturelle le Geneva*, 2: 23–64, 4 pls.

Joubin, L. 1895a. Contribution a l'Estude des Céphalopodes de l'Atlantique Nord. *Résultats des campagnes scientifiques accomplies sur yacht par Albert I Prince souverain de Monaco*, 9: 1–63, 6 pls.

⁎**Joubin, L.** 1895b. Céphalopodes recueillis dans l'estomac d'cachalot, capture aux isles Acores. *Comptes rendus des seances de l'Academie des Sciences*, 121: 1172–1174, 1 fig.

⁎**Joubin, L.** 1896. Observations sur divers Céphalopodes. Premiere Note: *Abraliopsis pfefferi* (nov. gen. et spec.). *Bulletin de la Societe Scientifique et Medicale de l'Ouest*, 5(1): 19–35, 10 figs.

⁎**Joubin, L.** 1898a. Note sur une nouvelle famille de Céphalopodes. *Annales des Sciences Naturelles, Zoologie*, (series 8)6: 279–292, 9 figs.

⁎**Joubin, L.** 1898b. Sur quelques céphalopodes du Musée Royale de Leyde et description de trois espèces nouvelles. *Notes from the Leyden Museum*, 20(2): 21–28.

⁎**Joubin, L.** 1898c. Observations sur divers Céphalopodes. Quatrieme note: *Grimalditeuthis richardi*. *Bulletin de la Société Zoologique de France*, 23: 101–113, 2 figs.

⁎**Joubin, L.** 1900. Cephalopodes provenant des campagnes de la Princesse-Alice (1891–1897). *Resultats des campagnes scientifiques accomplies sur son yacht par Albert I Prince souverain de Monaco*, 17: 1–135, 15 pls.

⁎**Joubin, L.** 1912. Sur les Céphalopodes captures en 1911 par S.A.S. le Prince de Monaco. *Comptes Rendus des seances de l'academic des Sciences*, 154: 395–397.

⁎**Joubin, L.** 1913. Estudes préliminaires sur les Céphalopodes recueillis au cours des croisières de S.A.S. le Prince de Monaco. 3^{e} Note: *Mastigoteuthis magna* nov. sp. *Bulletin de l'Institut Oceanographique*, 275: 1–11, 1 fig.

⁎**Joubin, L.** 1916. Estudes préliminaires sur les Céphalopodes recueillis au cours des croisières de S.A.S. le Prince de Monaco. 4^{e} Note: *Chiroteuthis portieri* nov. sp. *Bulletin de l'Institut Océanographique*, 317: 1–10, 3 figs.

*****Joubin, L.** 1919. Estudes preliminaires dur les Céphalopodes recueillis au cours des croisières de S.A.S. le Prince de Monaco. 7e Note: *Cycloteuthis sirventi* nov. gen. et sp. *Bulletin de l'Institut Oceanographique*, 351: 1–7, 2 figs.

*****Joubin, L.** 1920. Céphalopodes provenant des Campagnes de la Princesse-Alice (1898–1910). *Résultats des Campagnes scientitiques accomplies sur son yacht par Albert I Prince souverain de Monaco*, 54 :1–95, 16 pls.

*****Joubin, L.** 1924. Contributin a l'Éstude des Céphalopodes de l'Atlantique nord. *Resultats des Campagnes scientifiques accomlies sur son yacht par Albert I Prince souverain de Monaco*, 67: 1–113, 14 pls.

*****Joubin, L.** 1931. Notes preliminaires sur les Céphalopodes des croisières du DANA (1921–1922), 3e Partie. *Annals de l'Institut Oceanographique*, (new series)10(7): 169–211, 48 figs.

*****Joubin, L.** 1932. Note sur l'appareil reproducteur d'un céphalopode nouveau: *Chiropsis mega*. *Bulletin de la Societe Zoologique de France*, 57: 288–291.

*****Joubin, L.** 1933. Notes préliminaires sur les Céphalopodes des croisières du DANA (1921–1922), 4e Partie. *Annals de l'Institut Océanographiques*, 13(1): 1–49, 48 figs.

Joy, J.B. 1990. The fishery biology of *Todarodes sagittatus* in Shetland waters. *Journal of Cephalopod Biology. 1(2): 1–19.*

Juanico, M. 1983. Squid maturity scales for population analysis. *In*: J.F. Caddy, ed. Advances in Assessement of World Cephalopod Resources. *FAO Fisheries Technical Paper*, 231: 341–378.

*****Judkins, H., D.A. Ingrao & C.F.E. Roper.** (2009). First records of *Asperoteuthis acanthoderma* (Lu 1977) (Cephalopoda: Oegopsida: Chiroteuthidae) from the North Atlantic Ocean, Straits of Florida. *Proceedings of the Biological Society of Washington*, 122(2): 162–170.

Kajimura, H., C.H. Fiscus & R.K. Stroud. 1980. Food of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, Dall's porpose, *Phocoenoides dalli* and northern fur seal, *Callorhinus ursinus*, off California and Washington: with appendices on size and food of Dall's porpoise from Alaskan waters. *NOAA Technical Memo*, 33 p.

Kami, A.S., K. Miyajima & T. Abe. 2003. Development and comparative test of squid liver artificial bait for tuna longline. *Fisheries Science*, 69(2): 288–292.

Kang, D., T. Mukai, K. Iida, D. Hwang & J.G. Myoung. 2005. The influence of tilt angle on the acoustic target strength of the Japanese common squid (*Todarodes pacificus*). *ICES Journal of Marine Science*, 62(4): 779–789.

Kang, D., K. Iida, K. Mukai & J. Kim. 2006. Density and sound speed contrasts of the Japanese common squid *Todarodes pacificus* and their influence on acoustic target strength. *Fisheries Science Tokyo*, 72(4): 728–736.

Kang, D., D. Hwang, T. Mukai, K. Iida & K. Lee. 2006. Acoustic target strength of live Japanese common squid (*Todares pacifica [pacificus]*) for applying biomas estimation. *Journal of the Korean Fisheries Society*, 37(4): 345–353.

Kang, Y.J., Y.H. Kim, Y.K. Hong, J.Y. Park & K.Y. Park. 1996. A population genetic analysis of the common squid, *Todarodes pacificus* Steenstrup in the Korean waters. *Journal Korean Fishery Society*, 29(3): 320–331 (in Korean with English summary).

Kapel, F.O. & L.A. Angantyr. 1989. Feeding patterns of harp seals (*Phoca groenlandica*) in coastal waters of West Greenland, with a note on offshore feeding. *Copenhagen Denmark ICES*, 29 pp.

Kariyama, M., M. Nakamura, R. Edpalina, J.R. Bower, H. Yamaguchi, R.V. Walker & K.W. Myers. 2000. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fisheries Oceanography*, 13(3): 197–207.

Kariyama, M., M. Nakamura, M. Yamaguchi, H. Ueda, G. Anma, S. Takagi, K.Y. Aydin, R.V. Walker & K.W. Myers. 2000. Feeding ecology of sockeye and pink salmon in the Gulf of Alaska. *NPAFC Bulletin, Japan*, 2: 55–63.

Karnik, N.S., & S.K. Chakraborty. 2001. Length-weight relationship and morphometric study on the squid *Loligo duvauceli* (d'Orbigny) (Mollusca: Cephalopoda) off Mumbai (Bombay) waters, west coast of India. *Indian Journal of Marine Sciences*, 30: 261–263.

Karnik, N.S., S.K. Chakraborty, A.K. Jaiswar, R.P. Swamy, R. Rajaprasad, S. Boomireddy & A.F. Rizvi. 2003. Growth and mortality of Indian squid, *Loligo duvauceli* (d'Orbigny) (Mollusca: Cephalopoda: Teuthoidea) from Mumbai waters, India. *Indian Journal of Marine Sciences*, 32: 67–70.

*****Karpov, K.A. & G.M. Cailliet.** 1978. Feeding dynamics of *Loligo opalescens*. *California Department of Fish and Game, Fishery Bulletin*, 169: 45–66.

***Karpov, K.A. & G.M. Cailliet.** 1979. Prey composition of the market squid, *Loligo opalescens* Berry, in relation to depth and location of capture, size of squid, and sex of spawning squid. *Reports of California Cooperative Oceanic Fisheries Investigations*, 20: 51–57.

Kasamatsu, C., S. Kimura, M. Kagawa & K. Hatae. 2004. Identification of high molecular weight proteins in squid muscle by western blotting analysis and postmortem rheological changes. *Bioscience, Biotechnology and Biochemistry*, 68(5): 1119–1124.

***Kashiwada, J. & C.W. Recksiek.** 1978a. Possible morphological indicators of population structure in the market squid, *Loligo opalescens*. *In*: Biological, oceanographic and acoustic aspects of the market squid, *Loligo opalescens* Berry. *Fishery Bulletin of the California Department of Fish and Game*, p. 99–111.

***Kashiwada, J. & C.W. Recksiek.** 1978b. Beaks of the market squid, *Loligo opalescens*, as tools for predator studies. *Reports of California Cooperative Oceanic Fisheries Investigations*, 20: 65–69.

Kasim, H.M. 1985. Population dynamics of the squid *Loligo duvaucelii* D'Orbigny (Cephalopoda) in Saurashtra waters. *Journal of the Marine Biological Association of India*, 1985. 27(1–2): 103–112.

Kaspiris, P. & P. Tsiambaos. 1984. Some uncommon cephalopods from western Korinthiakos Gulf (Mollusca-Dibranchiata). *Biljeske Notes*, 49: 1–5.

Katagan, T. & A. Kocatas. 1990. Note preliminaire sur les Cephalopodes des les Eaux Turques. *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 32: 242.

Katagan, T., A. Salman & H.A. Benli. 1993. The cephalopod fauna of the Sea of Marmara. *Israel Journal of Zoology*, 39: 255–261.

Katara, I. & A. Palialexis. 2003. Relations among fisheries and environmental data in Greek seas using remote sensing and GIS. 7th Hellenic Symposium on Oceanography and Fisheries Chersonissos, Greece, 6–9 May 2003, Abstracts, 193 p.

Kato, M. & I. Mitani. 2001. Comparison of catch, CPUE, and sea surface temperature in the fishing ground between good and poor fishing years for the suqid jigging fishery target New Zealand southern arrow squid *Nototodarus sloanii* in New Zealand waters. *Bulletin of the Kanagawa Prefectural Fisheries Research Institute*, 6: 35–46.

Katsanevakis, S., M. Thessalou-Legake, C. Karlou-Riga, E. Lefkaditou, E. Dimitriou & G. Verriopoulos. 2007. Information-theory approach to allometric growth of marine organisms. *Marine Biology*, 151(3): 949–959.

Katugin, O.N. 1993. Genetic variation in the squid *Berryteuthis magister* (Berry, 1913) (Oegopsida: Gonatidae). *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 201–213.

Katugin, O.N. 1995. Genetic differentiation in *Berryteuthis magister* from the North Pacific. *Copenhagen Denmark ICES*, 199: 459–467.

***Katugin, O.N.** 1999. Intraspecific genetic variation and population differentiation of the squid *Berryteuthis magister* in the North Pacific Ocean. *Russian Journal of Marine Biology*, 25(1): 34–45.

***Katugin, O.N.** 2000a. A new subspecies of the schoolmaster gonatid squid, *Berryteuthis magister* (Cephalopoda: Gonatidae), from the Japan Sea. *Veliger*, 43(1): 82–97.

Katugin, O.N. 2000b. Studies of biochemical genetic population structure of the common squid (*Todarodes pacificus* Steenstrup, 1880) from the Japan Sea. I. Genetic variation of the species as revealed from protein electrophoresis. *Ruthenica*, 10(1): 53–70.

***Katugin, O.N.** 2002. Patterns of genetic variability and population structure in the North Pacific squids *Ommastrephes bartramii*, *Todarodes pacificus* and *Berryteuthis magister*. *Bulletin of Marine Science*, 71(1): 383–420.

Katugin, O.N. 2003. The gonatid squids – why do some of them become watery upon maturation? *In*: Cephalopod International Advisory Council Symposium 2003, Phuket. Abstract: 46 p.

***Katugin, O.N.** 2004. Squids of the family Gonatidae from the North Pacific Ocean and their genetic differentiation: controversial issues in the systematics and phylogeny. *Ruthenica*, 14(1): 73–87.

***Katugin, O.N. & A.Y. Merzlyakov.** 2002. Spent females of *Gonatus madokai* (Teuthida: Oegopsida) from the Okhotsk Sea. *In*: *1st International Workshop of Squids, 2nd International Symposium of Pacific Squids*, Abstract, p. 39–40.

Katugin, O.N. & N.M. Mokrin. 2001. Studies of biochemical genetic population structure of the common squid (*Todarodes pacificus* Steenstrup, 1880) from the Japan Sea. II. Genetic differences between intraspecific seasonal cohorts. *Ruthenica*, 11(1): 57–76.

Katugin, O.N. & G.A. Shevtsov. 2004. Patterns of distribution and biology of the North Pacific oceanic squid *Berryteuthis anonychus* with implications for the species life cycle. Abstract In: PICES XIII, Annual Meeting, Honolulu, Hawaii, USA, Abstract: 6–7.

***Katugin, O.N. & G.A. Shevtsov.** 2006. Early life stages of the Gonatidae (Teuthida: Oegopsida): ontogenetic changes in external morphology. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 80.

Katugin, O.N. & E.V. Slobodskoy. 2004a. Size structure and genetic variability in the squid *Ommastrephes bartramii* (Cephalopoda, Ommastrephidae) from the northwest Pacific Ocean. *In*: "*Mollusks of the Northeastern Asia and Northern Pacific: Biodiversity, Ecology, Biogeography and Faunal History*", Vladivostok, Russia: 69–72.

Katugin, O.N. & E.V. Slobodskoy. 2004b. Population structure of the North Pacific oceanic squid *Ommastrephes bartramii* as inferred from variability in biological traits and genetic markers. *PICES 13th Annual Meeting Book of Abstracts*, 7 p.

Katugin, O.N. & N.N. Zuev. 2004. Distribution of cephalopods near the bottom in the northwestern Bering Sea. *In*: *Molluscs of the Northeastern Asia and Northern Pacific: Biodiversity, Ecology, Biogeography and Faunal History*, Vladivostok, Russia: 72–75.

Katugin, O.N. & N.N. Zuev. 2007. Distribution of cephalopods in the upper pelagic northwestern Bering Sea in autumn. *Reviews in Fish Biology and Fisheries*, 17(2–3): 283–294.

Katugin, O.N., A.M. Berkutova & G.E. Gillespie. 2004a. Morphometric variation in the gladii of the squid *Berryteuthis magister* (Berry, 1913) from different regions of the North Pacific. *In*: *Molluscs of the Northeastern Asia and Northern Pacific: Biodiversity, Ecology, Biogeography and Faunal History*, Vladivostok, Russia: 62–66.

***Katugin, O.N., G.A. Shevtsov & M.A. Zuev.** 2004b. Distribution, biology, and life cycle of *Gonatus madokai* (Cephalopoda, Gonatidae) in the Sea of Okhotsk and Pacific waters off the Kuril Islands. *In*: *Molluscs of the Northeastern Asia and Northern Pacific: Biodiversity, Ecology, Biogeography and Faunal History*, Vladivostok, Russia: 66–69.

Katugin, O.N., G.A. Shevtsov & M.A. Zuev. 2006a. Distribution and life cycle patterns of the squids *Gonatopsis octopedatus* and *Gonatopsis japonicus* (Cephalopoda: Gonatidae) in the northwestern Pacific Ocean. Abstract *In*: *PICES XV*, Annual Meeting, Yokohama, Japan: 54–55.

***Katugin, O.N., N.N. Zuev & V.D. Didenko.** 2006b. Spatial and vertical distribution of cephalopods in the western Bering Sea in autumn 1990. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 81.

***Katugin, O.N., G.A. Shevtsov & M.A. Zuev.** 2008. Distribution of squid *Gonatopsis japonicus* (Cephalopoda, Gonatidae) in the Sea of Okhotsk and northwestern Pacific Ocean. *Zoologicheskyi Zhurnal (Russian Zoological Journal)*, 87(8): 899–911 (In Russian, English summary).

Katugin, O.N., A.R. Lindgren, E. Amezquite & M.K. Nishiguchi. 2006c. Squids of the family Gonatidae – genetic relationships. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 36.

***Katugin, O.N., A.Y. Merzlyakov, N.S. Vanin & A.F. Volkov.** 2004c. Distribution patterns for the gonatid squid *Gonatus madokai* in the Okhotsk Sea in spring 2002. *PICES Scientific Report*, 26: 158–161.

Katugin, O.N., G.A. Shevtsov, V.D. Didenko & E.V. Slobodskoi. 2002. Distribution of *Berryteuthis anonychus* (Gonatidae, Oegopsida) in the North Pacific Ocean. *In*: *1st International Workshop of Squids, 2nd International Symposium of Pacific Squids*, La Paz, Baja California Sur, Mexico, Abstract: 41–43.

***Katugin, O.N., G.A. Shevtsov, M.A. Zuev & A.V. Dakus.** 2007. Patterns of size structure and ecology in the northern gonate squid (*Boreoteuthis borealis*) in the Okhotsk Sea and northwestern Pacific Ocean. *In*: *PICES XVI*, Annual Meeting, Victoria, Canada, Abstract: 152.

***Katugin, O.N., G.A. Shevtsov, M.A. Zuev, A.M. Berkutova & E.V. Slobodskoy.** 2005. Spatial and seasonal distribution of the squid *Okutania anonycha* (Pearcy et Voss, 1963) (Cephalopoda: Gonatidae) in the northwestern Pacific Ocean and adjacent areas. *Ruthenica*, 15(1): 65–79.

Kaufman, M.R., Y. Ikeda, C. Patton, G. Van Dykhuizen & D. Epel. 1988. Bacterial symbionts colonize the accessory nidamental gland of the squid *Loligo opalescens* via horizontal transmission. *Biological Bulletin Marine Biological Laboratory Woods-Hole*, 19(1): 36–43.

Kawabata, A. 2005. Target strength measurements of suspended live ommastrephid squid, *Todarodes pacificus*, and its application in density estimations. *Fisheries Science*, 71(1): 63–72.

Kawabata, A. 2006. Distribution and biomass of the Japanese common squid, *Todarodes pacificus*, estimated by acoustic survey in the Pacific coastal waters off the northern Japan. *PICES XV.* Book of Abstracts, p. 141.

Kawabata, A., A. Yatsu, Y. Ueno, S. Suyama & Y. Kurita. 2006. Spatial distribution of the Japanese common squid, *Todarodes pacificus*, during its northern migration in the western North Pacific Ocean. *Fisheries Oceanography*, 15(2): 113–124.

Kawahara, M., I.G. Gleadall & Y. Tsukahara. 1998. A note on the fibre-optic light-guides in the eye photophores of *Watasenia scintillans*. *South African Journal of Marine Science*, 20: 123–127.

Kawakami, T. 1976. Squids found in the stomach of sperm whales in the northwestern Pacific. *Scientific Reports of the Whales Researach Institute*, Tokyo. 28: 145–151.

Kawakami, T. 1976. The fishery biological study on a squid *Nototodarus sloani sloani* (Gray) in the New Zealand waters. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 85: 31–104.

Kawakami, T. 1980. A review of sperm whale food. *Scientific Report of the Whales Research Institute*, 32: 199–218.

***Kawakami, T. & T. Okutani.** 1981. A note on identity of ommastrephid squids of the genus *Nototodarus* exploited in the New Zealand waters. *Bulletin of the Toyai Regional Fishery Research Laboratory*, 105: 17–30.

Kawakami, T., M. Hamabe & R. Saito. 1973. A preliminary note on the ecology of the ommastrephid squid *Nototodarus sloani sloani* (Gray) in New Zealand Waters. 2. Studies on the catch by jigs on the ground off the northwest coast of South Island of New Zealand in February and March 1972. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 70: 1–23.

Kawamura, S. & M. Hirai. 1993. Evaluation of hydrographic conditions on the fluctuation in catches of common squid during period of northward migration in the waters around Sado Island in the Japan Sea. *Bulletin Japan Sea National Fisheries Research Institute*, 43: 83–92.

Kawasaki, K.I., T. Ooizumi & S. Hayashi. 1993. Liver lipids in the firefly squid *Watasenia scintillans* of Toyama Bay. *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 4: 57–59.

Kawasaki, K.I., T. Ooizumi, S. Hayashi & K. Hayashi. 1994. Lipid class and fatty acid composition of liver of firefly squid *Watasenia scintillans*. *Bulletin of the Japanese Society of Science and Fishery*, 60(2): 247–251.

Kawasaki, K. & S. Kakuma. 1998. Biology and fishery of *Thysanoteuthis rhombus* in waters around Okinawa, Southwestern Japan. *In*:T. Okutani, ed. Large Pelagic Squids. *Japan Marine Fishery Resource Research Center, Tokyo*, 183–189.

Kazmi, Q.B. & R. Naushaba. 2003. Cephalopods, Sepioidea (Cuttlefish), Teuthoidea (Squids), Ocotopoda (Octopuses). *Marine Fauna of Pakistan, University of Karachi*, Series II: 23 pp.

Ke, P.J., B. Smith-Lall & G.R. Pond. 1981. Quality enhancement of Canadian Atlantic squid (*Illex illecebrosus*) by various low temperature operations. *Proceedings of the meeting of the Commission, Institut International du Froid*, 513–516 pp.

Kear, A.J. 1992. The diet of Antarctic squid: comparison of conventional and serological gut contents analyses. *Journal of Experimental Marine Biology and Ecology*, 156(2): 161–178.

***Keferstein, W.** 1866. Kopffüsser: Cephalopoda Cuvier. *In*: H.G. Bronn, Die Klassen und Ordnungen des Thierreiches: Weichthiere (Malacozoa). *Leipzig und Heidelberg*, 1862–1866: 1307–1464, pls 110–136.

Kemps, H.A., J.A. Totterdall, T. Nishida & H.S. Gill. 1999. Preliminary analysis on the diet and feeding ecology of juvenile southern bluefin tuna, *Thunnus maccoyii*, in relation to the southern coastal waters of Western Australia. *Southern Bluefin Tuna Recruitment Monitoring and Tagging Program, Hobart, CRIMP*, 16 pp.

***Kent, W.S.** 1874. Note on a gigantic cephalopod from Conception Bay, Newfoundland. *Proceedings of the Zoological Society of London*, 1874(2): 178–182.

Kennedy, M.S. 1982. The parasites of some eastern Australiasqid and their possible use as biological markers. Bachelor of Science (Honors) thesis, Department of Parasitology, University of Queensland, Australia.

Khromov, D.N. 1990. Cephalopods of the Vietnamese waters: the fauna and distribution patterns. *ICES/1990 Shell*, Paper. 12: 1–8.

Kidokoro, H. 2002. Development of reproductive organs and changes in nutritional state during the spawning migration of the Japanese common squid (*Todarodes pacificus*). *Bulletin of Marine Science*, 71(2): 1129.

***Kidokoro, H. & K. Mori.** 2004. Stock assessment methods and management procedure of *Todarodes pacificus* in Japan. *ICES Council Meeting Documents, Copenhagen*. No. 2004.

Kier, W.M. 1992. Squid cross-striated muscle: the evolution of a specialized muscle fiber type. *Bulletin of Marine Science*, 49(1–2): 389–403.

Kier, W.M. 1996. Muscle development in squid: ultrastructural differentiation of a specialized muscle fiber type. *Journal of Morphology*, 229: 271–288.

Kim, H.R., C.B. Ahn, D.S. Lee, D.S. Kim & J.H. Pyeun. 1995. Processing of protein concentrate and recovery of bioactive n–3 series fatty acids from squid viscera. *Bulletin of National Fisheries Research Development Agency, Korea*, 51: 95–112.

Kim, J.H., H.Y. Seo & K.S. Kim. 2004. Analysis of radiolytic products of lipid in irradiated dried squids (*Todarodes pacificus*). *Journal of Food Protection*, 67(8): 1731–1735.

Kim, J.J., S. Kim & H.H. Lee. 2007. Summer occurrence and transport process of common squid (*Todarodes pacificus*) paralarvae in the East China Sea. *The Changing North Pacific: Previous Patterns, Future Projections and Ecosystem Impacts*, p. 179.

Kim, S.M., O.D. Bank & K.T. Lee. 1994. The development of squid *Todarodes pacificus* sik-hae in the Kang-Nung district. 3. The effects of garlic concentrations on the properties of sik-hae. *Bulletin Korean Fisheries Society*, 27(4): 357–365.

Kim, S.M., O.D. Bank & K.T. Lee. 1994. The development of squid *Todarodes pacificus* sik-hae in the Kang-Nung district. 4. The effects of red pepper and grain contents on the properties of squid sik-hae. *Bulletin Korean Fisheries Society*, 27(4): 366–372.

Kim, S.M., Y.J. Cho & K.T. Lee. 1994. The development of squid (*Todarodes pacificus*) sik-hae in Kang-Nung district. 2. The effects of fermentation temperatures and periods on chemical and microbial changes, and the partial purification of protease. *Bulletin Korean Fisheries Society*, 27(3): 223–231.

Kim, S.M., I.H. Jeong & Y.J. Cho. 1994. The development of squid (*Todarodes pacificus*) sik-hae in Kang-Nung district. 1. The effects of fermentation temperatures and periods on the properties of squid sik-hae. *Bulletin Korean Fisheries Society*, 27(3): 215–222.

Kim, S.M., S.M. Park, H.M. Choi & K.T. Lee. 1997. Rheological properties of chitosan manufactured from the pens of domestic *Todarodes pacificus* and *Ommastrephes bartramii* squid. *Bulletin Korean Fisheries Society*, 30(5): 859–867.

Kim, Y.H. 1993. Population analysis of the common squid *Todarodes pacificus* Steenstrup in the Korean waters. Ph.D. thesis. *Department of Marine Biology, National Fisheries, University of Pusan*, 106 pp. (in Korean, with English summary).

Kim, Y.M., Y.M. Jeong & J.H. Hong. 1993. Processing conditions for low-salted squid jeotkal. *Bulletin Korean Fisheries Society*, 26(4): 312–320.

Kimura, S., Y. Sugiura, N. Kato & Y. Hanaoka. 1994. Occurrence of a mucin-type glycol protein in nidamental gland mucosubstance from the squid *Illex argentinus*. *Fisheries Science*, 60: 193–198.

Kimura, S., Y. Higuchi, M. Aminaka, J.R. Bower & Y. Sakurai. 2004. Chemical properties of egg-mass mucin complexes of the Ommastrephid squid *Todarodes pacificus*. *Journal of Molluscan Studies*, 70(2): 117–121.

King, A.J., S.A. Adamo & R.T. Hanlon. 2003. Squid egg mops provide sensory cues for increased agonistic behaviour between male squid. *Animal Behaviour*, 66(1): 49–58.

Kinoshita, T. 1989. Age and growth of the loliginid squid, *Heterololigo bleekeri*. *Bulletin of the Seikai Regional Fisheries Research Lab*., 67: 59–68 [in Japanese, with English abstract].

Kinoshita, Y., T. Yoshioka, K. Konno & Y. Sakurai. 2006. Study on the post-mortem change in skin colour of squid *Todarodes pacificus*: development of techniques for the preservation of squid. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 81.

Kirk, T.W. 1882. Descriptions of new Cephalopods. *Transactions and Proceedings of the New Zealand Institute*, 14(42): 283–286, 1 pl.

Kirkwood, R. & G. Robertson. 1997. Seasonal change in the foraging ecology of emperor penguins on the Mawson Coast, Antarctica. *Marine Ecology Progress Series*, 156: 205–223.

Kirsch, P.E., S.J. Iverson, W.D. Bowen, S.R. Kerr & R.G. Ackman. 1998. Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Science*, 55(6): 1378–1386.

***Kishi, M.J., K. Nakajima, M. Fujii & T. Hashioka.** 2007. Environmental factors which affect growth of Japanese common squid, *Todarodes pacificus*, analyzed by a bioenergetics model coupled with a lower trophic ecosystem model. *Journal of Marine System*, 78(2): 278–287.

Kishimoto, H. & H. Kohno. 1992. Development of the luminous organ in the purpleback flying squid, *Sthenoteuthis oualaniensis*, as shown by alcian blue stain techniques. *Bulletin of the Institute of Oceanographic Research and Development, Tokai University*, 13: 71–83.

Kito, Y., K. Narita, M. Seidou, M. Michinomae, J.C. Partridge & P.J. Herring. 1992. Porphyropsin and new deep–sea visual pigment with 4-hydroxyretinal are found in some mesopelagic cephalopods in Atlantic. *Zoological Science*, 9(6): 1230.

Kiyofuji, H. & S.I. Saitoh. 2004. Use of nighttime visible images to detect Japanese common squid *Todarodes pacificus* fishing areas and potential migration routes in the Sea of Japan. *Marine Ecology Progress Series*, 276: 173–186.

Kizikawa, H. 1986. Biological research of the spear squid fisheries of the Japan Sea Southwest Region I. On growth and maturity of the specimens collected by trawling. *Shimane Prefecture Fisheries Experimental Station*, 4: 67–82. [In Japanese].

Klages, N.T.W. 1989. Food and feeding ecology of emperor penguins in the eastern Weddell Sea. *Polar Biology*, 9(6): 385–390.

Klages, N.T.W., A.B. Willis & G.J.B. Ross. 1992. Variability in the diet of the Cape gannet at Bird Island, Algoa Bay, South Africa. *South African Journal of Marine Science*, 12: 675–687.

***Kluchnik, T.S. & Ya. Starobogatov.** 1978. List of species and the distribution of oceanic squid larvae in the eastern Atlantic. *In*: I.M. Likharev, ed. Molluscs: their systematics, evolution and significance. *Malacological Review*, 11(1–2): 132.

Klumov, S.K. & V.L. Yukhov. 1975. *Mesonychoteuthis hamiltoni* Robson, 1925 (Cephalopoda, Oegopsida) and its significance in the feeding of sperm whale in Antarctic waters. *Antarktika*, 14: 159–189.

Knudsen J. & R. Roeleveld. 1991. Henrik J. Posselt: *Todarodes sagittatus* (Lmk.) Stp. An anatomical study with remarks on relationships between the genera of the ommastrephid family. *Steenstrupia*, 17: 161–196.

Kobayashi, G., K. Masuda, G. Anma, T. Meguro, H. Yamaguchi & S. Takagi. 1986. Distribution and abundance of three species of squids along 155 degree W. longitude. *Bulletin of the Faculty of Fisheries, Hokkaido University*, 37(3): 181–189.

Kobayashi, H. & Y. Yamaguchi. 1988. Studies on fishing depth and difference in catch by color of jigs for purpleback flying squid *Symplectoteuthis oualaniensis* and luminous flying squid *Eucleoteuthis luminosa*. *Japanese Society of Science and Fisheries*, 54(6): 919–927.

Koen-Alonso, M. & P. Yodzis. 2005. Multispecies modeling of some components of the marine community of northern and central Patagonia, Argentina. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(7): 1490–1512.

Komai, T., C. Kawabata, M. Amano, B.R. Lee & E. Ichishima. 2004. *Todarepsin*, a new cathepsin D from hepatopancreas of Japanese common squid (*Todarodes pacificus*). *Comparative Biochemistry and Physiology, Part B: Biochemistry and Molecular Biology*, 137(3): 373–382.

Komai, T., C. Kawabata, H. Tojo, Sh. Gocho & E. Ichishima. 2007. Purification of serine carboxypeptidase from the hepatopancreas of Japanese common squid *Todarodes pacificus* and its application for elimination of bitterness from bitter peptides. *Fisheries Science*, 73(2): 404–411.

Kong, I., M. Clarke & R. Escribano. 1995. Feeding of *Paralichthys adspersus* (Steindachner, 1867) in the northern Chile. Osteichthyes: Paralichthyidae. *Revista de Biología Marina*, 30(1): 29–44.

Korneliussen, T. 1984. Getting into the European squid market. *Infofish Mark. Dig.*, 4: 36–38.

Koronkiewicz, A. 1980. Size, maturity, growth and food of squid *Illex argentinus* (Castellanos, 1960). *ICES Council Meeting*, 18: 18 pp.

Koronkiewicz, A. 1986. Growth and life cycle of squid *Illex argentinus* from Patagonic and Falkland shelf and Polish fishery of squid for this region, 1978 1985. *ICES Council Meeting*, 1986/K27: 16 pp.

Koronkiewicz, A. 1988. Biological characteristics of jumbo squid (*Dosidicus gigas*) caught in open waters of the eastern Central Pacific from October to December 1986. *Copenhagen Denmark ICES,* 14 pp.

***Korzun, Yu.V. & D.O. Alekseyev.** 1991. Taxonomic position of *Loligo singhalensis* (Cephalopoda, Loliginidae). *Zoologicheskij Zhurnal*, 70: 23–27 [In Russian].

***Korzun, Yu.V., K. Nesis, C.M. Nigmatullin, A.A. Ostapenko & M.A. Pinchukov.** 1979. New data on the distribution of squids, family Ommastrephidae, in the world ocean. *Oceanology*, 19(4): 472–475.

Koval, L.I. 1984. Genetic-biochemical differentiation of the orangeback squid, *Sthenoteuthis pteropus*. *In* K.Ja. Batal'jants, ed. *Intraspecific Differentiation in Marine Commercial Fishes and Invertebrates*. Kaliningrad: AtlantNIRO Publication: 77–82 (In Russian).

Koyama, J., N. Nanamori & S. Segawa. 2000. Bioaccumulation of waterborne and dietary cadmium by Oval squid, *Sepioteuthis lessoniana*, and its distribution among organs. *Marine Pollution Bulletin*, 40(11): 961–967.

***Kripa, V., K.P. Nair, K. Vidyasagar, G.S. Rao, A.P. Lipton, K.K. Appukuttan, P.V. Srinivasan, M.E. Rajapandian, P. Natarajan, K. Ramadoss, N. Burayya, K.T. Thomas & P. Achayya.** 1996. Cephalopod resources in southeast and northeast coasts of India and Andaman-Nicobar waters. *In*: V.K. Pillai, S.A.H. Abidi, V. Ravindran & K.K. Balachandran, eds. Proceedings of the Second Workshop on Scientific Results of Forv Sagar Sampada. *New Delhi, India Department of Ocean Development*, pp. 445–451.

Kristensen, T.K. 1977. Hatching, growth and distribution of juvenile *Gonatus fabricii* (Mollusca: Cephalopoda) in Greenland waters. *Astarte*, 10: 21–28.

Kristensen, T.K. 1977. Scanning electron microscopy of hook development in *Gonatusfabricii* (Lichtenstein, 1818) (Mollusca: Cephalopoda). *Videnskabelige Meddalelson fra Dansk Naturhistorisk Foreningi Kjabenhaun*, 140: 111–116.

***Kristensen, T.K.** 1980a. Periodical growth rings in cephalopod statoliths. *Dana*, 1: 39–51.

***Kristensen, T.K.** 1980b. Multivariate statistical analysis of geographic variation in the squid *Gonatus fabricii* (Lichtenstein, 1818) (Mollusca, Cephalopoda). *Haliotis*, 10(2): 83.

***Kristensen, T.K.** 1981. First record of a mature female of the squid *Gonatus fabricii* (Lichtenstein, 1818) (Cephalopoda: Teuthoidea). *Steenstrupia*, 7(5): 101–108.

Kristensen, T.K. 1982. Multivariate statistical analysis of geographic variation in the squid *Gonatus fabricii* (Lichtenstein, 1818) (Mollusca: Cephalopoda). *Malacologia*, 22(1–2): 581–586.

Kristensen, T.K. 1983. *Gonatus fabricii*. In: Boyle, P.R. (ed) Cephalopod life cycles. Volume I – Species Accounts. *Academic Press, London*, pp. 159–173.

Kristensen, T.K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. *Meddr Grønland Biosci*, 13: 1–20.

***Krohn, A.** 1845. Ueber einen neuen cephalopoden (*Octopodoteuthis*). *Archiv für Naturgeschichte*, 11:47–49, 6 figs.

***Krohn, A.** 1847. Nachtrage zu den Aufsatzen uber Tiedemannia, *Octopodoteuthis* und Alciopa. *Archiv für Naturgeschichte*, 13:36–40, 1 pl.

Kubo, I. 1966. Squids and octopuses. *Fisheries Biology*, II, pp. 188–264.

Kubodera, T. 1989 Young squids collected with 10–foot IKPT net during the JARE 28 cruise, 1987. Proceedings of the NIPR Symposium. *Polar Biology*, 2: 71–77.

Kubodera, T. 1992. Biological characteristics of the gonatid squid *Berryteuthis magister magister* (Cephalopoda: Oegopsida) off northern Hokkaido, Japan. *Memoirs of the National Science Museum, Tokyo*, 25: 111–123.

Kubodera, T. 1993. Upper bathyl cephalopods off eastern Cape Erimo, Hokkaido, Japan. *National Science Museum, Tokyo*, 26: 83–88.

***Kubodera, T.** 1994. Systematical and ecological studies of pelagic cephalopods in the eastern tropical Pacific. Preliminary Report of the Hakuho Maru Cruise KH-90-2, eastern tropical Pacific. *Ocean Research Institute*, 53–56.

Kubodera, T. 1995. Giant squid from sperm whale stomach contents. *Aquabiology*, 17(6): 482–487 [Japanese].

***Kubodera, T.** 1996. Cephalopod fauna off Sanriku and Joban districts northeastern Japan. *Memoirs of the National Science Museum of Tokyo*, (29): 187–207.

Kubodera, T. 1998. Cephalopod fauna around the continental shelf of the East China Sea. *Memoirs of the National Science Museum of Tokyo*, 31: 187–210.

*** Kubodera, T.** 2000. Class Cephalopoda. *In* T. Okutani, ed. *Marine Mollusks in Japan. Tokai University Press, Tokyo*, 1173 pp.

*** Kubodera, T.** 2006a. *Gonatopsis japonicus* Okiyama 1969. Version 30 May 2006. http://tolweb.org/Gonatopsis_japonicus/26877/2006.05.30 in The Tree of Life Web Project, http://tolweb.org/

*** Kubodera, T.** 2006b. *Gonatopsis makko* Okutani & Nemoto 1964. Version 30 May 2006. http://tolweb.org/Gonatopsis_makko/26878/2006.05.30 in The Tree of Life Web Project, http://tolweb.org/

*** Kubodera, T. & K. Jefferts.** 1984a. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific, Part I. *Bulletin of the National Science Museum, Tokyo*, series A, 10(4): 91–106.

*** Kubodera, T. & K. Jefferts.** 1984b. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda: Oegopsida), in the northern North Pacific, Part II. *Bulletin of the National Science Museum, Tokyo*, series A, 10(4):165–193.

Kubodera, T. & N. Miyazaki. 1993. Cephalopods eaten by short-finned pilot whales, *Globicephala macrorhynchus*, caught off Ayukawa, Ojika Peninsula, in Japan, in 1982 and 1983. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 215–227.

*** Kubodera, T, & K. Mori.** 2005. First-ever observations of a live giant squid in the wild. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 272(1581): 2583–2586.

*** Kubodera, T. & T. Okutani.** 1977. Description of a new species of gonatid squid, *Gonatus madokai*, n. sp., from the northwest Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). *Venus*, 36(3): 123–151, 3 figs, 4 pls.

*** Kubodera, T. & T. Okutani.** 1981. *Gonatus middendorffi*, a new species of gonatid squid from the northern North Pacific, with notes on morphological changes with gorwth and distribution in immature stages (Cephalopoda: Oegopsida). *Bulletin of the National Science Museum, Tokyo, series A (Zoology)*, 7(1): 7–26.

Kubodera, T. & T. Okutani. 1986. New and rare cephalopods from the Antarctic waters. *In*: T. Hoshiai, Y. Ohyama, eds. *Proceedings of the eighth symposium on Polar Biology*, 44: 129–143.

Kubodera, T. & K. Shimazaki. 1989. Cephalopods from the stomach contents of the pomfret (*Brama japonica* Hilgendorf) caught in surface gillnets in the northern North Pacific. *Journal of Cephalopod Biology*, 1(1): 71–83.

Kubodera, T. & H. Yamada. 1998. Cephalopod fauna around the continental shelf of the East China Sea. *Memoirs of the National Science Museum of Tokyo*, 31: 187–210.

*** Kubodera, T., Y. Koyama & K. Mori.** 2007a. Observations of wild hunting behaviour and bioluminescence of a large deep sea, eight-armed squid, *Taningia danae*. *Proceedings of the Royal Society B*, 274: 1029–1034.

Kubodera, T., H. Watanabe & T. Ichii. 2007b. Feeding habits of the blue shark, *Prionace glauca*, and salmon shark, *Lamna ditropis*, in the transition region of the Western North Pacific. *Reviews in Fish Biology and Fisheries*, 17(2–3): 111–124.

*** Kubodera, T., F.G. Hochberg, R.E. Young & M. Vecchione.** 2006a. *Berryteuthis* Naef, 1921. Version 30 May 2006. http://tolweb.org/Berryteuthis/19765/2006.05.30 in The Tree of Life Web Project, http://tolweb.org/

*** Kubodera, T., F.G. Hochberg, R.E. Young & M. Vecchione.** 2006b. *Eogonatus* Nesis, 1972. *Eogonatus tinro* Nesis 1972. Tree of Life, http://tolweb.org/

*** Kubodera, T., F.G. Hochberg, R.E. Young & M. Vecchione.** 2006c. *Gonatopsis* Sasaki, 1920. Version 30 May 2006 (under construction). http://tolweb.org/Gonatopsis/18764/2006.05.30 in The Tree of Life Web Project, http://tolweb.org/

*** Kubodera, T., F.G. Hochberg, R.E. Young & M. Vecchione.** 2006d. *Gonatus* Gray, 1849. Version 31 May 2006 (under construction). http://tolweb.org//Gonatus/19767/2006.05.31 in The Tree of Life Web Project, http://tolweb.org/

*** Kubodera, T., U. Piatkowski, T. Okutani & M.R. Clarke.** 1998. Taxonomy and Zoogeography of the family Onychoteuthidae (Cephalopoda: Oegopsida). *In* N.A. Voss, M.V. Vecchione, R.B. Toll, & M.J. Sweeney, eds. *Systematics and Biogeography of Cephalopods, Vol. II, Smithsonian Contributions to Zoology*, 586: 277–292.

Kubota, T., K. Iizuka & T. Okutani. 1982. Some biological aspects of *Abralia andamanica* from Suruga Bay, Japan (Cephalopoda: Enoploteuthidae). *Journal of the School of Marine Science and Technology of Tokai University*, 15: 333–343.

Kubota, T., T. Fukui. & T. Okutani. 1993. Cephalopods incidentally caught with shirasu boat seine from Suruga Bay in 1988, 1990 and 1991, with the catalogue of cephalopods hitherto recorded from the bay. *Journal of the Faculty of Marine Science and Technology, Tokai University*, 35: 77–91.

Kubota, T., H. Sakai, H. Nagai, K. Matsubara & T. Okutani. 1998. Diversity and vertical distribution of the paralarvae of pelagic cephalopods in Suruga Bay, central Japan. *Journal of the School of Marine Science and Technology of Tokai University*, 46: 67–86.

Kudikina, N.P. 1983. Quantitative distribution of steroid hormones in some species of tropical Cephalopods. Starobogatov, Ya.I.; Nesis, K.N. [Eds]. Taxonomy and ecology of Cephalopoda. *Scientific papers. USSR Academy of Science, Zoology Institute*, Leningrad. 1983: 1–148. Chapter pagination: 142.

Kudikina, N.P. 2006. The ontogenetic dynamic of steroids hormones quantitative contain in squid and octopus. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 82.

***Kumagai, N., H. Kiyofuji & S.I. Saitoh.** 2006. Distributions of squid fishing grounds and their relationship to sea surface temperature and chlorophyll-a concentration in the Japan Sea. *PICES XV. Book of Abstracts*, p. 144.

Kumagai, N., H. Kiyofuji, H. Kidokoro & S.I. Saitoh. 2007. Prediction and of Japanese common squid (*Todarodes pacificus*) fishing grounds using generalized additive models in the Japan/East Sea. *The Changing North Pacific: Previous Patterns, Future Projections and Ecosystem Impacts*, p.179.

Kuo, J.D., M. Peleg & H.O. Hultin. 1990. Tensile characteristics of squid mantle. *Journal of Food Science*, 55(2): 369–371.

Kuramochi, T., T. Kubodera & N. Miyazaki. 1993. Squids eaten by Dall's porpoises, *Phocoenoides dalli* in the north western North Pacific and in the Bering Sea. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 229–240.

Kurihara, H., H. Togawa & M. Hatano. 1993. Concentration of cadmium in livers of several kinds of squids and an approach to its elimination. *Bulletin of Faculty of Fisheries Hokkaido University*, 44(1): 32–38.

Kuroiwa, M. 1998. Exploration of the jumbo flying squid, *Dosidicus gigas*, resources in the southeastern Pacific Ocean with notes on the history of jigging survey vy the Japan Marine Resources Research Center. *In*: T. Okutani, ed. Large Pelagic Squids. *Japan Marine Fishery Resources Research Center*, Tokyo. 89–105 pp.

Kuwahara, K. & K. Osako. 2003. Effect of sodium gluconate on gel formation of Japanese common squid mantle muscle. *Bulletin of the Japanese Society of Scientific Fisheries*, 69(4): 637–642.

Labe, L.L. 2000. Catch rate of oceanic squid by jigging method in the South China Sea Area 3: Western Philippines. *Proceedings of the third Technical Seminar on Marine Fishery Resources Survey in the South China Sea, Area 3: Western Philippines*, 41: 19–31.

Lafont, A. 1871. Note pour servir à la fauna de la Gironde contenant la liste des animaux marins dont la presence à ete constatée à Arcochon pendant les annees 1869–1870. *Actes de la Société Linneénne Bordeaux*, 28: 237–279, 5 plates.

Laidre, K.L., M.P. Heide-Jørgensen, O.A. Jørgensen & M.A. Treble. 2004. Deep–ocean predation by a high Arctic cetacean. *ICES Journal of Marine Science*, 61: 430–440.

Laidre, K.L. & M.P. Heide-Joergensen. 2005. Winter Feeding Intensity of Narwhals (*Monodon monoceros*). *Marine Mammal Science*, 21(1): 45–57.

Lake, S., H. Burton & J. van den Hoff. 2003. Regional temporal and time–scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Marine Ecology Progress Series*, 254: 293–305.

Lakshmanan, P.T., T.S.G. Iyer, P.D. Antony & K. Gopakumar. 1998. K-Value, an Index for estimating fish quality during iced storage. *In*: M.S. Hameed & B.M. Kurup, eds. Technological advancements in fisheries. *Proceedings of the National Symposium on Technological Advancements in Fisheries and its Impact on Rural Development held at Cochin by School of Industrial Fisheries, Cochin University of Science and Technology during December 5 to 7, 1995 Cochin India* (CUSAT), 388–399.

***Lamarck, J.B.** 1798. Extrait d'un mémoire sur le genre de la Séche, du Calmar et Poulpe, vulgairement nommés, Polypes de Mer. *Bulletin des Sciences, par la Société Philomatique de Paris*, 2(5): 129–131.

***Lamarck, J.B.** 1799. Sur les genres de la seche, du calmar et du poulpe. Mémoires de la Société d'Histoire Naturelle de Paris, 1: 1–25, 2 pls.

∗**Landman, N.H., J.K. Cochran, R. Serrato, J. Mak, C.F.E. Roper & C.C. Lu.C.** 2004. Habitat and age of the giant squid (*Architeuthis sanctipauli*) inferred from isotopic analyses. *Marine Biology*, 144(4): 685–691.

∗**Lane, F.W.** 1957. Kingdom of the Octopus, the life-history of the Cephalopoda. 287 pp. London.

Lane, F.W. 1960. The kingdom of the Octopus; the life history of the Cephalopoda, Sheridan House, New York, 300 pp.

Lange, A.M.T. 1980. The biology and population dynamics of the squid *Loligo pealei* (LeSueur) and *Illex illecebrosus* (LeSueur) from the northwest Atlantic. *M.Sc. Thesis, University of Washington*, 178 pp.

∗**Lange, A.M.T.** 1981. Yield-per-recruit analysis for squid, *Loligo pealei* and *Illex illecebrosus*, from the Northwest Atlantic. *Journal of Shellfish Research*, 1(2): 197–207.

Lange, A.M.T. 1991. Alternative survey indices for predicting availability of longfin squid to seasonal Northwest Atlantic fisheries. *N. Am. J. Fish. Manage.*, 11(3): 443–450.

Lange, A.M.T. & M.P. Sissenwine. 1980. Biological considerations relevant to the management of squid (*Loligo pealei* and *Illex illecebrosus*) of the northwest Atlantic. *Marine Fisheries Review*, 42(7–8): 23–38.

∗**Lange, A.M.T. & M.P. Sissenwine.** 1983. Squid resources of the Northwest Atlantic. *In*: J.F. Caddy, ed. Advances in Assessment of World Cephalopod Resources. *FAO Fisheries Technical Paper*, 231: 21–54.

Lange, A.M.T. & G.T. Waring. 1992. Fishery interactions between long-finned squid (*Loligo pealei*) and butterfish (*Peprilus triacanthus*) off the northeast USA. *Journal of Northwest Atlantic Fishery Science*, 12: 49–62.

∗**Lange, A.M.T., M.P. Sissenwine & E.D. Anderson.** 1984. Yield analysis for the long-finned squid, *Loligo pealei* (LeSueur). *Copenhagen Denmark ICES*, 1984. 41 pp.

Langille, S.M. & T.A. Gill. 1984. Postmortem metabolism of short-finned squid muscle (*Illex illecebrosus*). *Comparative Biochemistry and Physiology*, 79B(3): 361–367.

∗**Lansdell, M. & J. Young.** 2007. Pelagic cephalopods from eastern Australia: species composition, horizontal and vertical distribution determined from the diets of pelagic fishes. *Reviews in Fish Biology and Fisheries*, 17(2–3): 125–138.

Lapa Guimaraes, J., M.A.A. da Silva, P.E. de Felicio & E.S.C. Guzman. 2002. Sensory, colour and psychrotrophic bacterial analyses of squids (*Loligo plei*) during storage in ice. *Food Science and Technology*, 35(1): 21–29.

Lapa Guimaraes, J., P.E. de Felicio & E.S.C. Guzman. 2005. Chemical and microbial analyses of squid muscle (*Loligo plei*) during storage in ice. *Food Chemistry*, 91(3): 477–483.

∗**LaPylaie, B. de** 1825. Notice sur l'encornet des pecheurs; *Loligo piscatorum. Annales des Sciences Naturelles, Paris*, 4: 319–335, pl 16.

Lapko, V.V. & O.A. Ivanov. 1993. Composition and distribution of fauna in the sound-scattering layer in Kuril waters of the Pacific Ocean. *Okeanologiya (Russian Journal of Oceanology)*, 33(4): 574–578. (In Russian).

Laptikhovsky, V.V. 1989. Diurnal vertical migrations of squid *Todarodes angolensis* Adam (Cephalopoda, Ommastrephidae) off Namibia. *Okeanologiya Oceanology*, 29: 836–837.

Laptikhovsky, V.V. 1990. Species composition and distribution of cephalopods in the shelf and continental slope waters off Namibia. *USSR Institute of Economics and Information in Fisheries*, 20 pp. [In Russian].

Laptikovsky, V.V. 1995. Mortality and production of the squid *Sthenoteuthis pteropus* (Steenstrup) Oegopsida, Ommastrephidae) in the eastern tropical Atlantic. *Biology and Population Dynamics of Fishes and Invertebrates in the Atlantic Ocean – Atlantniro*, 142–154 pp.

Laptikovsky, V.V. 1999a. Improved mathematical model to study the duration of embryogenesis in cephalopod molluscs. *Ruthenica*, 9: 141–146.

∗**Laptikovsky, V.V.** 1999b. Fecundity and spawning in squid of families Enoploteuthidae and Ancistrocheiridae (Cephalopoda: Oegopsida). *Scientia Marina (Barcelona)*, 63(1): 1–7.

Laptikovsky, V.V. 1999c. First data on fecundity of the squid *Abralia veranyi* (Cephalopoda: Enoploteuthidae). *Journal of the Marine Biological Association of the United Kingdom*, 79(6): 1135–1136.

Laptikhovsky, V.V. 2000. Fecundity of the squid *Loligo vulgaris* Lamarck, 1798 (Myopsida, Loliginidae) of northwest Africa. *Scientia Marina*, 64: 275–278.

Laptikhovsky, V.V. & A.I. Arkhipkin. 2001. Oogenesis and gonad development in the cold water loliginid squid *Loligo gahi* (Cephalopoda: Myopsida) on the Falkland shelf. *Journal of Molluscan Studies*, 67(4): 475–482.

*****Laptikhovsky, V.V. & A.I. Arkhipkin.** 2003a. The reproductive features of a mature female of the deep sea planktonic squid *Galiteuthis glacialis* (Cephalopoda: Cranchiidae) from the Southern Ocean. *Polar Research*, 22(2): 395–397.

Laptikhovsky, V.V. & A.I. Arkhipkin. 2003b. An impact of seasonal squid migrations and fishing on the feeding spectra of subantarctic notothenioids *Patagonotothen ramsayi* and *Cottoperca gobio* around the Falkland Islands. *Journal of Applied Ichthyology*, 19(1): 35–39.

Laptikhosky, V.V. & S.A. Murzov. 1990. Record of an epipelagic egg mass of the orangeback squid *Sthenoteuthis pteropus* (Steenstrup, 1855), in the eastern tropical Atlantic. *Biologija Morya*, 3: 62–63 (In Russian with English abstract).

Laptikovsky, V.V. & C.M. Nigmatullin. 1993. Egg size, fecundity and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *ICES Journal of Marine Science*, 50: 393–403.

*****Laptikovsky, V.V. & C.M. Nigmatullin.** 1999. Egg size and fecundity in females of the subfamilies Todaropsinae and Todarodinae (Cephalopoda: Ommastrephidae). *Journal of the Marine Biological Association of the United Kingdom*, 79(3): 569–570.

Lapitkhovsky, V.V. & C.M. Nigmatullin. 2005. Aspects of female reproductive biology of the orange-back squid, *Sthenoteuthis pteropus* (Steenstrup) (Oegopsina: Ommastrephidae) in the eastern tropical Atlantic. *Scientia Marina (Barcelona)*, 69(3): 383–390.

Laptikhovsky, V.V. & A.A. Zorikova. 1992. Fecundity and some features of reproductive biology of the squid *Todarodes angolensis* in Namibian waters. *Mar. Biol.*, 18(5–6): 51–61.

Laptikhovsky, V.V. & A.A. Zorikova. 1993. Fertility and some features of reproductive biology of squid *Todarodes angolensis* in waters of Namibia. *Russian Journal of Marine Biology., 18: 172–179.*

Laptikhovsky, V.V., A.I. Arkhipkin & A.C. Henderson. 2001. Feeding habits and dietary overlap in spiny dogfish *Squalus acanthias* (Squalidae) and narrowmouth catshark *Schroederichthys bivius* (Scyliorhinidae). *Journal of the Marine Biological Association of the United Kingdom*, 81(6): 1015–1018.

Laptikhovsky, V.V., A.I. Arkhipkin & H.J.T. Hoving. 2007. Reproductive biology in two species of deep-sea squids. *Marine Biology*, 152(4): 981–990.

*****Laptikhovsky, V.V., A. Salman & H. Moustahfid.** 2005. Morphological changes at maturation and systematics in the squid genus *Alloteuthis*. *Phuket Marine Biological Center Research Bulletin*, 66: 187–193.

Laptikhovsky, V.V., A.I. Arkhipkin, D.A.J. Middleton & L.R. Butcher. 2002a. Ovary maturation and fecundity of the squid *Loligo gahi* on the southeast shelf of the Falkland Islands. *Bulletin of Marine Science*, 71, 449–464.

*****Laptikhovsky V., A. Salman, B. Önsoy & T. Katagan.** 2002b. Systematic position and reproduction of squid of the genus *Alloteuthis* (Cephalopoda: Loliginidae) in the eastern Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, 82: 983–985.

Lapko, V.V. 1995. The role of squids in the Okhotsk Sea communities. *Okeanologiya*, 35(5): 737–742.

LaRoe, E.T. 1971. The culture and maintenance of the lolinginid squids *Sepioteuthis sepioidea* and *Doryteuthis plei*. *Marine Biology*, 9–25.

Lasut, M.T., F.B. Boneka & G.F.N. Mamangkey. 2000. Descriptions of loliginid squid *Uroteuthis bartschi* Rehder, 1945 (Cephalopoda: Loliginidae) and other edible squids from northern Minahasa peninsular waters, north Sulawesi, Indonesia. *Proceedings of the 10th International Congress and Workshop of the Tropical Marine Mollusc Programme (TMMP), 20–30 October 1999, hosted by the Ministry of Fisheries of the Socialist Republic of Vietnam, conducted in Hanoi and Haiphong in collaboration with RIMP, RIA 1 and RIA3*. 21(1): 267.

Latif, M.S.A. 1982. Malaysian squid resources. IPFC (Indo-Pacific Fishery Commission) Report of the Third Session of the Standing Committee on Resources Research and Development. Sidney, Australia, 28 April–4 May 1982. *FAO Fisheries Report*, 175: 118–120.

*****Latreille, P.A.** 1825. Familles naturelles du regne animal, exposees succinctement et dans un ordre analytique, avec l'indication de leurs genres. *Paris, J.B. Bailliere*, 570 pp.

Laubscher, R., D. Durholtz & M.R. Lipinski. 2006. Methodology of loliginid statolith data processing for ageing studies. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 82.

Laughlin, R.A. & R.J. Livingston. 1982. Environmental and trophic determinants of the spatial/temporal distribution of the Brief squid (*Lolliguncula brevis*) in the Apalachicola Estuary (North Florida, USA). *Bulletin of Marine Science*, 32(2): 489–497.

Lavall, R.L., O.B.G. Assis & S.P. Campana-Filho. 2007. beta-Chitin from the pens of *Loligo* sp.: Extraction and characterization. *Bioresource Technology*, 98(13): 2465–2472.

Lawson, J.W., A.M. Magalhaes & E.H. Miller. 1998. Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Marine Ecology Program Series*, 164: 13–20.

Lazzeretti, A., A. Voliani & A. Zucchi. 1995. Note on a specimen of *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae) caught in the northern Tyrrhenian Sea. *Biologia Marina Mediterrean*, 2(2): 493–494.

Le Corre, M., Y.I. Cherel, F. Lagarde, H. Lormee & P. Jouventin. 2003. Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird *Phaethon rubricauda*. *Marine Ecology Progress Series*, 255: 289–301.

Lea, C.E. 1978. Pelagic cephalopods of Gulf Stream cyclonic rings. *M.Sc. Thesis*. Texas A&M Univ. 60 pp.

* **Lea, C.E.** 1985. Pelagic cephalopods of the Florida Current. *Texas A and M University. Ph.D. Dissertation*, 235 pp.

* **Leach, W.E.** 1817. Synopsis of the orders, families, and genera of the class Cephalopoda. *In*: W.E. Leach & R.P. Nodder, eds. *The Zoological Miscellany; being Descriptions of New or Interesting animals*, 3(30): 137–141.

Learson, R.J. 2000. Preservation of Squid Quality. *In*: Marine and Freshwater Products Handbook. *Technomic Publishing Co.*, pp. 339–342.

Lee, H.H., M.H. Son & S. Kim. 2006. Distribution of common squid, *Todarodes pacificus* (Cephalopoda: Ommastrephidae), larvae in the East China Sea in the early 2000s. *PICES XV. Book of Abstracts*, p. 142.

Lee, J.H., B.D. Choi, K.H. Lee & H.S. Ryu. 1989. Flavor components in the squid processing. *Bulletin of Korean Fishery Society*, 22(5): 370–374.

Lee, M.L. & P.B. Sun. 1990. Comparison on the autolysis of Argentina squid (*Illex argentinus*) and Falkland squid (*Martialia hyadesi*). *In*: R. Hirano & I. Hanyu, eds. *Proceedings of the Second Asian Fisheries Forum, Tokyo*, pp. 881–884.

Lee, N.G. & Y.J. Cho. 1996. Effect of washing and additives on gel formation of squid surimi. *Journal of the Korean Fishery Society*, 29(6): 754–760.

Lee, P.G., P.E. Turk, W.T. Yang & R.T. Hanlon. 1994. Biological characteristics and biomedical applications of the squid *Sepioteuthis lessoniana* cultured through multiple generations. *Biological Bulletin of the Marine Biology Laboratory, Woods-Hole*, 186: 328–341.

Lee, S.D., Y.S. Son & Y.C. Kim. 1985. A study on the vertical distribution of common squid, *Todarodes pacificus* (Steenstrup) in the eastern waters of Korea. *Journal of Fish, Fisheries Research and Development Agency, Pusan*, 36: 23–28.

Lefkaditou, E. 2006a. Life history of *Loligo vulgaris* on the shelf of the Thracian Sea (NE Mediterranean). *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 43.

Lefkaditou, E. 2006b. Fisheries and demographic structure of *Loligo vulgaris* in the Mediterranean Sea. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 83.

Lefkaditou, E. 2007. Review of Cephalopod fauna in Hellenic waters. *In*: C. Papaconstantinou, A. Zenetos, V. Vassilopoulou & G. Tserpes, eds. *State of Hellenic Fisheries*, II, 4, 62–69. *Athens, HCMR Publications*.

Lefkaditou, E. & G.D. D' Onghia. 2001. *Loligo forbesi* and Ommastrephid squids by-catches on the north-eastern Ionian slope: preliminary analysis of stock structure based on exploratory trawling. *Scientific Council Research Document NAFO*, 01/144, 6 pp.

* **Lefkaditou, E. & L. Maiorano.** 2001. New record of *Galiteuthis armata* (Cephalopoda: Cranchiidae) in the Mediterranean Sea. *Rapp. Comm. Int. Mer. Medit.*, 36: 293.

Lefkaditou, E. & Y. Poulopoulos. 1998. Cephalopod remains in the stomach-content of Beaked Whales, *Ziphius cavirostris* (Cuvier, 1823), from the Ionian Sea. *Rapport de la Commission Internationale pour la Mer Méditerranée*, 35: 460–461.

Lefkaditou, E., M. Corsini-Foka & G. Kondilatos. 2009. Description of the first Lessepsian squid migrant *Sepioteuthis lessoniana* (CEPHALOPODA: Loliginidae) from the Aegean Sea (Eastern Mediterranean). *Mediterranean Marine Science*, 10 (2) (In press). Available on-line at: http://www.medit-mar-sc.net/contents/index.html.

Lefkaditou, Å., P. Maiorano & Ch. Mytilineou. 2001a. Cephalopod species captured by deep-water exploratory trawling in the eastern Ionian Sea. NAFO Special Symposium on Deep-Sea Fisheries, Varadero, Cuba, September 2001, NAFO SCR Doc.01/131, 8 pp.

***Lefkaditou, E., C. Papaconstantinou & K. Anastasopoulou.** 1999. Juvenile cephalopods collected in the midwater macroplankton over a trench in the Aegean Sea (northeastern Mediterranean). *Israel Journal of Zoology*, 45(3): 395–405.

Lefkaditou, E., C.Y. Politou & C. Papaconstantinou. 2000. Notes on *Brachioteuthis riisei* (Steenstrup, 1882) and *Ancitroteuthis lichtensteini* (Orbigni, 1839) (Cephalopoda: Teuthoidea) found in the Aegean Sea. *Belgian Journal of Zoology*, 130: 71–75.

Lefkaditou, E., Ch. Mytilineou, P. Maiorano & G. D' Onghia. 2001b. Cephalopod species captured by deep-water exploratory trawling in the northeastern Ionian Sea. *In*: J.A. Moore & J.D.M. Gordon, eds. *Symposium of deep sea fisheries*, NAFO, ICES, 131: 431–440.

Lefkaditou, E., C. Papaconstantinou, A. Tsangridis & P. Leondarakis. 2001c. Contribution of cephalopods to the artisanal and trawl fisheries in the Thracian Sea (Greece). Proceedings of the 10th Panellenic Congress of Ichthyologists, Chania, Greece, Oct 18–20, 2001. *Panellenic Ichthyological Association*, pp. 45–48.

Lefkaditou, E., P. Sanchez, A. Tsangidis & A. Adamidou. 1998. A preliminary investigation on how meteorological changes may affect beach-seine catches of *Loligo vulgaris* in the Thracian Sea (Eastern Mediterranean). *In*: A.I.L. Payne, M.R. Lipinski, M.R. Clarke & M.A.C. Roeleveld, eds. “Cephalopod Biodiversity, Ecology and Evolution”. *South African Journal of Marine Science*, 20: 453–461.

***Lefkaditou, E., P. Peristeraki, P. Bekas, G. Tserpes, Ch.Y. Politou & G. Petrakis.** 2003. Cephalopod distribution in the southern Aegean Sea. *Mediterranean Marine Science*, 4(1): 79–86.

Legand, M., P. Bourret, P. Fourmanoir, R. Grandperrin, A. Gueredrat, A. Michel, P. Rancurel, R. Repelin & C. Roger. 1972. On trophic relationships at higher levels of the food chain in the tropical Pacific Ocean. *Proceedings of the Pacific Science Congress,* 12(1): p.159.

Leite, T.S., L.C.A. Andrade, R.A. Santos, M. Haimovici & J.E.L. Oliveira. 2006. Identification of cephalopod fauna of the Archipelago of Saint Peter and Saint Paul, the most isolated island in Brazil. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 84.

Lelli, S., A. Belluscio, P. Carpentieri & F. Colloca. 2005. Ecologia trofica di *Illex coindetii* e *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) nel Mar Tirreno centrale. *Biologia Marina Mediterranea*, 12: 531–534.

Lelli, S., A. Belluscio, P. Carpentieri & F. Colloca. 2006. Feeding of *Illex coindetti* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in the central Tyrrhenian Sea. *Biologia Marina Mediterranea*, 12(1):531–534.

Leos, R.R. 1998. The biological characteristics of the Monterey Bay squid catch and the effect of a two-day-per-week fishing closure. *Reports of California Cooperative Oceanic Fisherie Investigations,* 39: 204–211.

***Lesson, R.P.** 1830–1831. Mollusques, Anellides et Vers. *In*: Voyage autour du monde sur la corvette de la Majeste, la Coquille, pendant les annees 1822–1825 sous le commandement du capitaine Duperrey. *Paris, Zoologie*, 2(1): 471 pp. [pp. 1–24 = 1830, pp. 25–471 = 1831]; Atlas, Mollusques, 16 pls [pls 1–9 = 1830, pls 10–16 = 1831]. [See Sherborn and Woodward (1906) for dates of publication].

***Lesueur, C.A.** 1821. Descriptions of several new species of cuttlefish. *Journal of the Academy of Natural Sciences of Philadelphia*, 2(1): 86–101.

***Lesueur, C.A.** 1824. Description of a new species of cephalopod of the genus *Loligo*. *Journal of the Academy of Natural Science of Philadelphia*, 3(2):282–284, 1 pl.

***Lesueur, C.A. & N.M. Petit.** 1807. Atlas Historique. *In*: F. Peron, ed. Voyage de decouvertes aux terres Australes sur les corvettes le Geographe, le Naturaliste, et la Geolette le Casuarina, pendant 1800–1804. 2 volumes, atlas and 14 maps, 1807–1816, 41 pls.

Leta, H.R. 1987a. Descricion de los huevos, larvas y juveniles de *Illex argentinus* (Ommastrephidae) y juveniles de *Loligo brasiliensis* (Loliginidae) en la Zona Com’n de Pesca Argentino Uruguaya. *Publ. Cient. INAPE 1987*, 1(1): 1–8.

∗**Leta, H.R.** 1987b. Primer hallazgo de *Lycoteuthis diadema* y *Octopoteuthis megaptera* para aguas urugauayas y descripcion de un nueva especie del genero *Pholidoteuthis* (Cephalopoda: Teuthoidea). *Publicaciones Cientificas, Instituto Nacional de Pesca, Montevideo*, 1(1): 9–25.

Leta, H.R. 1989. Exploratory and experimental jigging for red squid (*Ommastrephes bartramii*) and short finned squid (*Illex argentinus*) in the Uruguayan sector of the Argentine-Uruguayan common fishing zone (winter 1986). *Frente Maritimo*, 5A: 29–37.

Levi, D., M.G. Andreoli, G. Gioiello, P. Jereb, G. Norrito & G. Pernice. 1999. Trawl surveys forecasting. *In*: J.A. Bertrand & G. Relini, Co-ordinators. "Assessment of demersal resources by direct methods in the Mediterranean and the adjacent seas", Pisa (Italy), 18–21 March 1998. *Aquatic Living Resources*, 12(3): 112–128.

Levitina, M.V. 1993; 1992. Glycolipids in the optic ganglia of three species of squid. *Russian Journal of Marine Biology*, 18,(5–6): 192–195; 18(5–6): 78–81.

Li, J. & L. Yan. 2004. Quantity distribution of *Todarodes pacificus* and its relation with environment in the East China Sea. *Marine Fisheries Haiyang Yuye*, 26(3): 193–198.

∗**Li, J., J. Yang & H. Pang.** 1995. Study on the ecological growth efficiency of five marine fishes. *Marine Sciences, Qingdao*, 3: 52–54.

Li, S.F., L.P. Yan, H.Y. Li, J.S. Li & J.H. Cheng. 2006. Spatial distribution of cephalopod assemblages in the region of the East China Sea. *Journal of Fishery Sciences of China/Zhongguo Shuichan Kexue*, 13(6): 936–944.

∗**Li, Y., G. Chen & D. Sun.** 2000. Analysis of the composition of fishes in the Pearl River estuarine waters. *Journal of Fisheries of China*, 24(4): 312–317.

Liao, C.-H., K.-T. Lee, M.-A. Lee & T.-Y. Liu. 2005. A study on fishing composition of torch-lighted fishery in the northern waters of Taiwan. *Journal of the Fisheries Society of Taiwan*, 32(1): 57–58.

Libertelli, M.M., G.A. Daneri, U. Piatkowski, N.R. Coria & A.R. Carlini. 2004. Predation on cephalopods by *Pygoscelis papua* and *Arctocephalus gazella* at South Orkney Islands. *Polish Polar Research*, 25(3–4): 267–2.

∗**Lichtenstein, H.C.** 1818. *Onychoteuthis*, Sepien mit Krallen. *Isis oder Encyclopadische Zeitung*, 1818(9):1591–1592, 1 pl.

Lick, R. & U. Piatkowski. 1998. Stomach contents of a northern bottlenose whale (*Hyperoodon ampullatus*) stranded at Hiddensee, Baltic Sea. *Journal of the Marine Biological Association of the United Kingdom*, 78(2): 643–650.

Lieberman, E.M., N.J. Abbott & S. Hassan. 1989. Evidence that glutamate mediates axon-to-Schwann cell signaling in the squid. *Glia*, 2(2): 94–102.

Lim, N.S.H., K.J. Everuss, A.E. Goodman & K. Benkendorff. 2007. Comparison of surface microfouling and bacterial attachment on the egg capsules of two molluscan species representing Cephalopoda and Neogastropoda. *Aquatic Microbial Ecology*, 47(3): 275–287.

∗**Lima, P.A., M.L. Coelho, J.P. Andrade & E.R. Brown.** 1995. Patterns of schooling behaviour in *Alloteuthis subulata* (Cephalopoda: Loliginidea). *Copenhagen Denmark ICES*, 9 pp.

Lin, J.K. & D.C. Hurng. 1989. Potentiation of ferrous sulphate and axcorbate on the microbial transformation of endogenous trimethylamine N-oxide to trimethylamine and dimethylamine in squid extracts. *Food and Chemical Toxicology*, 27(9): 613–618.

Lin, L. & B.F. Li. 2006. Radical scavenging properties of proein hydrolysates from jumbo flying squid (*Dosidicus eschrichitii* Steenstrup) skin gelatin. *Journal of the Science of Food and Agriculture*, 86(14): 2290–2295.

∗**Lindgren, A., R.E. Young & K.M. Mangold.** 2008. Pyroteuthidae Pfeffer 1912. The fire squid. Version 23 April 2008. http://tolweb.org/Pyroteuthidae/19637/2008.04.23 in The Tree of Life Web Project, http://tolweb.org/

Lindgren, A.R., O.N. Katugin, M.K. Nishiguchi & E. Amezquita. 2004. Phylogenetic relationships among the Gonatidae (Cephalopoda, Teuthida, Oegopsida) based on DNA sequence data. *In*: "*Mollusks of the Northeastern Asia and Northern Pacific: Biodiversity, Ecology, Biogeography and Faunal History*", Vladivostok, Russia: 89–92.

∗**Lindgren, A.R., O.N. Katugin, E. Amezquita & M.K. Nishiguchi.** 2005. Evolutionary relationships among squids of the family Gonatidae (Mollusca: Cephalopoda) inferred from three mitochondrial loci. *Molecular Phylogenetics and Evololution*, 36: 101–111.

Ling, J. & Y. Zheng. 2000. Stock assessment of cephalopoda in East China Sea and Yellow Sea. *Marine Fisheries Haiyang-Yuye Shanghai*, 2000(2): 60–62.

***Linnaeus, C. von,** 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Edition, 10(1), 824 pp.

Lipinski, M.R. 1979. Universal maturity scale for the commercially important species. The results of maturity classification of *Illex illecebrosus* (LeSueur, 1821) population for years 1973–1977. Res. Doc. 79/II/38, Serial No.5364, ICNAF, 40 pp.

***Lipinski**, M.R. 1983. A description of a new species of enoploteuthid cephalopod, *Abralia siedleckyi* spec. nov., with some remarks on *Abralia redfieldi* G. Voss, 1955. *Veliger*, 25(3): 255–265, 8 figs.

Lipinski, M.R. 1985. Laboratory survival of *Alloteuthis subulata* (Cephalopoda: Loliginidae) from the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom*, 65: 845–855.

Lipinski, M.R. 1986. Methods for the validation of squid age from statoliths. *Journal of the Marine Biological Association of the United Kingdom*, 66: 505–526.

Lipinski, M.R. 1987. Food and feeding of *Loligo vulgaris reynaudii* from St. Francis Bay, South Africa. *In*: A.I.L. Payne, J.A. Gulland & K.H. Brink eds. “The Benguela and comparable frontal systems”, 5: 557–564.

Lipinski, M.R. 1990a. Changes in pH in the caecum of *Loligo vulgaris reynaudii* during digestion. *South African Journal of Marine Science*, 9: 43–51.

Lipinski, M.R. 1990b. The distribution of cephalopods in South African waters and world-wide. *South African Comm. Fishermen*, 2: 10–11.

***Lipinski**, M.R. 1992. Cephalopods and the Benguela ecosystem: trophic relationships and impact. *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. *Benguela trophic functioning. South Africa*, 12: 791–802.

Lipinski, M.R. 1993a. Description of mature males of the histioteuthid cephalopod *Histioteuthis atlantica* (Hoyle, 1885) (Cephalopoda: Oegopsida) from the South Atlantic Ocean. *South African Journal of Marine Science*, 13: 51–62.

Lipinski, M.R. 1993b. The deposition of statoliths: a working hypothesis. *In*: T. Okutani, R.K. O’Dor & T. Kubodera, eds. Recent advances in cephalopod fisheries biology. *Tokai University Press*, 241–262.

Lipinski, M.R. 1994. Differences among basic biological parameters in a population of chokka squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) sampled by three methods. *South African Journal of Marine Science*, 14: 281–286.

Lipinski, M.R. 1997 Morphology of giant squid *Architeuthis statoliths*. *South African Journal of Marine Science*, 18: 299–303.

Lipinski, M.R. 1998a. Cephalopod life cycles: patterns and exceptions. *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 439–447.

***Lipinski**, M.R. 1998b. The external diverticulum of the anterior vena cava in some cephalopods: A preliminary description. *South African Journal of Marine Science*, 20: 37–40.

***Lipinski**, M.R. 2001. Preliminary description of two new species of Cephalopods (Cephalopoda: Brachioteuthidae) from South Atlantic and Antarctic waters. *Bulletin of the Sea Fisheries Institute, Gdynia*, 152: 3–14.

Lipinski, M.R. & J.H.M. David. 1990. Cephalopods in the diet of the South African fur seal (*Arctocephalus pusillus pusillus*). *Journal of Zoology, London*, 221: 359–374.

***Lipinski**, M.R. & D.M. **Durholtz.** 1994. Problems associated with ageing squid from their statoliths: towards a more structured approach. *In*: P.G. Rodhouse, U. Piatkowski & C.C. Lu eds. Southern Ocean cephalopods: life cycle and populations. *Antarctic Science*, 6(2): 215–222.

Lipinski, M.R. & T.B. Linkowski. 1986. Some aspects of the biology of squid *Moroteuthis ingens* (Onychoteuthidae) from New Zealand waters. *Report of Fisheries Institute, Gdynia*, 21: 97–105.

Lipinski, M.R. & T.B. Linkowski. 1988. Food of the squid *Ommastrephes bartramii* Lesueur, (1821) from the south-west Atlantic Ocean. *South African Journal of Marine Science*, 6: 43–46.

Lipinski, M.R. & M.A. Soule. 2006. Elements of behaviour of loliginid squid in a large concentration. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 85.

Lipinski, M.R. & M.A. Soule. 2007a. A new direct method of stock assessment of the loliginid squid. *Reviews in Fish Biology and Fisheries*, 17(2–3): 437–453.

Lipinski, M.R. & M.A. Soule. 2007b. Disintegration of a large concentration of loliginid squid as a response to predation. *Reviews in Fish Biology and Fisheries*, 17(2–3): 477–485.

***Lipinski, M.R. & K. Turoboyski.** 1983. The ammonium content in the tissues of selected species of squid (Cephalopoda: Teuthoidea). *Journal of Experimental Marine. Biology and Ecology*, 69(2): 145–150.

Lipinski, M.R. & L.G. Underhill. 1995. Sexual maturation in squid: quantum or continuum? *South African Journal of Marine Science*, 15: 207–223.

***Lipinski, M.R. & R.E. Young.** 2008. Brachioteuthidae Pfeffer 1908. Version 06 July 2008. http://tolweb.org/Brachioteuthidae/19409/2008.07.06 in The Tree of Life Web Project, http://tolweb.org/

Lipinski, M.R., M.D. Durholtz & L.G. Underhill. 1988. Field validation of age readings from the statoliths of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) and an assessment of associated errors. *ICES Journal of Marine Science*, 55(2): 240–257.

Lipinski, M.R., R. Laubscher & D. Durholtz. 2006. Hatching dates and the timing of spawning in the chokka squid. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 86.

Lipinski, M.R., W.K. Macy & D.M. Durholz. 2002. Comparison of LM - and SEM - derived ages of *Loligo pealeii*. *Bulletin of Marine Science*, 71(2): 1130.

***Lipinski, M.R., F.A. Naggs & M.A. Roeleveld.** 2000. Catalogue of types of recent cephalopods in the collection of the Natural History Museum, London. *Annales Zoologici (Warszawa)*, 50(1): 101–120.

Lipinski, M.R., A. Payne & B. Rose. 1992. The importance of cephalopods as prey for hake and other groundfish in South African waters. *South African Journal of Marine Science*, 12: 651–662.

Lipinski, M.R., M.A. Roeleveld & L.G. Underhill. 1993. Comparison of the Statoliths of *Todaropsis eblanae* and *Todarodes angolensis* (Cephalopoda: Ommastrephidae) in South African Waters. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Fisheries Biology. Tokai University Press, Tokyo*, 263–273.

***Lipinski**, **M.R., I. Hampton, W.H.H. Sauer & C.J. Augustyn.** 1998a. Daily net emigration from a spawning concentration of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) in Kromme Bay, South Africa. *ICES Journal of Marine Science*, 55(2): 258–270.

***Lipinski**, **M.R., D.S. Butterworth, C.J. Augustyn, J.K.T. Brodziak, G. Christy, S. des Clers, G.D. Jackson, R.K. O'Dor, D. Pauly, L.V. Purchase, M.J. Roberts, B.A. Roel, Y. Sakurai & W.H.H. Sauer.** 1998b. Cephalopod fisheries: a future global upside to past overexploitation of living marine resources? *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 463–469.

Littnan, C.L., J.P.Y. Arnould & R.G. Harcourt. 2007. Effect of proximity to the shelf edge on the diet of female Australian fur seals. *Marine Ecology Progress Series*, 338: 257–267.

Liu, B. & X. Chen. 2004. Preliminary study on the relationship between the distribution of production of *Illex argentinus* and SST in the Southwest Atlantic Ocean in 2001. *Marine Fisheries/Haiyang Yuye*, 26(4): 326–331.

Llewellyn, J. 1984. The biology of *Isancistrum subulatae* n.sp., a monogenean parasitic on the squid, *Alloteuthis subulata*, at Plymouth. *Journal of the Marine Biological Association of the United Kingdom*, 64(2): 285-302.

Lloret, J. & J. Lleonart. 2002. Recruitment dynamics of eight fishery species in the northwestern Mediterranean Sea. *Scientia Marina*, 66(1): 77–82.

Lo, Z.T., C.S. Chen, T.S. Chiu & C.C. Hsu. 2005. Migration pattern of seasonal cohort of *Ommastrephes bartramii* in the North Pacific. *Journal of Fisheries Society of Taiwan*, 32(1): 121.

Loffler, D.L. & M. Vecchione. 1993. An unusual squid paralarva (Cephalopoda) with tentacular photophores. *Proceedings of Biological Society of Washington*, 106(3): 602–605.

Lombarte, A., P. Sanchez & B. Morales-Nin. 1997. Intraspecific shape variability in statoliths of three cephalopod species. *In*: S.v. Boletsky, P. Fioroni & A. Guerra, eds. *Functional Morphology of Cephalopods*, Banyuls ser Mer, France, 47(2): 165–169.

Long, T.M., R.T. Hanlon, A. ter Maat & H.M. Pinsker. 1989. Non associative learning in the squid, *Lolliguncula brevis*. *Marine Behavior and Physiology*, 16(1): 1–9.

Longhurst, A. 1998. Ecological Geography of the Sea, San Diego, *Academic Press*.

***Lönnberg, E.** 1896. Notes on some rare cephalopoda. Ofversigt af Kong. *Vetenskaps-Akademiens Forhandlingar,* 53(8): 603–612, 4 figs.

***Lönnberg, E.** 1898. On the cephalopods collected by the Swedish Expedition to Tierra del Fuego, 1895–96. *Svenska Expeditionen till Magellanslanderna*, 2(4): 49–64, 2 pls.

Lopes, S.S., M.L. Coelho & J.P. Andrade. 1997. Analysis of oocyte development and potential fecundity of the squid *Loligo vulgaris* from the waters of southern Portugal. *Journal of the Marine Biological Association of the United Kingdom*, 77(3): 903–906.

Lordan, C. 2001. Investigations into the fisheries and biology of ommastrephid squid species in Irish waters. Ph.D. thesis, Aquaculture Development Centre, Department of Zoology and Animal Ecology, Cork, National University of Ireland.

Lordan, C. & J. Casey. 1999. The first evidence of offshore spawning in the squid species *Loligo forbesi*. *Journal of the Marine Biological Association of the United Kingdom*, 79: 379–381.

***Lordan, C., G.M. Burnell & T.F. Cross.** 1998a. The diet and ecological importance of *Illex coindetii* and *Todaropsis eblanae* (Cephalopopda: Ommastrephidae) in Irish waters. *In*: A.I.L. Payne, M.R. Lipinski & M.A.C. Roeleveld, eds. Cephalopod Biodiversity, Ecology and Evolution. *South African Journal of Marine Science*, 20: 153–163.

Lordan, C., M.A. Collins & C. Perales-Raya. 1998b. Observations on morphology, age and diet of three *Architeuthis* caught off the west coast of Ireland in 1995. *Journal of the Marine Biological Association of the United Kingdom*, 78: 903–917.

Lordan, C., M. Collins, G. Burnell & T. Cross. 1995. The significance of squid in Irish fisheries. *Copenhagen Denmark ICES*, 11 pp.

***Lordan, C., M.A. Collins, L. Key & E.D. Browne.** 2001a. The biology of the ommastrephid squid, *Todarodes sagittatus*, in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 81(2): 299–306.

Lordan, C., S. Warnes, T.F. Cross & G.M. Burnell. 2001b. The distribution and abundance of cephalopod species caught during demersal trawl surveys west of Ireland and in the Celtic Sea. *Irish Fisheries Investigation New Series*, 8: 26 pp.

Lorentsen, S.H., N. Klages & N. Roev. 1998. Diet and prey consumption of Antarctic petrels *Thalassoica antarctica* at Svarthamaren, Dronning Maud Land, and at sea outside the colony. *Polar Biology*, 19(6): 414–420.

Loukashkin, A.S. 1977. On the biology of the market squid, *Loligo opalescens*, a contribution toward the knowledgeof its food habits and feeding behaviour. *Reports of California Cooperative Oceanic Fisheries Investigations*, 18: 109–111.

Lowry, M.S. & J.V. Carretta. 1999. Market squid (*Loligo opalescens*) in the diet of California sea lions (*Zalophus californianus*) in southern California (1981–1995). *Reports of California Cooperative Oceanic Fisheries Investigations*, 40: 196–202.

***Lu, C.C.** 1973. Systematics and zoogeography of the squid genus *Illex* (Oegopsida: Cephalopoda). Ph.D. Thesis, Memorial University of Newfoundland, Canada, 389 pp.

***Lu, C.C.** 1977. A new species of squid, *Chiroteuthis acanthoderma*, from the Southwest Pacific (Cephalopoda, Chiroteuthidae). *Steenstrupia*, 4:179–188, 14 figs.

***Lu, C.C.** 1982. First record of *Todaropsis eblanae* (Ball, 1841) in the Pacific Ocean. *Venus, Japanese Journal of Malacology*, 41(1): 67–70.

Lu, C.C. 1986. Smallest of the largest-first record of giant squid larval specimen. *Australian Shell News*, 53: 9.

Lu, C.C. 1997. A new species of squid, *Chiroteuthis acanthoderma* from the Southwest Pacific (Cephalopoda, Chiroteuthidae). *Steenstrupia*, 4(16): 179–188.

Lu, C.C. 1998a. Order Sepioidea. Pp. 504–51. *In*: P.L Beesley, G.J.B. Ross, & A. Wells, eds. *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5*. CSIRO Publishing: Melbourne, Part A xvi 563 pp.

Lu, C.C. 1998b. Order Vampyromorpha. Pp. 542–545. *In*: P.L. Beesley, G.J.B. Ross & A. Wells, eds. *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5. CSIRO Publishing*: Melbourne, Part A xvi 563 pp.

Lu, C.C. 1998c. Order Octopoda. Pp. 545–563. *In*: P.L. Beesley, G.J.B. Ross, & A. Wells, eds. *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5. CSIRO Publishing*: Melbourne, Part A xvi 563 pp.

Lu, C.C. 2000. Diversity of cephalopoda from the waters around the Tong-Sha Island (Pratas Islands), South China Sea. Proceedings of the 2000 Cross-strait Symposium on Bio-Diversity and Conservation, Chow Y.S., Hsieh, F.K., Wu, S.H., Chou, W.H. (eds). Taichung: National Museum of Natural Science. p. 201–214.

Lu, C.C. 2002. Cephalopod production from the waters around Taiwan. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. *Cephalopod Biomass and Production. Bulletin of Marine Science*, 71(1): 465–471.

*****Lu, C.C.** 2005. A new family of myopsid squid from Australasian waters (Cephlopoda: Teuthida. *Phuket Marine Biological Center Research Bulletin*, 66: 71–82, figs 1–9.

*****Lu, C.C. & M.R. Clarke.** 1974. Two new species of cranchiid cephalopod from the North Atlantic, *Uranoteuthis bilucifer* n. gen., n. sp. and *Galiteuthis triluminosa* n. sp. *Journal of the Marine Biological Association of the United Kingdom*, 54:985–994, 4 figs.

*****Lu, C.C. & M.R. Clarke.** 1975a. Vertical distribution of cephalopods at 40°N, 53°N and 60°N at 20°W in the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 55: 143–163.

*****Lu, C.C. & M.R. Clarke.** 1975b. Vertical distribution of cephalopods at 11°N, 20°W in the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 55: 369–389.

Lu, C.C. & M.C. Dunning. 1982. Identification guide to Australian arrow squid (family Ommastrephidae). *Victorian Institute Marine Scientific Technical Report*, 2.

Lu, C.C. & J.U. Phillips. 1985. An annotated checklist of Cephalopoda from Australian waters. *Occasional Papers from the Museum of Victoria*, 2: 21–36.

*****Lu, C.C. & C.F.E. Roper.** 1979. Cephalopods from Deepwater Dumpsite 106 (Western Atlantic): Vertical Distribution and Seasonal Abundance. *Smithsonian Contributions to Zoology*, 288: 36 pp.

Lu, C.C. & R.W. Tait. 1983. Taxonomic studies on *Sepioteuthis* Blainville (Cephalopoda; Loliginidae) from the Australian region. *Proceedings of the Royal Society of Victoria*, 95(4): 181–204.

*****Lu, C.C. & R. Williams.** 1994a. Contribution to the biology of squid in the Prydz Bay region. *Antarctica. Antarctic Science*, 6(2): 223–229.

Lu, C.C. & R. Williams. 1994b. *Kondakovia longimana* Filippova (Cephalopoda: Onychoteuthidae) from the Indian Ocean sector of the Southern Ocean. *Antarctic Science*, 6: 231– 234.

*****Lu, C.C. & R.E. Young.** 2005. Australiteuthidae Lu, 2005. *Australiteuthis aldrichi* Lu, 2005. Version 20 September 2005. http://tolweb.org/Australiteuthis_aldrichi/52671/2005.09.20 in The Tree of Life Web Project, http://tolweb.org/

*****Lu, C.C., R. Boucher-Rodoni & A. Tillier.** 1995. Catalogue of types of recent Cephalopoda in the Muséum national d'Histoire naturelle (France). *Bulletin of the Muséum national d'Histoire naturelle, Paris*, 4e sér., 17A(3–4): 307–343.

*****Lu, C.C., C.F.E. Roper & R.W. Tait.** 1985. A revision of *Loliolus* (Cephalopoda; Loliginidae), including *L. noctiluca*, a new species of squid from Australian waters. *Proceedings of the Royal Society of Victoria*, 97(2): 59–85.

Lubimova, T.G. 1985. Results of Soviet investigations of the distribution and ecology of pelagic squids (Oegopsida) in the Southern Ocean. *Selected papers presented to the scientific committee of CCAMLR*, 79–111.

Lucena, F.M., T. Vaske, Jr., J.R. Ellis & C.M. O' Brien. 2000. Seasonal variation in the diets of bluefish, *Pomatomus saltatrix* (Pomatomidae) and striped weakfish, *Cynoscion guatucupa* (Sciaenidae) in southern Brazil: implications of food partitioning. *Environmental Biology of Fishes*, 57(4): 423–434.

*****Lucero, M.T. & J. Poulsen.** 2005. Betaine transport in giant fiber lobes of the squid *Lolliguncula brevis*. *Phuket Marine Biological Center Research Bulletin*, No. 66: 229–234, 4 figs.

Lumare, F. 1970. Nota sulla distribuzione di alcuni cefalopodi del Mar Tirreno. *Boll. Pesca Piscic. Idrobiol.*, 25(2): 313–344.

Lum-Kong, A. 1992. A histological study of the accessory reproductive organs of female *Loligo forbesi* (Cephalopoda: Loliginidae). *Journal of Zoology*, 226(3): 469–490.

*****Lum-Kong, A. & T.S. Hastings.** 1992. The accessory nidamental glands of *Loligo forbesi* (Cephalopoda: Loliginidae): Characterization of symbiotic bacteria and preliminary experiments to investigate factors controlling sexual maturation. *Journal of Zoology*, 228(3): 395–403.

Lum-Kong, A., G.J. Pierce & C. Yau. 1992. Timing of spawning and recruitment in *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, 72: 301–311.

Lydersen, C., I. Gjertz & J.M. Weslawski. 1989. Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. *Polar Research*, 25(153): 107–114.

Lydersen, C., L.A. Angantyr, O. Wiig & T. Oritsland. 1991. Feeding habits of northeast Atlantic harp seals (*Phoca groenlandica*) along the summer ice edge of the Barents sea. *Canada Journal of Fisheries and Aquatic Science*, 48(11): 2180–3.

Lykkeboe, G. & K. Johansen. 1982. A cephalopod approach to rethinking about the importance of the Bohr and Haldane effects. *Pacific Science*, 36(3): 305–314.

Lynnes, A.S. & P.G. Rodhouse. 2002. A big mouthful for predators: the largest recorded specimen of *Kondakovia longimana* (Cephalopoda: Onychoteuthidae). *In* P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(2): 1087–1090.

MacAskie, I.B. 1971. Range extension for the squid *Abraliopsis (Watasenia) felis*. *Journal of Fisheries Research Board, Canada*, 28(4): 620–621.

* **MacDonald, R. & W.J. Clench.** 1934. Descriptions of a new genus and two new species of squids from the North Atlantic. *Occasional Papers of the Boston Society of Natural History*, 8:145–152, 9 figs.

Macewicz, B.J., J.R. Hunter & N.C.H. Lo. 2003. Lifetime fecundity of the market squid, *Loligo opalescens*, with application to monitoring escapement. *In*: O.S. Kjesbu, J.R. Hunter & P.R. Witthames, eds. Report of the Working Group on Modern Approaches to Assess Maturity and Fecundity of Warm and Cold water Fish and Squids. *Havforsknings Instituttet*, 12: 79–85.

Macewicz, B.J., J.R. Hunter, N.C.H. Lo & E.L. LaCasella. 2004. Fecundity, egg deposition, and mortality of market squid (*Loligo opalescens*). *Fishery Bulletin*, 102(2): 306–327.

MacLeod, C.D., G.J. Pierce & M.B. Santos. 2004. Geographic and temporal variations in strandings of beaked whales (Ziphiidae) on the coasts of the UK and the Republic of Ireland from 1800–2002. *Journal of Cetacean Research and Management*, 6(1): 79–86.

MacNaughton, R., E. Rogan, V. Hernandez-Garcia & C. Lordan. 1998. The importance of cephalopods in the diet of blue shark (*Prionace glauca*) south and west of Ireland. *Copenhagen, Denmark ICES*, 12 pp.

Macy, W.K. 1980. The ecology of the common squid, *Loligo pealei* LeSueur, 1821, in Rhode Island waters. *Ph.D. Thesis, University of Rhode Island*, 236 pp.

Macy, W.K. 1982a. Development and application of an objective method for classifying long-finned squid, *Loligo pealei*, into sexual maturity stages. *Fishery Bulletin*, 80: 449–459.

Macy, W.K. 1982b. Feeding patterns of the long-finned squid, *Loligo pealei*, in New England waters. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 162(1): 28–38.

* **Macy, W.K.** 1995a. The application of digital image processing to ageing long-finned squid *Loligo pealei*, using the statolith. *In*: D.H. Secor, J.M. Dean & S.E. Campana, eds. Recent Developments in Fish Otolith Research. *University Of South Carolina Press*, 283–302.

* **Macy, W.K.** 1995b. Recruitment of long-finned squid in New England (USA) waters. *ICES Council Meeting, Aalborg (Denmark)*, 21–29 Sep 1995.

Macy, W.K. & J.K.T. Brodziak. 2001. Seasonal maturity and size at age of *Loligo pealeii* in waters of southern New England. *ICES Journal of Marine Science*, 58(4): 852–864.

Madan, J.J. & M.J. Wells. 1997. A ‘hyaline’ layer in the skin of squids. *Journal of the Marine Biological Association of the United Kingdom*, 77(4): 1247–1250.

Madeira di Beneditto, A.P. & R.M. Arruda Ramos. 2001. Biology and conservation of the franciscana (*Pontoporia blainvillei*). *Journal of Cetacean Research and Management*, 3(2): 185–192.

Madeira di Beneditto, A.P.M. & R.M. Arruda Ramos. 2004. Biology of the marine tucuxi dolphin (*Sotalia fluviatilis*) in southeastern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 84(6): 1245–1250.

Madureira, L., R. Habiaga, C. Soares, S. Weigert, C. Ferreira, D. Eliseire & A.C. Duvoisin. 2005. Identification of acoustic records of the Argentinian calamar *Illex argentinus* (Castellanos, 1960) along the outer shelf and shelf break of the south and southeast coast of Brazil. *Fisheries Research (Amsterdam)*, 73(1–2): 251–257.

Madureira, L.S.P., R.G.P. Habiaga, A.C. Duvoisin, D. Eliseire, C.F. Soares, F. Cristina, S.C. Weigert, C.S. Ferreira & A. Pablo. 2006. Identification of the acoustic record of the Argentinian squid *Illex argentinus* (Castellanus, 1960) from the continental shelf of the south and southeastern region of Brazil. *Instituto Oceanografico, Sao Paulo*, 1–32.

Maharaj, G. & B.A. Roel. 2000. Fishing effort in the South African Chokka squid jig fishery. 10th Southern African Marine Science Symposium SAMSS 2000: *Land, Sea and People in the New Millennium, Abstracts*.

Major, P.F. 1986. Notes on a predator-prey interaction between common dolphins (*Delphinus delphis*) and short-finned squid (*Illex illecebrosus*) in Lydonia submarine canyon, western North Atlantic Ocean. *Journal of Mammalogy*, 67(4): 769–770.

Makinodan, Y., T. Nakagawa & M. Hujita. 1993. Effect of cathepsins on textural change during ripening of Ika-shiokara (salted squid preserves). *Bulletin of the Japanese Society of Scientific Fisheries*, 59(9): 1625–1629.

Malzone, C., M. Wilson & P. Iampietro. 2006. Advances in the evaluation of acoustic beamformed backscatter data for fisheries applications. *Journal of the Acoustical Society of America*, 120(5, pt. 2): 3018.

Mandic, S. & J. Stjepcevic. 1983. Economical important species of cephalopods in South Adriatic. *Studies Mar.*, 13–14: 215–222.

Mandic, S., J. Stjepcevbic & R. Dragonovic. 1982. Migration's occurrences with some Cephalopoda species in the South Adriatic. *Studies Mar.*, 11–12: 95–102.

* **Mangold, K.** 1974. Cephalopods collected during the Polymede I and II cruises in the Mediterranean. *Rapport P.V. Reun, de la Commission International pour l'Exploration Scientifique de la Mer Mediterranée, Monaco*, 22(7): 67.

Mangold, K. 1983. Food, feeding and growth in cephalopods. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Proceedings of the workshop on the biology and resource potential of cephalopods. Memoirs of the National Museum Victoria*, 44: 81–94.

Mangold, K. 1987. Reproduction. *In*: P.R. Boyle Ed. "Cephalopod Life Cycles. Comparative reviews". Vol. II. *Academic Press, London*, 157–200.

* **Mangold K. & S.V. Boletzky.** 1987. Céphalopodes. *In*: W. Fischer, M.-L. Bauchot & M. Schneider, eds. Fiches FAO d'identification des especes pour les besoins de la peche. (Révision 1). Méditerranée et mer Noire. Zone de peche 37. Volume I. *Végétaux et Invertébrés*, 1: 634–714.

Mangold, K., M.R. Clarke & C.F.E. Roper. 1998. Class Cephalopoda. *In*: P.L. Beesley, G.J.B. Ross, & A. Wells, eds. *Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5. CSIRO Publishing*: Melbourne, Part A: 451–484.

Mangold, K., C.C. Lu & F.A. Aldrich. 1969. A reconsideration of forms of squid of the genus *Illex* (Illicinae, Ommastrephidae). II. Sexual dimorphism. *Canadian Journal of Zoology*, 47: 1153–1156.

* **Mangold-Wirz, K.** 1963. Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie et Milieu*, 13(suppl): 285 pp.

Mangum, C.P. 1991. Salt sensitivity of the haemocyanin of eury- and sthenohaline squids. *Comparative Biochemistry and Physiology* A, 99: 159–161.

* **Mann, T.** 1984. Spermatophores. Development, structure, biochemical attributes and role in the transfer of spermatozoa. *Springer-Verlag, Berlin*, 215 pp.

* **Mann, T., A.W. Martin & J.B. Tiersch.** 1966. Spermatophores and spermatophoric reaction in the giant octopus of the North Pacific, *Octopus dofleini martini*. *Nature, London*, 211: 1279–1282.

* **Mann, T., A.W. Martin & J.B. Tiersch.** 1970. Male reproductive tract, spermatophores and spermatophoric reaction in the giant octopus of the North Pacific, *Octopus dofleini martini*. *Proceedings of the Royal Society of London, Series B*, 175: 31–61.

Mannini, P. & C. Volpi. 1989. Nota sulla presenza e distribuzione di alcuni cefalopodi del Tirreno settentrionale. *Oebalia*, 15 (2): 693–701.

* **Manoch, R.** 1998. Re-examination of *Loligo sumatrensis* d'Orbigny, 1835 along the eastern coast of the Gulf of Thailand. *Thai Marine Fisheries Research Bulletin*, 6: 11–16.

Marabello, F., L. Guglielmo, A. Granata & O. Sidoti. 1996. Studi preliminari sulle abitudini alimentari di *Todarodes sagittatus* (Cephalopoda) nel Tirreno meridionale. *In*: G. Albertelli, A. De Maio & M. Piccazzo eds. Atti dell'11° Congresso dell'Associazione Italiana di Oceanologia e Limnologia (Sorrento, 26–28 Ottobre 1994), *Genova, A.I.O.L.*, pp. 271–278.

Marano, C.A., M. Martino, M.C. Marzano, L. Ceriola & N. Ungaro. 2006. Taglia di prima maturita' di *Illex coindetii* (Verany, 1839) nell'Adriatico meridionale. *Biologia Marina Mediterranea*, 13 (1 Part II): 881–883.

Marian, J.E.A.R. & O. Domaneschi. 2006 Spermatophore formation in Loliginidae: morphology, histology and histochemistry of the spermatophoric organ of *Loligo plei*, *L. sanpaulensis* and *Lolliguncula brevis*. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 44.

* **Markaida, U.** 2006a. Food and feeding of jumbo squid *Dosidicus gigas* in the Gulf of California and adjacent waters after the 1997–98 el Niño event. *Fisheries Research*, 79(1–2): 16–27.

* **Markaida, U.** 2006b. Population structure and reproductive biology of jumbo squid *Dosidicus gigas* from the Gulf of California after the 1997–1998 el Niño event. *Fisheries Research*, 79(1–2): 28–37.

Markaida, U. & F.G. Hochberg. 2005. Cephalopods in the diet of swordfish (*Xiphias gladius*) caught off the west coast of Baja California, Mexico. *Pacific Science*, 59(1): 25–41.

Markaida, U. & O. Sosa-Nishizaki. 1998. Food and Feeding Habits of Swordfish *Xiphias gladius* L., off Western Baja California. *Biology and Fisheries of Swordfish*, 142: 245–260.

* **Markaida, U. & O. Sosa-Nishizaki.** 2001. Reproductive biology of jumbo squid *Dosidicus gigas* in the Gulf of California, 1995–1997. *Fisheries Research*, 54(1): 63–82.

* **Markaida, U. & O. Sosa-Nishizaki.** 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the United Kingdom*, 83(3): 507–522.

* **Markaida, U., C. Quinonez-Velazquez & O. Sosa-Nishizaki.** 2004. Age, growth and maturation of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Fisheries Research*, 66(1): 31–47.

* **Markaida, U., J.J.C. Rosenthal & W.F. Gilly.** 2005. Tagging studies on the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. *Fishery Bulletin*, 103(1): 219–226.

Martin, A.R. & M.R. Clarke. 1986. The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. *Journal of the Marine Biological Association of the United Kingdom*, 66(4): 779–790.

Martin, B. & B. Christiansen. 1997. Diets and standing stocks of benthopelagic fishes at two bathymetrically different midoceanic localities in the northeast Atlantic. *Deep Sea Research*, I 44(4): 541–558.

* **Martin, R. & J. Voight.** 1987. The neurosecretory system of the octopus vena cava: a neurohemal organ. *Experientia*, 43: 537–543.

Martinez, P., A. Sanjuan & A. Guerra. 2002. Identification of *Illex coindetii*, *I. illecebrosus* and *I. argentinus* (Cephalopoda: Ommastrephidae) throughout the Atlantic Ocean; by body and beak characters. *Marine Biology*, 141(1): 131–143.

* **Martinez, P., P. Belcari, A. Sanjuan & A. Guerra.** 2005a. Allozyme analysis of geographical and seasonal variation of *Illex coindetii* (Cephalopoda: Ommastrephidae) from Central Mediterranean and Iberian Atlantic. *Journal of Marine Biology Association of the United Kingdom*, 85: 177–184.

* **Martinez, P., M. Perez-Losada, A. Guerra & A. Sanjuan.** 2005b. First genetic validation and diagnosis of the short-finned squid species of the genus *Illex* (Cephalopoda: Ommastrephidae). *Marine Biology*, 148: 97–108.

Martinez-Portela, C.J. 1992. Cephalopod fisheries in the Malvinas/Falkland Islands area and international waters of the Patagonian shelf. Proceedings of the second world cephalopod conference, squid' 91 Madrid. Hotel Castellana, Madrid, Spain, 11, 12 and 13 November 1991. Infofish, Kuala Lumpur Malaysia, *Turnbrige Wells UK, Agra Europe*, London Ltd., 15–41.

Martinez-Vega, J.A., L.E. Cruz-Suarez & D. Ricque-Marie. 2000a. Evaluation of different body parts of the giant squid (Dosidicus gigas) powdered as meal in balanced diets for shrimp (*Litopenaeus vannamei*) feeding. *Ciencia y mar*, 4(11): 11–18.

Martinez-Vega, J.A., L.E. Cruz-Suarez & D. Ricque-Marie. 2000b. Body composition and drying process of the giant squid *Dosidicus gigas*. *Ciencia y mar*, 4(11): 35–38.

Martins, A.L.G. & J.A.A. Perez. 2002. Sistemática e biologia reprodutiva da lula *Lolliguncula* sp. no litoral catarinense. *Anais do XXIV Congresso Brasileiro de Zoologia*, Itajaí, SC, p. 662.

* **Martins, H.R.** 1982. Biological studies of the exploited stock of *Loligo forbesi* (Cephalopoda) in the Azores. *Journal of the Marine Biological Association of the United Kingdom*, 62: 799–808.

Martins, H.R. & Porteiro, F.M. 1988. The exploited stock of *Loligo forbesi* in the Azores: Additional notes on biology and fisheries. *Copenhagen Denmark ICES*, 7 pp.

Martins, M.C. 1997. The statoliths of *Loligo vulgaris* and *L. forbesi* hatchlings: preliminary morphological study. *In*: S.v. Boletsky, P. Fioroni & A. Guerra, eds. *Functional Morphology of Cephalopods. Banyuls sur Mer, France, Laboratoire Arago*, 47(2): 171–176.

Martins, R., F. Rebordao & M. Sobral. 2000. Fishing with the xavega beach seine gear. Relatorios cientificos e tecnicos. *Instituto de Investigacao das Pescas e do Mar*, 48: 32 pp.

***Martins, R.S. & J.A.A. Perez.** 2006a. Occurrence of loliginid paralarvae around Santa Catarina Island, Southern Brazil. *Pan American Journal of Aquatic Sciences*, 1(1): 24–27.

***Martins, R.S. & J.A.A. Perez.** 2006b. Cephalopods and fish attracted by night lights in coastal shallow-waters, off southern Brazil, with the description of squid and fish behaviour. *Revista de Etologia*, 8: 27–34.

***Martins, R. S. & J.A.A. Perez.** 2007. The ecology of loliginid squid in shallow waters around Santa Catarina Island, Southern Brazil. *Bulletin of Marine Science*, 80(1): 125–145.

Martos, P. & M.C. Piccolo. 1988. Hydrography of the Argentine continental shelf between 38° and 42°S. *Continental Shelf Research*, 8: 1043–1056.

***Massy, A.L.** 1907. Preliminary notice of new and remarkable cephalopods from the south-west coast of Ireland. *Annals and Magazines of Natural History*, (series 7)20: 377–384.

***Massy, A.L.** 1916. The cephalopoda of the Indian Museum. *Records of the Indian Museum*, 12: 185–247.

Masuda, S., K. Yokawa, A. Yatsu & S. Kawahara. 1998. Growth and population structure of *Dosidicus gigas* in the southeastern Pacific Ocean. pp. 107–118. *In*: T. Okutani ed. Large Pelagic Squids. *Japan Marine Fishery Resources Research Center*, Tokyo. 269 pp.

Matallanas, J., M. Casadevall, M. Carrasson, J. Boix & V. Fernandez. 1995. The food of *Seriola dumerili* (Pisces: Carangidae) in the Catalan sea (western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, 75(1): 257–60.

Mathger, L.M. 2003. The response of squid and fish to changes in the angular distribution of light. *Journal of the Marine Biological Association of the United Kingdom*, 83(4): 849–856.

Mathger, L.M. & E.J. Denton. 2001. Reflective properties of iridophores and fluorescent 'eyespots' in the lolignid squid *Alloteuthis subulata* and *Loligo vulgaris*. *Journal of Experimental Biology*, 204: 2103–2118.

Matos-Correia, L. De & M.M. de Matos-Correia. 1989. Flying squid in the anchovy industry. *Squid 89 Lisbon: The first world cephalopods conference*, pp. 140–152.

Matsuda, S., F. Hanaoka, T. Kato & M. Hamabe. 1972. Recruitment and underlying mechanism of common squid stock in the southwestern waters of Japan. *Research Repport, Tech. Couns. Agr. For. Fish.*, 57: 10–30.

Matsui, S., M. Seidou, S. Horiuchi, I. Uchiyama & Y. Kito. 1988a. Adaptation of a deep-sea cephalopod to the photic environment. Evidence for three visual pigments. *Journal of General Physiology*, 92(1): 55–66.

Matsui, S., M. Seidou, I. Uchiyama, N. Sekiya, K. Hiraki, K. Yoshihara & Y. Kito. 1988b. 4-Hydroxyretinal, a new visual pigment chromophore found in the bioluminescent squid, *Watasenia scintillans*. *Biochemical and Biophysical Acta*, 966(3): 370–374.

Matsumiya, M., K. Miyauchi & A. Mochizuki. 2003. Purification and some properties of a chitinase isozyme from the liver of Japanese common squid *Todarodes pacificus*. *Fisheries Science*, 69(2): 427–429.

Matsuo, K., M. Miyagawa, M. Kanda & K. Yamaoka. 1997. Feeding habits of fishes of rocky shore at Ibukijima Island, in the Inland Sea. *Bulletin of Marine Sciences and Fisheries, Kochi University*, 17: 41–61.

Matsuo, M., Y. Abe, Y. Saruta & N. Okada. 1995. Mollusk genes encoding lysine tRNA(UUU) contain introns. *Gene*, 165(2): 249–253.

Matsuo, M., T. Yokogawa, K. Nishikawa, K. Watanabe & N. Okada. 1995. Highly specific and efficient cleavage of squid tRNA super (Lys) catalyzed by magnesium ions. *Journal of Biological Chemistry*, 270(17): 10097–10104.

Matsuoka, M., M. Tokimura, H. Fujita & T. Kitajima. 1993. A consideration on differences of catch compositions between daytime and nighttime bottom trawl samplings in the East China Sea. *Bulletin of the Sekai National Fisheries Research Institute, Seisuiken Kenpo*, 70: 1–9.

Mattlin, R.H. 1994. Seals and sea birds-fisheries interactions: Report of a workshop, Wellington, 1992. *New Zealand Fisheries Occas. Publication*, 8: 96 pp.

Maul, G.E. & W.J. Rees. 1956. The cephalopoda of Madeira: records and distribution. *Bulletin of the British Museum (Natural History) Zoology*, 3(6): 259–281.

Maunder, M.N., P.J. Starr & R. Hilborn. 2000. A Bayesian analysis to estimate loss in squid catch due to the implementation of a sea lion population management plan. *Marine Mammal Science*, 16(2): 413–426.

Maurer, R.O. & R.E. Bowman. 1985. Food consumption of squids (*Illex illecebrosus* and *Loligo pealei*) off the northeastern United States. *NAFO Scientific Council Studies*, 9: 117–124.

Maxwell, M.R. & R.T. Hanlon. 2000. Female reproductive output in the squid *Loligo pealeii*: Multiple egg clutches and implications for a spawning strategy. *Marine Ecology Progress Series*, 199: 159–170.

Maxwell, M.R. & R.T. Hanlon. 2002. Female reproductive output in the squid *Loligo pealeii*: multiple egg clutches and implications for a spawning strategy. *Bulletin of Marine Science*, 71(2): 1131.

Maxwell, M.R., K.M. Buresch & R.T. Hanlon. 2000. Pattern of inheritance of microsatellite loci in the squid *Loligo pealeii* (Mollusca: Cephalopoda). *Marine Biotechnology*, 2: 517–521.

Maxwell, M.R., L.D. Jacobson & R.J. Conser. 2005. Eggs-per-recruit model for management of the California market squid (*Loligo opalescens*) fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(7): 1640–1650.

Maxwell, M.R., W.K. Macy, S. Odate & R.T. Hanlon. 1996. Evidence for multiple spawning by squids (*Loligo pealei*) in captivity. *Biological Bulletin*, 195(2): 225–226.

Maxwell, M.R., W.K. Macy, S. Odate & R.T. Hanlon. 1998. Evidence for multiple spawning by squids (*Loligo pealei*) in captivity. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 195(2): 225–226.

Maxwell, M.R., A. Henry, C.D. Elvidge, J. Safran, V.R. Hobson, I. Nelson, B.T. Tuttle, J.B. Dietz & J.R. Hunter. 2004. Fishery dynamics of the California market squid (*Loligo opalescens*), as measured by satellite remote sensing. *Fishery Bulletin*, 102(4): 661–670.

Mayake, H., T. Kubodera & T. Okutani. 2006. Cephalopods observed from submersibles and ROV – II. A gigantic squid in Sagami Bay. *Chiribotan*, 36(2): 38–41 (in Japanese).

McAllister, M.K., S.L. Hill, D.J. Agnew, G.P. Kirkwood & J.R. Beddington. 2004. A Bayesian hierarchical formulation of the De Lury stock assessment model for abundance estimation of Falkland Islands' squid (*Loligo gahi*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61(6): 1048–1059.

McArthur, T., E.C. Butler & G.D. Jackson. 2003. Mercury in the marine food chain in the Southern Ocean at Macquarie Island: an analysis of a top predator, Patagonian toothfish (*Dissostichus eleginoides*) and a mid-trophic species, the warty squid (*Moroteuthis ingens*). *Polar Biology*, 27(1): 1–5.

*** McConathy, D., R.T. Hanlon & R.F. Hixon.** 1980. Chromatophore arrangements of hatchling loliginid squids (Cephalopoda, Myopsida). *Malacologia*, 19(2): 279–288.

*** McCoy, F.** 1888. Natural History of Victoria. *Ommastrephes gouldi* (McCoy). *Prodromous of the Zoology of Victoria, Decade*, 17: 255–257, 2 pls.

McDaniel, J.I. & S.I. Emslie. 2002. Fluctuations in Adelie penguin prey size in the mid to late holocene, northern Marguerite Bay, Antarctic Peninsula. *Polar Biology*, 25(8): 618–623.

McGowan, J.A. 1954. Observations on the sexual behaviour and spawning of the squid *Loligo opalescens* at La Jolla, California. *California Department of Fish and Game Fishery Bulletin*, 40: 47–54.

*** McGowan, J.A. & T. Okutani.** 1968. A new species of enoploteuthid squid, *Abraliopsis (Watasenia) felis*, from the California Current. *Veliger*, 11(1):72–79, 2 pls.

*** McGrath, G.L & G.D. Jackson.** 2002. Egg production in the arrow squid *Nototodarus gouldi* (Cephalopoda: Ommastrephidae), fast and furious or slow and steady? *Marine Biology*, 141(4): 699–706.

McGrath-Steer, B.L. & G.D. Jackson. 2004. Temporal shifts in the allocation of energy in the arrow squid, *Nototodarus gouldi*: Sex specific responses. *Marine Biology*, 144(6): 1141–1149.

McKay, K. 2008. Caribbean Squid (*Sepioteuthis sepioidea*). *In*: J.B. Wood, ed. www.thecephalopodpage/Marine invertebratezoology webpage.

McKinnon, J. 1994 Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, in the coastal waters of central Peru. *Fishery Bulletin*, 92(3): 569–578.

McKinnon, J. & G. Jackson. 2006. Statolith and gladius aging of the southern arrow squid (*Nototodarus sloanii*). Cephalopod International Advisory Council Symposium 2006, Abstract: p. 47.

McLean, N., F.G. Hochberg & G.L. Shinn. 1987. Giant protistan parasites on the gills of cephalopods (Mollusca). *Diseases of Aquatic Organisms*, 3(2): 119–125.

McMahon, J. & W.C. Summers. 1971. Temperature effect on the developmental rate of squid (*Loligo pealei*) embryos. *Biological Bulletin*, 141: 561–567.

McSweeny, E.S. 1970. Description of the juvenile form of the Antarctic squid *Mesonychoteuthis hamiltoni* Robson, 1970. *Malacologia*, 10(2): 323–332.

Meister, G. 1972. Organogenesis of *Loligo vulgaris* Lam. (Mollusca, Cephalopoda, Teuthoidea, Myopsida, Loliginidae). *Zool. Jahrb. Anat. Ontog. Tiere*, 89(2): 247–300.

Meister, G. 1977. Investigations on vacuolized round cells in the blood of the embryos of different cephalopod species (Mollusca, Cephalopoda). *Zool. Jahrb., Abt. Anat. Ontog. Tiere*, 97(1): 54–67.

Meiyappan, M.M. & K.S. Mohamed. 2003. Cephalopods. *In*: J. M. Mohan & A. A. Jayaprakash, eds. Status of Exploited Marine Fishery Resources of India. *Central Marine Fisheries Institute, Kochi, India*, pp. 221–227.

Melin, S.R. 2002. The foraging ecology and reproduction of the California sea lion (*Zalophus californianus californianus*). *Dissertation Abstracts International Part B: Science and Engineering*, 63(3): 1135.

Mellink, E. & A.L. Romero Saavedra. 2005. Diet of California sea lions, *Zalophus californianus*, at San Jorge Island, northern Gulf of California, Mexico, 1998–1999. *Ciencias Marinas*, 31(2): 369–377.

Mello, R.M. De, J.P. Castello & K.M.F. Freire. 1992. Marine pelagic species association in southern Brazil during winter and spring. *Frente Maritimo*, 11: 63–69.

Melo, Y.C. & W.H.H. Sauer. 1998. Ovarian atresia in cephalopods. *South African Journal of Marine Science*, 20: 143–151.

Melo, Y.C. & W.H.H. Sauer. 1999. Confirmation of serial spawning in the chokka squid *Loligo vulgaris reynaudii* off the coast of South Africa. *Marine Biology*, 135(2): 307–313.

Melo, Y.C. & W.H.H. Sauer. 2000. A histological description of post-ovulatory follicles in *Loligo vulgaris reynaudii*. *In*: B. Norberg, O.S. Kjesbu, G.L. Taranger, E. Andersson & S.O. Stefansson, eds. “Reproductive Physiology of Fish”, 301 p.

Melo, Y.C. & W.H.H. Sauer. 2007. Determining the daily spawning cycle of the chokka squid, *Loligo reynaudii* off the South African Coast. *Reviews in Fish Biology and Fisheries*, 17(2–3): 247–257.

Mendis, E., N. Rajapakse, H.G. Byun & S.K. Kim. 2005. Investigation of jumbo squid (*Dosidicus gigas*) skin gelatin peptides for their in vitro antioxidant effects. *Life Sciences*, 77(17): 2166–2178.

Mercer, M.C. 1970a. The northern limit of the squid *Loligo pealei* LeSueur. *Le Naturaliste Canadien*, 97(6): 823–824.

***Mercer, M.C.** 1970b. The tropical loliginid squid *Sepioteuthis sepioidea* from the Northwest Atlantic. *Journal of Fisheries Research Board of Canada*, 27: 1892–1893.

Mercer, M.C. 1975. Modified Leslie-DeLury population models of the long-finned pilot whale (*Globicephala melaena*) and annual production of the short finned squid (*Illex illecebrosus*) based upon their interaction at Newfoundland. *Journal of Fisheries Research Board, Canada*, 32(7): 1145–1154.

Mercer, R.W. & M. Bucy. 1983. Experimental squid jigging off the Washington coast. *Marine Fisheries Review*, 45(7/9): 56–62.

***Mesnil, B.** 1977. Growth and life cycle of squid, *Loligo pealei* and *Illex illecebrosus*, from the northwest Atlantic. *Selected Papers ICNAF*, 2: 55–69.

Messenger, J.B. & J.Z. Young. 1999. The radular apparatus of cephalopods. *Philosophical Transactions of the Royal Society of London*, 354: 161–182.

Meyer, M. & M.J. Smale. 1991. Predation patterns of demersal teleosts from the Cape South and West coasts of South Africa. 1. Pelagic predators. *South African Journal of Marine Science*, 10: 173–191.

Mhitu, H.A., Y.D. Mgaya & M.A.K. Ngoile. 1999. Growth and reproduction analysis of the squid, *Sepioteuthis lesoniana*, in the coastal waters of Zanzibar. *Conference on Advances on Marine Sciences in Tanzania Zanzibar Tanzania IMS*, 74.

Michalsen, K. & K.H. Nedreaas. 1998. Food and feeding of Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in the Barents Sea and east Greenland waters. *Sarsia*, 83(5): 401–407.

Michel, E., Klett, A. & R.I. Ochoa. 1986. Preliminary study for determination of the giant squid *Dosidicus gigas* gonadic maturity. *Ciencias Pesqueras*, 5: 77–89.

Michinomae, M., Y. Kito, M. Seidou & K. Narita. 1991. Vision and bioluminescence of the firefly squid. *Zoology Science*, 8(6): 1036.

Michinomae, M., H. Masuda, M. Seidou & Y. Kito. 1990. Light and electron microscopic investigation of cellular architecture in the retina of the firefly squid, *Watasenia scintillans* 3. *Proceedings of the sixty first meeting of the Zoological Society of Japan, October 3–5, 1990, Niigata*, 7(6): 1027.

Michinomae, M., H. Masuda, M. Seidou & Y. Kito. 1994. Structural basis for wavelength discrimination in the banked retina of the firefly squid *Watasenia scintillans*. *Journal of Experimental Biology*, 193: 1–12.

***Middendorff, A.T.** 1849. Beitrage zu einer Malacozoologica Rossica. II–III. Aufzahlung und Beschreibung der zur Meeresfauna Russlands gehorigen Einschaler. *Memoires de l'Academie imperiale des Sciences de St. Petersbourg*, (series 6)6:329–610, 21 pls.

Mignino, L.A. & M.E. Paredi. Physico-chemical and functional properties of myofibrillar proteins from different species of mollusks. *Food Science and Technology*, 39(1): 35–42.

Mikheyev, E.V. & N.N. Kovalev. 2005. Adaptive role of pacific Cephalopods cholinesterase. *Transactions of the Pacific Research Fisheries Centre*, 143: 338–342.

Minobe, S. 1997. 50-70 year oscillation over the north Pacific and north America. *Geophysical Research Letters*, 24: 683–686.

Miske, V.C. 1996. Cephalopods of the deep-sea - insight into the world of the bathypelagic cephalopods. *Deutsche Museum der Meereskunde von Fischerei*, 12: 73–78 (in German).

***Miske, V.C.** 1998. The cephalopods of expedition 52b on FFS "Walther Herwig" to the mid-Atlantic ridge 1982. *Ph.D. dissertation, University of Rostock, Germany*, 158 pp. (in German).

Miura, Y.Y., Y. Matsubara, T. Ebihara, Y. Koyama, K. Ogawa-Goto, N. Isobe, S. Hattori & S. Irie. 2005. Cloning and nucleotide sequence of a novel 28-kDa protein from the mantle muscle of the squid *Todarodes pacificus* with homology to tropomyosin. *Comparative Biochemistry and Physiology, Part B: Biochemistry and Molecular Biology*, 141(1): 3–12.

Miyahara, K. & S. Gorie. 2005. Comparison of CPUEs in the diamond squid angling fishery off Hyogo Prefecture, the Sea of Japan. *Bulletin of the Hogo Prefectural Technology Center for Agriculture, Forestry and Fisheries*, 38: 15–23.

Miyahara, K., K. Fukui, T. Nagahama & T. Okatani. 2006a. First record of planktonic egg masses of the diamond squid, *Thysanoteuthis rhombus* Troschel, in the Sea of Japan. *Plankton and Benthos Research*, 1(1): 59–63.

Miyahara, K., K. Fukui, T. Ota & T. Minami. 2006b. Laboratory observations on the early life stages of the diamond squid *Thysanoteuthis rhombus*. *Journal of Molluscan Studies*, 72(2): 199–205.

Miyahara, K., T. Ota, T. Goto & S. Gorie. 2006c. Age, growth and hatching season of the diamond squid *Thysanoteuthis rhombus* estimated from statolith analysis and catch data in the western Sea of Japan. *Fisheries Research*, 80(2–3): 211–220.

***Miyahara, K., T. Ota, N. Kohno, Y. Ueta & J.R. Bower.** 2005. Catch fluctuations of the diamond squid *Thysanoteuthis rhombus* in the Sea of Japan and model to forecast CPUE based on analysis of environmental factors. *Fisheries Research*, 72(1): 71–79.

Miyanaga, S. & Y. Sakurai. 2006. Effect of temperature on the activity and metabolism of Japanese common squid (*Todarodes pacificus*) paralarvae. Cephalopod International Advisory Council Symposium 2006, Abstract.

Mladineo, I., D. Valic & M. Jozic. 2003. Spawning and early development of *Loligo vulgaris* Lamarck, 1798, under experimental conditions. *Acta Aadriatica*, 44(1): 77–83.

Mochizuki, Y., H. Mizuno, H. Ogawa, K. Ishimura, H. Tsuchiya & N. Iso. 1995. Changes of rheological properties of cuttlefish and squid meat by heat treatment. *Fisheries Science., 61(4): 680–683.*

Mohamed, K.S. 1993. Spawning congregations of Indian squid *Loligo duvaucelii* (Cephalopoda: Loliginidae) in the Arabian Sea off Mangalore and Malpe. *Indian Journal of Marine Science*, 22: 172–175.

***Mohamed, K.S.** 1996. Estimates of growth, mortality and stock of the Indian squid *Loligo duvaucelii* Orbigny, exploited off Mangalore, southwest coast of India. *Bulletin of Marine Science*, 58: 393–403.

Mohamed, K.S. & D. Nagaraja. 1991. Unusual occurrence of two species and rare occurrence of one species of neritic squids off Mangalore coast. *Indian Journal of Fisheries*, 38(1): 66–68.

Mohamed, K.S. & G.S. Rao. 1997. Seasonal growth, stock-recruitment relationship and predictive yield of the Indian squid *Loligo duvauceli* (Orbigny) exploited off Karnataka coast. *Indian Journal of Fisheries*, 44: 319–329.

***Mohan, P.C. & G.V. Rayudu.** 1986. Squid and cuttlefish in nearshore bottom waters off Visakhapatnam, India. *In*: M.F. Thompson *et al.*, eds. Biology of Benthic Marine Organisms. *Balkema, Rotterdam*, pp. 373–377.

Moiseev, P.A. 1989. Biological resources of the world ocean. *Agropromizdat Press, Moscow.* 368 pp. (In Russian).

Moiseev, S.I. 1989. Vertical distribution and behaviour of squid *Gonatus fabricii* (Cephalopoda, Gonatidae) in the North East Atlantic. *In*: D.E. Gershanovich, ed. *Underwater Observations in Biooceanological and Fisheries Research*, 53–60 pp.

Moiseev, S.I. 1992. Observation of the vertical distribution and behavior of nektonic squids using manned submersibles. *Bulletin of Marine Science*, 49(1–2): 446–456.

Moiseev, S.I. & C.M. Nigmatullin. 2002. The peculiarities of oceanic ommastrephid squids distribution in areas of underwater ridges. *In*: B.G. Ivanov & Ch.M.Nigmatullin, eds. VI All-Russian Conference on Commercial Invertebrates (3–6 September 2002, Kaliningrad-Lesnoe). Theses of reports. Moscow: *VNIRO Publication*, 152–155 (In Russian).

Mokrin, N.M. & O.N. Katugin. 2000. Stock dynamics, ecology, and population structure of the Japanese flying squid, *Todarodes pacificus*, in the Japan Sea. *In*: *PICES IX*, Annual Meeting, Hakodate, Hokkaido, Japan, Abstract: 98–99.

Mokrin, M.M., Yu.V. Novikov & Yu.I. Zuenko. 2002. Seasonal migrations and oceanographic conditions for concentration of the Japanese flying squid (T*odarodes pacificus* Steenstrup, 1880) in the northwestern Japan Sea. *Bulletin of Marine Science*, 71(1): 487–499.

***Molina, G.I.** 1782. Saggio sulla storia naturale del Chili. *Bologna, Stamperia di S. Tommaso d'Aquino*, 367 pp.

***Moller, H.P.C.** 1842. Index Molluscorum Groenlandiae. *Naturhistorisk Tidskrift, Copehagen*, 4(1): 76–97.

Moltschaniwskyj, N.A. 1995. Multiple spawning in the tropical squid *Photololigo* sp.: what is the cost in somatic growth? *Marine Biology*, 124: 127–135.

Moltschaniwskyj, N.A. & G.D. Jackson. 2000. Growth and tissue composition as a function of feeding history in juvenile cephalopods. *Journal of Experimental Marine Biology and Ecology*, 253(2): 229–241.

Moltschaniwskyj, N.A., & G.T. Pecl. 2003. Small-scale spatial and temporal patterns of egg production by the temperate loliginid squid *Sepioteuthis australis*. *Marine Biology*, 142: 509–516.

***Moltschaniwskyj, N.A. & G.T. Pecl.** 2007. Spawning aggregations of squid (*Sepioteuthis australis*) populations: a continuum of 'microcohorts'. *Reviews in Fish Biology and Fisheries*, 17(2–3): 183–195.

Moltschaniwskyj, N.A., G. Pecl & J. Lyle. 2002. An assessment of the use of short-term closures to protect spawning southern calamary aggregations from fishing pressure in Tasmania, Australia. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(1): 501–514.

Moltschaniwskyj, N., G. Pecl, J. Lyle, M. Haddon & M. Steer. 2003. Population dynamics and reproductive ecology of the southern calamari (*Sepioteuthis australis*) in Tasmania. TAFI, Hobart, Tas. (Australia), 159 pp.

Moltschaniwskyj, N.A., K. Hall, M.R. Lipinski, J.E.A.R. Marian, M. Nishiguchi, M. Sakai, D.J. Shulman, B. Sinclair, D.L. Sinn, M. Staudinger, R. Van Gelderen, R. Villanueva & K. Warnke. 2007. Ethical welfare considerations when using cephalopods as experimental animals. *Reviews in Fish Biology and Fisheries*, 17(2–3): 455–476.

Montague, T.L. & J.M. Cullen. 1988. The diet of the little penguin *Eudyptula minor* at Phillip Island, Victoria. *EMU*, 88(3): 138–149.

Monteiro, L.R., F.M. Porteiro & J.M. Goncalves. 1992. Inter- and intra-specific variation of mercury levels in muscle of cephalopods from the Azores. *Arquipelago Cienc. Nat. Life Earth Science*, 10: 13–22.

Montevecchi, W.A. 1993. Seabird indication of squid stock conditions. *Journal of Cephalopod Biology*, 2(2): 57–64.

Montevecchi, W.A. & R.A. Myers. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. *Marine Ecology Progress Series*, 117(1–3): 1–9.

Montevecchi, W.A., V.L. Birt & D.K. Cairns. 1988. Dietary changes of seabirds associated with local fisheries failures. *Biological Oceanography*, 5(3): 153–161.

Moon, T.W. & W.C. Hulbert. 1975. The ultrastructure of the mantle musculature of the squid *Symplectoteuthis oualaniensis*. *Comparative Biochemistry and Physiology*, B52(1): 145–149.

Moore, P.J. & M.D. Wakelin. 1997. Diet of the yellow-eyed penguin *Megadyptes antipodes*, South Island, New Zealand, 1991–1993. *Marine Ornithology*, 25(1–2): 17–29.

Moore, G.J., G. Robertson & B. Wienecke. 1998. Food requirements of breeding king penguins at Heard Island and potential overlap with commercial fisheries. *Polar Biology*, 20(5): 293–302.

Morales, E. 1958. Cefalopodos de Cataluna. I. *Investigacion Pesquera*, 11: 3–32.

* **Morales, E. & A. Guerra.** 1977. Teuthoidea: Oegopsida (Mollusca, Cephalopoda) del NW de Africa. *Investigacion Pesquera*, 41(2): 295–322.

Morales-Bojorquez, E. 2002. Comments about the relationship between temperature and giant squid catches. *Ciencias Marinas*, 28(2): 211–221.

Morales-Bojorquez, E. & M.O. Nevarez-Marinez. 2002. Stochastic estimation of the catchability and recruitment of the jumbo squid *Dosidicus gigas* (D'Orbigny, 1835) from the Gulf of California, Mexico. *Ciencias Marinas*, 28(2): 193–204.

Morales-Bojorquez, E., S. Martinez-Aguilar, R. Arreguin-Sanchez & M.O. Nevarez-Martinez. 2001c. Estimations of catchability-at-length for the jumbo squid (*Dosidicus gigas*) fishery in the Gulf of California, Mexico. *Reports of California Cooperative Oceanic Fisheries Investigations*, 42: 167–171.

Morales-Bojorquez, E., A. Hernandez-Herrera, M.O. Nevarez-Martinez, A.J. Diaz-de-Leon-Corral, G.I. Rivera-Parra & A. Ramos-Montiel. 1997. Population abundance of the giant squid (*Dosidicus gigas*) from the coast of Sonora, Mexico. *Oceanides*, 12(2): 89–95.

Morales-Bojorquez, E., A. Hernandez-Herrera, M.O. Nevarez-Martinez, M.A. Cisneros-Mata & F.J. Guerrero-Escobedo. 2001b. Population size and exploitation of giant squid (*Dosidicus gigas* D'Orbigny, 1835) in the Gulf of California, Mexico. 2001. *Scientia Marina (Barcelona)*, 65(1): 75–80.

* **More, A.G.** 1875. Notice of a gigantic cephalopod (*Dinoteuthis proboscideus*) which was stranded at Dingle, in Kerry, two hundred years ago. *The Zoologist, London*, (series 2)118:4526–4532.

Morejohn, G.V., J.T. Harvey & L.T. Krasnow. 1978. The importance of *Loligo opalescens* in the food web of Marine vertebrates in Monterey Bay. *California Fish and Game, Fish Bulletin*, 169: 67–98.

Moreno, A. 1993. Preliminary study on biological characters of *Alloteuthis subulata* and distribution of the genus *Alloteuthis* (Cephalopoda: Loliginidae) in Portuguese waters. *Copenhagen Denmark ICES*, 21 pp.

Moreno, A. 1995. Aspectos da biologia de *Alloteuthis subulata* e distribuicão de *Alloteuthis* spp. (Cephalopoda: Loliginidae) das águas portuguesas. *Relatórios Cientificos e Técnicos do Instituto Português de Investigação Maritima*, 8.

Moreno, A. 1998. Variação sazonal na distribuição e abundância dos cefalópodes da plataforma continental entre Espinho e Nazaré: resultados dos cruzeiros de agosto e novembro de 1996 no N/I "Mestre Costeiro". *Relatórios Cientificos e Técnicos do Instituto de Investigação das Pescas e do Mar*, 29: 23 pp.

Moreno, A. 2002. Morfologia e micro-estrutura dos estatolitos de lula, *Loligo vulgaris*. *Relatórios Cientificos e Técnicos do Instituto Português de Investigação Maritima.*, 86: 46 pp.

* **Moreno, A. & J.M.F. Pereira.** 1998. Cephalopod paralarval distribution in Iberian Atlantic waters. *Copenhagen Denmark ICES*, 8 pp.

Moreno, A. & C.S. Reis. 1995. Seasonal distribution of loliginid early young stages in the Portuguese continental shelf. *Copenhagen Denmark ICES*, 11 pp.

Moreno, A., M. Morais da Cunha & J.M.F. Pereira. 1993. Population biology of veined squid (*Loligo forbesi*) and European squid (Loligo vulgaris) from the Portuguese coast. *Copenhagen Denmark ICES*, 1993 39 pp.

Moreno, A., M. Morais da Cunha & J.M.F. Pereira. 1994. Population biology of veined squid (*Loligo forbesi*) and European squid (*Loligo vulgaris*) from the Portuguese coast. *Fisheries Research*, 21: 71–86.

Moreno A., J.M.F. Pereira & M. Morais da Cunha. 1996. Age and growth of the squid *Loligo vulgaris* from Portuguese waters. *ICES Council Meeting*,1996/K: 14, 17 pp.

Moreno A., J. Pereira & M. Morais da Cunha. (2005). Environmental influences on age and size at maturity of *Loligo vulgaris*. *Aquatic Living Resources*, 18: 377–380.

Moreno, A., M. Azevedo, J. Pereira & G.J. Pierce. 2007. Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. *Marine Biology Research*, 3(1): 49–59.

***Moreno, A., J. Pereira, C. Arvanitidis, J.P. Robin, D. Koutsoubas, C. Perales-Raya, M.M. Cunha, E. Balguerías & V. Denis.** 2002. Biological variation of *Loligo vulgaris* (Cephalopoda: Loliginidae) in the eastern Atlantic and Mediterranean. *Bulletin of Marine Science*, 71: 515–534.

Mori, J., T. Kubodera & N. Baba. 2001. Squid in the diet of northern fur seals, *Callorhinus ursinus*, caught in the western and central North Pacific Ocean. *Fisheries Research*, 52(1): 91–97.

Mori, K. & Y. Nakamura. 2003. Distribution of juvenile Japanese common squid *Todarodes pacificus* around the Kuroshio-Oyashio transition region. 2003. *Bulletin of the Japanese Society of Scientific Fisheries*, 69(1): 23–29.

***Mori, K., K. Tsuchiya & K. Takagi.** 2002. Distribution and community structure of epipelagic squids in the Kuroshio-Oyashio transition zone, western North Pacific. *Bulletin of Marine Science*, 71(2): 1131–1132.

Moriwaki, S. & Y. Ogawa. 1986. Influences of pelagic fishes as prey on the formation of fishing grounds for and catch fluctuations of *Loligo edulis*. *Bulletin of the Japanese Society of Fisheries Oceanography*, 50(2): 114–120.

Morris, C.C. 1991a. Methods for in situ experiments on statolith increment formation, with results for embryos of *Alloteuthis subulata*. *In*: P. Jereb, S. Ragonese and Boletzky, S. von, eds. Squid Age Determination Using Statoliths. Note Tecniche e Reprints dell'Istituto di Tecnologia della Pesca e del Pescato (Mazara del Vallo, Italy), Special Publication 1: 67–72.

Morris, C.C. 1991b. Statocyst fluid composition and its effects on calcium carbonate precipitation in the squid *Alloteuthis subulata* (Lamarck, 1798): Towards a model for biomineralization. *Bulletin of Marine Science*, 49(1–2): 379–388.

Morris C.C. 1993. Environmental effects on increment formation in embryonic statoliths of the squid *Alloteuthis subulata* (Myopsida: Loliginidae). *Journal of Cephalopod Biology*, 2(2): 23–33.

Morte, S., M.J. Redon & A. Sanz-Brau. 1997. Feeding habits of juvenile *Mustelus mustelus* (Carcharhiformes, Triakidae) in the western Mediterranean. *Cahiers de Biologie Marine*, 38: 103–107.

Moustafa, E.K., M.E.M. Yousef & M.A. Hamza. 1998a. Composition and quality of squid and cuttlefish as affected by hot smoking and subsequent frozen storage. In: Teutscher, F. (ed.) "Report and proceedings of the sixth FAO Expert Consultation on Fish Technology in Africa, Kisumu, Kenya, 27–30 August 1996", 574: 147–156.

Moustafa, E.K., M.E.M. Yousef & M.A. Hamza. 1998b. Hot smoking of squid and cuttlefish: A comparative study. *In*: F. Teutscher, ed. "Report and proceedings of the sixth FAO Expert Consultation on Fish Technology in Africa, Kisumu, Kenya, 27–30 August 1996", 574: 157–160.

Moustahfid, H. 2002. Age and growth of arrow squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) sampled in summer in Atlantic Moroccan waters. *Bulletin of Marine Science*, 71(1): 535–543.

***Moynihan, M. & A.F. Rodaniche.** 1982. The behavior and natural history of the Caribbean reef squid. Advances in Ethology, 25: 151 pp, New York, NY USA, Parey Scientific Publishers.

***Muntz, W.R.A.** 1976. On yellow lenses in mesopelagic animals. J*ournal of the Marine Biological Association of the United Kingdom*, 56: 963–976.

Muntz, W.R.A. 1995. Giant octopus and squid from Pliny to the Rev. Moses Harvey. *Archives of Natural History*, 22(1): 1–28.

Muntz, W.R.A. & M.S. Johnson. 1978. Rhodopsins of oceanic decapods. *Vision Research*, 18(5): 601–602.

Murata, M. 1983. Quantitative assessment of oceanic squid by means of jigging surveys. *Biological Oceanography*, 2(2–4): 433–456.

Murata, M. 1989. Population assessment, management and fishery forecasting for the Japanese common squid, *Todarodes pacificus*. *In*: J.F. Caddy, ed. *Marine Invertebrate Fisheries: Their Assessment and Management*. 613–636 pp.

Murata, M. 1990. Oceanic resources of squids. *Marine Behavior and Physiology*, 18:

Murata, M. & M. Ishii. 1977. Some information on the ecology of the oceanic squid, *Ommastrephes bartramii* (Lesueur) and *Onychoteuthis borealijaponicus* Okada, in the Pacific Ocean off northeastern Japan. *Bulletin of the Hokkaido Regional Fisheries Research Laboratory*, 42: 1–23.

Murata, M. & y. Nakamura. 1998. Seasonal migration and diel vertical migration of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific. *In*: T. Okutani, ed. Contributed Papers of the International Sympoium on Large Pelagic Squids. Tokyo: *JAMARC Publication*, 13–30.

Murata, M. & T. Okutani. 1975. Rare and interesting squid from Japan 6. An occurrence of *Gonatopsis japonicus* Okiyam in the Sea of Okhotsk. *Venus*, 33(4): 210–211.

Murata, M., M. Ishii & M. Osako. 1982. Some information on copulation of the oceanic squid *Onychoteuthis borealijaponica* Okada. *Bulletin of the Japanese Society of Scientific Fisheries*, 48(3): 351–354.

Murawski, S.A. 1993. Climate change and marine fish distributions: forecasting from historical analogy. *Transactions of the American Fisheries Society*, 122: 647–658.

Murayama, T., Y. Hiyama & S. Kasahara. 1993. Why is autumn the main spawning season of the common squid in the Japan Sea? *Bulletin Japan Sea National Fisheries Research Institute*, 43: 93–103.

Murueta, J.H.C. & F.L.G. Carreno. 2001. The effect on growth and protein digestibility of shrimp *Penaeus stylirrostris* fed with feeds supplemented with squid (*Dosidicus gigas*) meal dried by two different processes. 2001. *Journal of Aquatic Food Product Technology*, 10(3): 35–47.

Muus, B.J. 1959. Skallus, Søtænder, Blæksprutter. *Danmarks Fauna*, No. 65.

Muus, B.J. 1962. Cephalopoda. The Godthaab Expedition. *Meddr Grønland,* 81, 5: 1–23.

Nabhitabhata, J. 1995. Mass culture of cephalopods in Thailand. *World Aquaculture*, 26(2): 25–29.

Nabhitabhata, J. 1996. Life cycle of cultured big fin squid, *Sepioteuthis lessoniana* Lesson. *Proceedings of the sixth Workshop of the Tropical Marine Mollusc Programme TMMP conducted in India at Annamalai University, 12–20 June 1995*. Hylleberg, J. & Ayyakkannu, K. (eds), 16: 83–95.

Nabhitabhata, J., A. Panya, A. Sabaithip & P. Pichitra. 2000. Tolerance of eggs and hatchlings of neritic cephalopods to salinity changes. *Special publication, Phuket Marine Biological Center*, 25(pt. 1): 91–99.

Nabhitabhata, J., P. Nilaphat, P. Promboon, C. Jaroongpattananon, G. Nilaphat & A. Nateewathana. 1992. Taxonomic studies on loliginid squids (Cephalopoda: Loliginidae) from the Andaman Sea coast of Thailand. *Phuket Marine Biological Centre Research Bulletin*, 57: 1–40.

*\u2009**Nabhitabhata, J., P. Nilaphat, P. Promboon, C. Jaroongpattananon, G. Nilaphat & A. Reunreng.** 2005. Performance of simple large-scale cephalopod culture system in Thailand. *Phuket Marine Biological Center Research Bulletin*, 66: 337–350, 2 figs.

* **Naef, A.** 1912a. Teuthologische Notizen 1: Die Familien der Myopsiden. *Zoologischer Anzeiger*, 39(7): 241–244.

* **Naef, A.** 1912b. Teuthologische Notizen. 4. Die Gattungen der Loliginidae. *Zoologischer Anzeiger*, 39(25): 741–745.

* **Naef, A.** 1916. Systematische Übersicht der mediterranen Cephalopoden. *Pubblicazioni della Stazione Zoologica di Napoli*, 1: 11–19.

* **Naef, A.** 1921a. Das system der dibranchiaten Cephalopoden und die mediterranen arten derselben. *Mitteilungen aus der Zoologischen Station zu Neapel*, 22(16): 527–542, 1 fig.

Naef, A. 1921b. Die Cephalopoden. *Fauna und Flora des Golfes von Neapel, Monograph*, 35, 1(1)(part 1): 1–148, figs 1–62, pls 1–56.

* **Naef, A.** 1922. Die Fossilen Tintenfische. *Jena: Gustav Fischer*, 322 pp, 101 figs.

* **Naef, A.** 1923. Die Cephalopoden. *Fauna e Flora de Golfo di Napoli, Monograph*, 35, 1(1)(part 2):149–863, figs 63–473.

Naef, A. 1928. Cephalopod Embriology. *Fauna and Flora of the Bay of Naples. Monograph*, 35B, Part. I, Vol.II: 1–364.

Naef, A. 1928. Die Cephalopoden. *Fauna e Flora del Golgo di Napoli*, 1-357 pp.

Naef, A. 1928. Cephalopoda Embryology. *Fauna and Flora of the Bay of Naples, Monograph*, 35: Part I, Vol. II: 461 pp. 37 pls. (English translation, 2000).

Nagamatsu, M. 1974. Fish transportation – 3. Effect of dry ice and iron fish container on the freshness of fishes. *Bulletin of the Japanese Society of Scientific Fisheries*, 40(8): 759–765.

Nagasawa, K. 1993. Review of human pathogenic parasites in the Japanese comon squid (*Todarodes, pacificus*). *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology (Tokai Univeristy Press*, Tokyo), 293–312 pp.

Nagasawa, K. & F. Moravec. 2002. Larval anisakid nematodes from four species of squid (Cephalopoda: Teuthoidea) from the central and western North Pacific Ocean. *Journal of Natural History*, 36(8): 883–891.

Nagasawa, K., J. Mori & H. Okamura. 1998. Parasites as biological tags of stocks of neon flying squid (*Ommastrephes bartramii*) in the North Pacific Ocean. *In*: T. Okutani, ed. Contributed Papers of the International Symposium on Large Pelagic Squids. Tokyo: JAMARC Publication: 49–64.

Nagasawa, K., S. Takayanagi & T. Takami. 1993. Cephalopod tagging and marking in Japan: Review. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology (Tokai Univeristy Press, Tokyo)*, pp. 313–329.

Nagasawa, K., Y. Ueno, T. Azuma, M. Ogura, A.V. Startsev, I.M. Ivanova & J.F.T. Morris. 1996. Distribution and biology of epipelagic animals in the northern North Pacific Ocean and adjacent seas. 1. Fishes and squids in the southern Okhotsk Sea and western North Pacific Ocean off the Kuril Islands in the autumn of 1993. *Bulletin of National Research Institute Far Seas Fisheries*, 33: 149–170.

Nagashima, Y., H. Ebina, M. Tanaka & T. Taguchi. 1993. Effect of high hydrostatic pressure on the thermal gelation of squid mantle meat. *Food Res. Int.*, 26(2): 119–123.

Naidenova, N.N., Ch.M. Nigmatullin & A.V. Gaevskaya. 1985. The helminth fauna and host-parasite relations of squid, *Sthenoteuthis oualaniensis* (Lesson) (Cephalopoda, Ommastrephidae), in the Indian Ocean and the Red Sea. *In* W.J. Hargris ed. Parasitology and Pathology of Marine Organisms of the World Ocean. *NOAA Technical Report National Marine Fisheries Service*, 25, pp. 113–116.

Najd, A., A. Boumaaz & A. Dridi. 1997. Evolution of the abundance and demographic structure of *Octopus vulgaris* and *Loligo vulgaris* of Moroccan South Atlantic waters. Annex 3. *In*: M. Lamboeuf, ed. *Ad hoc Working Group on Cephalopods, 19–26 May 1997, Tenerife, Spain, Rome, Italy, FAO*, 63: 52–57.

Nakamura, Y. 1993. Vertical and horizontal movements of mature females of *Ommastrephes bartramii* observed by ultrasonic telementry. pp. 331–336. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology, Tokyo*, 372 pp.

Nakamura, Y. & Y. Sakurai. 1991. Validation of daily growth increments in statoliths of Japanese common squid, *Todarodes pacificus*. *Nippon Suisan Gakkaisi*, 57: 2007–2011.

Nakamura, Y. & Y. Sakurai. 1993. Age determination from daily growth increments in statoliths of some groups of Japanese common squid, *Todarodes pacificus*. *In:* T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo*, 339–344 pp.

Nakata, J. 1993. Long-term changes in catch and biological features of Japanese common squid (*Todarodes pacificus*) in waters off the east coast of Hokkaido. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology (Tokai Univeristy Press, Tokyo)*, pp. 343–350.

Nakata, J. 1984. Southward migration of the squid, *Todarodes pacificus* Steenstrup, from the southeastern waters of Hokkaido. , 26:1–10.

Nakaya, H. 1998. Studies on off-flavor in *Dosidicus gigas*. Pp. 127–130. *In*: T. Okutani, ed. Large Pelagic Squids, Japan. *Marine Fishery Resources Center, Tokyo*, 269 pp.

***Narasimham, K.A.** 2005. Molluscan Fisheries of India. Delhi, B.R. Pub., xiv, 362 p., tables, pls.

Narasimham, K.A., V. Kripa & K. Bala. 1993. Molluscan shellfish resources of India. *An overview. Indian Journal of Fisheries*, 40(1–2): 112–124.

***Nateewathana, A.** 1992. Taxonomic studies on loliginid squids (Cephalopoda: Loliginidae) from the Andaman Sea coast of Thailand. *Phuket Marine Biological Centre Research Bulletin*, 57: 1–40.

*__Nateewathana, A.__ 1995. New record of oceanic squids from Thai water, the Andaman Sea. *Research Bulletin of Phuket Marine Biology*, 60: 1–19.

Nateewathana, A. 1997. Two species of oceanic squids from the Andaman Sea, Indian Ocean. *In*: J. Hylleberg, ed. *Proceedings of the seventh Workshop of the Tropical Marine Mollusc Programme on Central and West Java*, 17(2): 453–464.

*__Nateewathana, A., A. Munprasit & P. Dithachey.__ 2000. Systematics and distribution of oceanic cephalopods in the South China Sea, Area 3: Western Philippines. *Proceedings of the Third Technical Seminar on Marine Fishery Resources Survey in the South China Sea, Area 3: Western Philippines, 13–15 July 1999, Bangkok, Thailand*, 41: 76–100.

Nateewathana, A., S. Siriraksophon & A. Munprasit. 2001. The systematics and distribution of oceanic cephalopods in the South China Sea, area 4: Vietnamese waters. *Special paper, Southeast Asian Fisheries Development Center*, 44: 169–180.

*__Natsukari, Y.__ 1976. Taxonomic and morphological studies on the loliginid squids. II. Descriptions and new records of *Doryteuthis sibogae* Adam, 1954, from Formosa. *Venus, Japanese Journal of Malacology*, 35(1): 15–23.

*__Natsukari, Y.__ 1983. Taxonomical and morphological studies on the loliginid squid. III. Nippololigo, a new subgenus of the genus *Loligo*. *Venus, Japanese Journal of Malacology*, 42: 313–318.

*__Natsukari, Y.__ 1984a. Taxonomical and morphological studies on the loliginid squid. IV. Two new genera of the family Loliginidae. *Venus, Japanese Journal of Malacology*, 43: 229–239.

*__Natsukari, Y.__ 1984b. Taxonomical and morphological studies on the loliginid squid. V. Re-description of the type specimen of *Loligo sumatrensis* d'Orbigny, 1835. *Venus, Japanese Journal of Malacology*, 43:260–263.

Natsukari, Y. 1991. Cuttlefish fisheries in Japan. Acta of the 1st International Symposium on the Cuttlefish *Sepia*. *Centre de Publications de l'Universitée de Caen*, pp. 345–348.

Natsukari, Y. & N. Komine. 1992. Age and growth estimation of the European squid, *Loligo vulgaris*, based on statolith microstructure. *Journal of the Marine Biological Association of the United Kingdom*, 72: 271– 280.

*__Natsukari, Y. & T. Okutani.__ 1975. Taxonomic and morphological studies on the loliginid squids. I. Identity of *Loligo chinensis* Gray, 1849. Redescription of the type specimen and taxonomic review. *Venus, Japanese Journal of Malacology*, 34: 85–91.

*__Natsukari, Y. & M. Tashiro.__ 1991. Neritic squid resources and cuttlefish resources in Japan. *Marine Behavior and Physiology*, 18(3): 149–226.

*__Natsukari, Y., T. Nakanose & K. Oda.__ 1988. Age and growth of the loliginid squid *Photololigo edulis* (Hoyle, 1885). *Journal of Experimental Marine Biology and Ecology*, 116: 177–190.

*__Natsukari, Y., Y. Nishiyama & Y. Nakanishi.__ 1986. A preliminary study on the isozymes of the loliginid *Photololigo edulis* (Hoyle, 1885). Report on the Cooperative Investigation of 'Shiro-ika', *Loligo edulis*, Inhabiting the Western Japan Sea, 2: 145–151.

Natsukari, Y., H. Mukai, S. Nakahama & T. Kubodera. 1993. Age and growth estimation of a gonatid squid, *Berryteuthis magister*, based on statolith microstructure (Cephalopoda: Gonatidae). *In* T. Okutani,R.K. O'Dor & T. Kubodera, eds. Recent Advances in Cephalopod Fisheries Biology. *Tokyo: Tokai University Press*, 351–364.

Navarro, J.C. & R. Villanueva. 2000. Lipid and fatty acid composition of early stages of cephalopods: an approach to their lipid requirements. *Aquaculture*, 183(1–2): 161–177.

Nazumi, T. 1975. Notes on the fishery and the ecology of the squid, *Thysanoteuthis rhombus* Troschel, in the San'in waters. *Bull. Hyuogo Prefectural Fish. Stat.*, 15: 5–34 (In Japanese).

Neethiselvan, N., V.K. Venkataramani & V. Sundararaj. 2002. Status of squid and cuttlefish resources of Thoothukkudi coast. *Suganthi Devadason Marine Research Institute (SDMRI) Research Publication*, 2: 104–110.

Nel, J. 1998. *Bucculatrix apicipunctella* Deschka & Huemer, 1997, synonyme de *Novotinea liguriella* Amsel, 1950 (Lep., Bucculatricidae, Tineidae). *Bulletin de la Societe Entomologique de France*, 103(4): 354.

Nel, D.C., J.R.E. Lutjeharms, E.A. Pakhomov, I.J. Ansorge, P.G. Ryan & N.T.W. Klages. 2001. Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Marine Ecology Progress Series*, 217: 15–26.

Nemoto, T., M. Okiyama & M. Takahashi. 1984. Aspects of the roles of squid in food chains of the Antarctic marine ecosystems. *In*: T. Hoshiai & M. Fukuchi, eds. *Proceedings of the Sixth Symposium on Polar Biology*, 32: 89–92.

Nemoto, T., M. Okiyama, N. Iwasaki & T. Kikuchi. 1988. Squid as predators on krill (*Euphausia superba*) and prey for sperm whales in the Southern Ocean. *In* D. Sahrhage, ed. *Antarctic Ocean and Resources Variability*, 292–296.

Nesis, K.N. 1965. Distribution and feeding of young squids *Gonatus fabricii* in the Labrador Sea and the Norwegian Sea. *Oceanology*, 5: 102–108.

*** Nesis, K.N.** 1971. A new form of squid, genus *Histioteuthis*, from the eastern Pacific. *Zoologicheskij Zhurnal*, 50(10): 1463–1471, 2 figs [In Russian].

*** Nesis, K.N.** 1972a. A review of the squid genera *Taonius* and *Belonella* (Oegopsida, Cranchiidae). *Zoological Zhurnal*, 51(3): 341–350.

*** Nesis, K.N.** 1972b. Two new species of gonatid squids from the north Pacific. *Zoological Zhurnal*, 51(9): 1300–1307.

Nesis, K.N. 1972c. Oceanic cephalopods of the Peru Current: horizontal and vertical distribution. *Okeanologiya*, 12(3):506–519.

*** Nesis, K.N.** 1973. Cephalopods of the eastern equatorial and southeastern Pacific. *Trudy Instituta Okeanologii/Transactions of the Institute of Oceanology*, 94: 188–242.

*** Nesis, K.N.** 1974a. Oceanic cephalopods of the southwest Atlantic Ocean. *In*: Z.A. Filatova, ed. *Biological investigations in the Atlantic sector of the Antarctic, Moscow, USSR Nauka*, 98: 51–75 (English Translation: Selected Translated Publications, 1965–1994. Kir R. Nesis. *Smithsonian Institution Libraries*, 2003, Vol 1, Part 1: 271–300).

Nesis, K.N. 1974b. A revision of the squid genera *Corynomma*, *Megalocranchia*, *Sandalops* and *Liguriella* (Oegosida Cranchiidae. Ichthyoplankton, deep sea fishes and squids from the World Ocean tropical waters. *Moscow, USSR, Nauka*, 96.

Nesis, K.N. 1976. Comparison of cephalopod faunas along the coasts of Central America. *In*: Likharev, Malacological Review, eds. *Molluscs: their systematics, evolution and significance*, 11(1–2): 127–128.

Nesis, K.N. 1977a. Population structure in the squid, *Sthenoteuthis oualaniensis* (Lesson, 1830) (Ommastrephidae), in the western tropical Pacific. *Trudy Institute of Oceanology of the Academy of Sciences USSR*, 107: 15–29 (In Russian with English abstract).

*** Nesis, K.N.** 1977b. *Mastigoteuthis psychrophila* sp.n. (Cephalopoda, Mastigoteuthidae) from the Southern Ocean. *Zoological Zhurnal*, 56(6): 835–842.

*** Nesis, K.N.** 1977c. Vertical distribution of pelagic cephalopods. *Zhurnal Obshchei Biologii*, 38(4): 547–557 (in Russian, English summary).

*** Nesis, K.N.** 1979a. Squid larvae of the Family Ommastrephidae (Cephalopoda). *Zoologicheskij Zhurnal*, 58(1): 17–28.

*** Nesis, K.N.** 1979b. A brief review of zoogeography of Australian–New Zealand pelagic realm (by Cephalopods). *Trudy Instituta Okeanologii im. P.P. Shirshova Akademii Nauk SSSR*, 106: 125–139.

*** Nesis, K.N.** 1979c. Squids of the family Ommastrephidae in the Australian–New Zealand region. *Trudy Instituta Okeanologii im. P.P. Shirshova Akademii Nauk SSSR*, 106: 140–146.

*** Nesis, K.N.** 1980. Taxonomic position of *Chiroteuthis famelica* Berry (Cephalopoda, Oegopsida). *Biulleten Moskoskae Obschestvo Ispytatekei Prirody, Otdel Biolodicheskii*, 85(4): 59–66 [In Russian].

*** Nesis, K.N.** 1982. Abridged key to the cephalopod molluscs of the world's oceans. *Moscow: Light and Food Industry Publishing House*, 385 pp. (In Russian; see Nesis, 1987 for abridged English translation).

*** Nesis, K.N.** 1982/1987. Cephalopods of the world. squids, cuttlefishes, octopuses and allies (translated from Russian by BS Levitov), ed. L.A. Burgess, 1987. *TFH Publications Inc., Ltd.*, 351 pp. *Neptune City, NJ and London.*

*** Nesis, K.N.** 1983. *Dosidicus gigas*. *In*: P. Boyle, ed. *Cephalopod Life Cycles, Vol. I. Academic Press*, p. 215–231.

Nesis, K.N. 1984. Cephalopods. Field card manual of plankton, Part 3. *Leningrad: Zoological Institute of the USSR Academy of Sciences*, 182 pp. (In Russian).

*** Nesis, K.N.**1985. Oceanic cephalopods: Distribution, life forms, evolution. *Nauka, Moscow*, 287 pp.

Nesis, K.N. 1989a. Teuthofauna of the Sea of Okhotsk. Biology of the squids *Berryteuthis magister* and *Gonatopsis borealis* (Gonatidae). *Zoological Zhurnal*, 68(9): 45–56.

***Nesis, K.N.** 1989b. Teuthofauna of the Sea of Okhotsk. Distribution and biology of off-shore species. *Zoological Zhurnal*, 68(12): 19–29.

Nesis, K.N. 1990. The Japanese *Gonatopsis*. The largest gonatid squid. *In*: A.P. Alexeyev *et al.*, eds. All – USSR Symposium "Reserve Raw Food Biological Resources of the Open Ocean and Seas of the USSR", *Kaliningrad, 20–33 March, 1990. Moscow*, pp. 133–136.

Nesis, K.N. 1992a. The diamondback squid, *Thysanoteuthis rhombus* Troschel, 1857: "A living fossil"? *Ruthenica*, 2 (2): 91–103.

Nesis, K.N. 1992b. Cephalopods of underwater rises in the ocean. *Docklady Akademii NAUK*, 322(5): 1003–1006.

***Nesis, K.N.** 1993a. Cephalopods of seamounts and submarine ridges. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 365–373.

***Nesis, K.N.** 1993b. Population structure of oceanic ommastrephids, with particular reference to *Sthenoteuthis oualaniensis*. *In T.* Oktani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology. Tokyo: Tokai University Press*, pp. 375–383.

***Nesis, K.N.** 1993c. Spent females of the deepwater squid *Gonatopsis octopedatus* Sasaki, 1920 (Gonatidae) in the epipelagic zone of the Okhotsk and Japan seas. *Ruthenica*, 3(2): 153–158.

***Nesis, K.N.** 1993d. Vertical migrations of micronektonic squids, *Pyroteuthis margaritifera* (Rueppell) and *Pterygioteuthis gemmata* Chun, based on hauls by nonclosing trawls. *Oceanology*, 33(1): 110–115.

***Nesis, K.N.** 1994. Warm-water squid and pelagic octopus species in Far East seas. *Oceanology*, 34(3): 410–416.

***Nesis, K.N.** 1995. Population dynamics of the squid *Berryteuthis magister* (Berry, 1913) in the western Bering Sea during the autumn spawning season. *Ruthenica*, 5(1): 55–69.

***Nesis, K.N.** 1997. Gonatid squids in the sub-Arctic North Pacific: ecology, biogeography, niche diversity and role in the ecosystem. *Advances in Marine Biology*, 32: 243–324.

***Nesis, K.N.** 1998. Biodiversity and systematics in cephalopods: unresolved problems require an integrated approach. *In*: A.I.L. Payne, M.R. Lipinski, M.R. Clarke & M.A.C. Roeleveld, eds. *South African Journal of Marine Science*, 20: 165–173.

***Nesis, K.N.** 1999a. Horizontal vertical distribution and some features of biology of the gonatid squid *Gonatus antarcticus* Lönnberg, 1898 (Cephalopoda). *Ruthenica*, 9(2): 129–139.

***Nesis, K.N.** 1999b. Cephalopoda. *In* D. Boltovskoy, ed. *South Atlantic Zooplankton*. *Backhuys Publishers*, Leiden, The Netherlands. I: 707–795.

Nesis, K.N. 1999c. The duration of egg incubation in high latitude and deep-sea cephalopods. *Russian Journal of Marine Biology*, 25(6): 499–506.

***Nesis, K.N.** 2000. Squid family Onychoteuthidae: phylogeny, biogeography, and way of life. *Zoological Zhurnal*, 79(3): 272–281 [in Russian, English summary].

Nesis, K.N. 2001. West Arctic and east Arctic distributional ranges of cephalopods. *Sarsia*, 86(1): 1–11.

***Nesis, K.N.** 2002. Life style strategies of recent cephalopods: a review. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(2): 561–579.

***Nesis, K.N.** 2003. Distribution of recent cephalopoda and implications for Plio-Pleistocene events. *In*: K. Warnke, H. Keupp & S.v. Boletsky, eds. *Coleoid cephalopods through time, Berliner Palaeobiologische Abhandlung*, 03: 199–224.

Nesis, K.N. 2004. What may the geographic distribution of recent cephalopods tell about their plio-pleistocene migrations? *In*: A.I. Kafanov, ed. *Main Problems in Marine Biogeography: In memory of the academician O.G. Kussakin, Vladivostok, Dalnauka*, 112–131 (In Russian, English summary).

Nesis, K.N. & D.L. Ivanov. 2005. Cephalopoda. *In*: Yu.I. Kantor & A.V. Sysoev, eds. Catalogue of molluscs of Russia and adjacent countries. *Moscow, KMK Scientific Press Ltd.*, 401–409 (In Russian).

***Nesis, K.N. & N.P. Nezlin.** 1993. Intraspecific groupings of gonatid squids. *Russian Journal Aquatic Ecology*, 2(2): 91–102.

***Nesis, K.N. & C.M. Nigmatullin.** 1979. The distribution and biology of the genus *Ornithoteuthis* Okada, 1927 and *Hyaloteuthis* Gray, 1849 (Cephalopoda, Oegopsida). *Bulletin of the Moscow Society of Naturalists, Biology*, 84(1): 50–63 [in Russian].

Nesis, K.N. & I.V. Nikitina. 1984. A redescription of *Chiroteuthis joubini* Voss, 1967 (Cephalopoda, Chiroteuthidae). *In*: A.P. Kuznetsov & N. Vinogradova, eds. “Structure, formation and distribution of the ocean bottom fauna”, 119: 145–153.

***Nesis, K.N. & I.V. Nikitina.** 1986a. A new family of abyssal squids (Cephalopoda, Oegopsida) from the south-eastern Atlantic. *Zoologicheskij Zhurnal*, 65(1):47–54.

***Nesis, K.N. & I.V. Nikitina.** 1986b. New genus and species of squid of the family Neoteuthidae (Cephalopoda, Oegopsida) from the Southeast Pacific. *Zoologicheskij Zhurnal*, 65(2): 290–294.

***Nesis, K.N. & I.V. Nikitina.** 1987. Resescription of *Abralia steindachneri* and revision of subgenus systematics of the genus *Abralia* (Cephalopoda, Enoploteuthidae). *Zoologicheskij Zhurnal*, 66(11):1693–1705, 9 figs [In Russian].

***Nesis, K.N. & I.V. Nikitina.** 1990. Revision of the squid family Lepidoteuthidae. *Zoologicheskij Zhurnal*, 69(10): 38–49.

***Nesis, K.N. & I.V. Nikitina.** 1992. New records of oceanic squids *Walvisteuthis virilis* Nesis and Nikitina, 1986 and *Nototeuthis dimegacotyle* Nesis and Nikitina, 1986.

***Nesis, K.N. & I.V. Nikitina.** 1996. Vertical distribution of squids in the southern Okhotsk Sea and north-western Pacific off Kurile Islands (in 1992). *Russian Journal of Aquatic Ecology*, 4(1): 9–24 (1995).

Nesis, K.N. & G.A. Shvetsov. 1977a. The neritic squids (family Loliginidae) in the waters of the Soviet Far East. *Biologiya Morya, Vladivostok*, 1977(3): 70–71 [in Russian, English summary].

Nesis, K.N. & G.A. Shevtsov. 1977b. First data on abyssal cephalopods on the Sea of Okhotsk. *Biologiya Morya, Vladivostok*, 1977(5): 76–77 [in Russian, English summary].

Nesis, K.N. & G.A. Shevtsov. 1977. First data on abyssal cephalopods of the Sea of Okhotsk. *Biologiva Morya*, (5): 76–77 (Russian with English translation).

Nesis, K.N., O.N. Katugin & A.V. Ratnikov. 2004. Pygmy cuttlefish *Idiosepius paradoxus* (Ortmann, 1888) (Cephalopoda) – first record of Idiosepiidae in Russian seas. *Ruthenica*, 12 (1): 81–84.

Nesis, K.N., C.M. Nigmatullin & I.V. Nikitina. 1998a. Spent females of deepwater squid *Galiteuthis glacialis* under the ice at the surface of the Weddell Sea (Antarctic). *Journal of Zoology*, 244(2): 185–200.

***Nesis, K.N., M.A.C. Roeleveld & I.V. Nikitina.** 1998b. A new genus and species of onychoteuthid squid (Cephalopoda, Oegopsida) from the southern Ocean. *Ruthenica*, 8(2): 153–168.

Nesis, K.N., A.M. Amelekhina, A.R. Boltachev & G.A. Shevtsov. 1985. Records of giant squids of the genus *Architeuthis* in the North Pacific and South Atlantic. *Zoological Zhurnal*, 64(4): 518–528.

Nevarez-Martinez, M.O. & E. Morales-Bojorquez. 1997. The proportional escapement and the use of the biological reference point F sub (%BR), for the exploitation of the giant squid, *Dosidicus gigas*, from Gulf of California, Mexico. *Oceanides*, 12(2): 97–105.

Nevarez-Martinez, M.O., F.J. Mendez-Tenorio, C. Cervantes-Valle, J. Lopez-Martinez & M.L. Anguiano-Carrasco. 2006. Growth, mortality, recruitment, and yield of the jumbo squid (*Dosidicus gigas*) off Guaymas, Mexico. *Fisheries Research*, 79(1–2): 38–47.

Nevarez-Martinez, M.O., A. Hernandez-Herrera, E. Morales-Bojorquez, A. Balmori-Ramirez, M.A. Cisneros-Mata & R. Morales-Azpeitia. 2000. Biomass and distribution of the jumbo squid (*Dosidicus gigas*; d’Orbigny, 1835) in the Gulf of California, Mexico. *Fisheries Research*, 49(2): 129–140.

Neves, A., I. Figueiredo, T. Moura, C. Assis & L.S. Gordo. 2007. diet and feeding strategy of *Galeus melastomus* in the continental slope off southern Portugal. *Vie et milieu*, 57(3): 165–169.

Ni, J., J. Li & Y. Xu. 1992. Preliminary observation on the feeding habits and reproduction of *Triakis scyllium*. *Journal of oceanography of Huanghai and Bohai Seas, Qingdao*, 10(1): 42–46.

Nichols, R.B., R.A. Robertson & B.E. Lindsay. 2001. Northern New England commercial fishermen and open ocean aquaculture: An analysis of how commercial fishermen perceive the government, fishing and their way of life. *In*: C.J. Bridger & T.H. Reid, eds. Open Ocean Aquaculture IV Symposium. *Mississippi–Alabama Sea Grant Consortium*, p. 77.

Nigmatullin, C.M. 1972. To the question on schooling behaviour of the orangeback squid, *Ommastrephes pteropus* Steenstrup. Behaviour of Aquatic Invertebrates. *Borok: Institute of the Biology of Inland Waters of the Academy of Sciences USSR Publication*, 86–92 (In Russian).

Nigmatullin, C.M. 1975. The food of commercial cephalopods from the shelf waters off Spanish Sahara and Mauritania. Oceanological studies, fishery biology and fisheries in the Atlantic Ocean and the Baltic Sea, vol. 58 (in Russian, abstract in English).

*__Nigmatullin, C.M.__ 1976. A new record of the giant squid *Architeuthis* from the equatorial Atlantic. *Biologiya Morya (Marine Biology), Vladivostok*, 4: 29–31.

*__Nigmatullin, C.M.__ 1979. Main stages of the evolutionof the squid family Ommastrephidae (Cephalopoda, Oegopsida). *In* V.L. Wagin, ed. *Problems of Evolutionary Morphology, Kazan University Press, Kazan*, p. 210–219 (In Russian).

*__Nigmatullin, C.M.__ 1989a. Squids of the open oceans. *In*: V.V. Ivchenko, ed. Fisheries development in the open ocean. *Kaliningrad Publishing House, Kaliningrad*, pp. 26–48 (in Russian).

*__Nigmatullin, C.M.__ 1989b. The most abundant squid species of the southwest Atlantic and a synopsis of the ecology of *Illex argentinus*. *Frente Maritimo*, 5, 71–81. [Las espécies de calamar mas abundantes del Altántico sudoeste y synopsis sobre la ecologia del calmar (*Illex argentinus*)].

*__Nigmatullin, C.M.__ 1992 [1991]. Systematics, phylogeny and morpho-function evolution of squids of the family Ommastrephidae. *Bulletin of Marine Science*, 49(1–2): p. 666 [Abstract].

*__Nigmatullin, C.M.__ 2000. New subfamily Todaropsinae (Cephalopoda: Ommastrephidae) and its place in the family evolution. *In* A.F. Alimov, B.I. Sirenko & E.N. Egorova, eds. *Marine Mollusks: Taxonomy, Ecology and Phylogeny. 5th (14th)Conference on the Study of Mollusks*. Zoological Institute of RAS Press, St. Petersburg. pp. 63–64 [Abstract].

*__Nigmatullin, C.M.__ 2002a. Preliminary estimation of total stock size and production of ommastrephid squids in the world ocean. *Bulletin of Marine Science*, 71(2): p. 1134.

*__Nigmatullin, C.M.__ 2002b. Ovary development, potential and actual fecundity and oocyte resorption in coleoid cephalopods: a review. *In*: K. Warnke, ed. International Symposium "Coleoid cephalopods through time", Berlin, Sept. 17–19, 2002. *Berliner Palaobiologische Abhandungen*, 1: 82–84.

*__Nigmatullin, C.M.__ 2004. Estimation of biomass, production and fishery potential of ommastrephid squids in the world oceans and problems of their fishery forecasting. *ICES Council Meeting* 2004/CC: 06, 20 pp.

Nigmatullin, C.M. 2006. Fecundity and oocyte stock development in Antarctic squids. *Cephalopod International Advisory Council Symposium 2006, Abstract*, p. 90.

*__Nigmatullin, C.M. & A.I. Arkhipkin.__ 1998. A review of the biology of the diamondback squid *Thysanoteuthis rhombus* (Oegopsidae: Thysanoteuthidae). *In*: T. Okutani,ed. Large Pelagic Squids. *Japan Marine Fishery Resource Research Center, Tokyo*, 155–181.

Nigmatullin, C.M. & V.V. Laptikhovsky. 1994. Reproductive strategies in the squids of the family Ommastrephidae. *Ruthenica*, 4(1): 79–82.

*__Nigmatullin, C.M. & V.V. Laptikhovsky.__ 1999. Reproductive biology in females of the subfamilies Todaropsinae and Todarodinae (Cephalopoda: Ommastrephidae). *Ruthenica*, 9(1): 63–75.

Nigmatullin, C.M. & A.S. Shchetinnikov. 1992. Ecology, resources and results of experimental fishing for epipelagic squids in the waters of the Democratic Republic of Sao Tome e Principe. *Fishery Biology Studies of Marine Invertebrates, VNIRO*, pp. 134–149.

Nigmatullin, C.M. & O.A. Shukhalter. 2001. The macro-ecosystem variations of the helminth fauna in ommastrephid squid, *Sthenoteuthis oualaniensis*, from the Indian Ocean and eastern tropical Pacific. *International Council for the Exploration of the Sea, Council Meeting*, 2001/K:21: 11 pp.

Nigmatullin, C.M. & A.N. Vovk. (1972). The biology of the short-finned squid (*Illex coindetii* Verany, 1837) of the Angola coast. *Trudy AtlantNIRO*, 42: 162–166.

*__Nigmatullin, C.M., A.I. Arkhipkin & R.M. Sabirov.__ 1991a. Structure of the reproductive system of the squid, *Thysanoteuthis rhombus* (Cephalopoda: Oegopsidae). *Journal of Zoology, London*, 224: 271–283.

*__Nigmatullin, C.M., A.I. Arkhipkin & R.M. Sabirov.__ 1995. Age, growth and reproductive biology of the diamond-shaped squid *Thysanoteuthis rhombus* (Oegopsidae: Thysanoteuthidae). *Marine Ecology Progress Series*, 124: 73–87.

*__Nigmatullin, C.M., Yu.M. Froerman & Yu.N. Zheronkin.__ 2002a. Biomass of the jumbo squid *Dosidicus gigas* in the EEZ of Nicaragua and adjacent open waters. *Bulletin of Marine Science*, 71(2): 1132.

*__Nigmatullin, Ch.M., V.V. Laptikhovsky & H. Moustahfid.__ 2002b. Brief review on the ecology in the North African population of arrow squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae). *Bulletin of Marine Science*, 71(2): 581–590.

*__Nigmatullin, C.M., K.N. Nesis & A.I. Arkhipkin.__ 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopods: Ommastrephidae). *Fisheries Research*, 54(1): 9–19.

*__Nigmatullin, C.M., A.N. Parfenjuk & V.N. Nikolsky.__ 1991b. Ecology and resources of epipelagic nektonic squids in the Atlantic and southeastern part of the Pacific Ocean. *In*: State of the Fishing Industry's Biological Resources in the Central and South Atlantic and East Pacific Oceans. *Kaliningrad: AtlantNIRO Publication*, 142–177 (In Russian with English abstract).

*__Nigmatullin, C.M., A.V. Parfenjuk & R.M. Sabirov.__ 2002c. Distribution and biomass of the ommastrephid squids in the southeastern Pacific in the early 1980s. *Bulletin of Marine Science*, 71(2): 1132–1133.

*__Nigmatullin, C.M., R.M. Sabirov & V.P. Zalygalin.__ 2003. Ontogenetic aspects of morphology, size, structure and production of spermatophores in ommastrephid squids: An overview. *In*: K. Warnke, H. Keupp & S.v. Boletsky, eds. Coleoid cephalopods through time. *Berliner Palaeobiologische Abhandlung*, 3: 225–240.

Nigmatullin, C.M., A.V. Simin & A.Z. Sundakov. 2004. The stock and fishery variability of the Argentine squid *Illex argentinus* in 1982–2004 related to environmental conditions. ICES Council Meeting Documents Copenhagen. No. 2004.

Nigmatullin, C.M., V.Yu. Tsygankov & R.M. Sabirov. 1983. On the taxonomic status of the early–maturing and late–maturing forms of the squid, *Sthenoteuthis oualaniensis* (Lesson). *In*: Ya.I. Starobogatov & K.N. Nesis eds. Taxonomy and Ecology of Cephalopods. Leningrad. *Zoological Institute of the Academy of Sciences USSR Publication*, pp. 94–96 (In Russian).

Nikolsky, V.N., G.V. Zuev & C.M. Nigmatullin. 1986. Some results of the study of the Atlantic orangeback squid, *Sthenoteuthis pteropus*, and prospects of its stock utilization. *In* B.G. Ivanov, ed. Resources and Perspectives of the Squid Utilization in the Oceans. *Moscow: VNIRO Publication*, pp. 12–28. (In Russian with English abstract).

Ninh, T.D. 2007. Water-soluble and lipid-soluble arsenic compounds in Japanese Flying Squid *Todarodes pacificus*. *Journal of Agricultural and Food Chemistry*, 55(8): 3196–3202.

Nirmale, V., B.B. Nayak, S. Kannappan & S. Basu. 2002. Antibacterial effect of the Indian squid, *Loligo duvauceli* (d'Orbigny), INK. *Journal of the Indian Fisheries Association*, 29: 65–69.

Nishida, H., I. Uchiyama & K. Hirakawa. 1998. Possibility of forecasting the abundance of the firefly squid *Watasenia scintillans* immigrating into Toyama Bay, southern Japan Sea. *Bulletin of Japan Sea National Fisheries Research Institute*, 48: 37–49.

Nishimura, S. 1966. Notes on the occurrence and biology of the oceanic squid, *Thysanoteuthis rhombus* Troschel, in Japan. *Publications of the Seto Marine Biological Laboratory*, 14(4): 327–349.

Nitisewojo, P. & H.O. Hultin. 1986. Characteristics of TMAO degrading systems in Atlantic short finned squid (*Illex illecebrosus*). *Journal of Food Biochemistry*, 10(2): 93–106.

*__Nixon, M.__ 1983. *Teuthowenia megalops*. *In*: P.R. Boyle, ed. Cephalopod Life Cycles. Volume 1. *Species accounts*, 233–247.

Nixon, M. 1987. Cephalopod diets. *In*: P.R. Boyle, ed. Cephalopod Life Cycles, Vol. II Comparative Reviews. *Academic Press, London*, pp. 201–219.

*__Nixon, M. & J.Z. Young.__ 2003. The Brains and Lives of Cephalopods. *Oxford University Press*, 392 pp.

Nobes, C., J. Baverstock & H. Saibil. 1992. Activation of the GTP-binding protein Gq by rhodopsin in squid photoreceptors. *Biochemical Journal.*, 287(2): 545–54.

*__Nobre, A.__ 1936. Moluscos Marinhos de Portugal. *Porto*, Vol. 2, 378 pp., 6 pls.

Nolan, C.P., I.J. Strange, E. Alesworth & D.J. Agnew. 1998. A mass stranding of the squid *Martialia hyadesi* Rochebrune and Mabille, 1889 (Teuthoidea: Ommastrephidae) at New Island, Falkland Islands. *South African Journal of Marine Science*, 20: 305–310.

Nootmorn, P. & C. Chotiyaputta. 2002. Species diversity, biomass and community structure of cephalopods off Adang-Rawi Archipelago, Thailand. *Bulletin of Marine Science*, 71(2): 591–600.

Nootmorn, P. & A. Yakoh. 2006. Reproductive biology of purpleback flying squid *Sthenoteuthis oualaniensis* (Lesson, 1830) in the Andaman Sea. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 91.

Noriyuki, T., O. Sayaka, I. Yurzuru, Y. Akihiko, K. Hideaki & S. Wataru. 2000. Geographical variations in carbon and nitrogen stable isotope ratios in squid. *Journal of the Marine Biological Association of the United Kingdom*, 80(4): 675–684.

*__Norman, M.__ 2000. Cephalopods, a World Guide. *ConchBooks, Hackenheim, Germany*, 320 pp., 800 figs.

Norman, M.D. & C.C. Lu. 1997. Sex in giant squid. *Nature*, 389(6652): 683–684.

*__Norman, M.D. & C.C. Lu.__ 2000. Preliminary checklist of the cephalopods of the South China Sea. *Raffles Bulletin of Zoology, Supplement*, 8: 539–567.

Nottage, J.D., S.S. Montgomery, R.J. West & K. Graham. 2007. Cephalopod diversity in commercial fisheries landings of New South Wales, Australia. *Reviews in Fish Biology and Fisheries*, 17(2–3): 271–281.

Novikov, Y., E.V. Slobodskoy & G.A. Shevtsov. 2007. Influence of oceanological conditions on the distribution and biological features of the mass squid species in the South Kuril Region. *Russian Academy of Sciences*, 47(2): 238–244.

Nowara, G.B. & T.I. Walker. 1998. Effects of time of solar day, jigging method and jigging depth on catch rates and size of Gould's squid, *Nototodarus gouldi* (McCoy), in southeastern Australian waters. *Fisheries Research*, 34: 279–288.

*__Nunes, J.A.C., L.T. Chaves, R. Maia-Nogueira & C.L.S. Sampaio.__ 2007. Association between juvenile reef fish and the Caribbean reef squid *Sepioteuthis sepioidea* on north-eastern Brazilian coastal reefs. *Journal of the Marine Biological Association of the United Kingdom*, 87(3): 761–762.

Nyegaard, M. 2001. An analysis of reproductive behaviour, demography, diet, and spatial distribution of the Eurepean common squid (*Alloteuthis subulata*) in the Irish Sea. *Master thesis, University Tromsø.*

Nyegaard, M., A. Arkhipkin & P. Brickle. 2004. Variation in the diet of *Genypterus blacodes* (Ophidiidae) around the Falkland Islands. *Journal of Fish Biology*, 65(3): 666–682.

O'Dor, R.K. 1982. Respiratory metabolism and swimming performance of the squid, *Loligo opalescens*. *Canadian Journal of Fishery and Aquatic Science*, 39: 580–587.

*__O'Dor, R.K.__ 1983. *Illex illecebrosus*. *In*: P.R. Boyle, ed. Cephalopod Life Cycles. *Academic Press, London*, 1: 175–199.

O'Dor, R.K. 1988. Limitations on locomotor performance in squid. *Journal of Applied Physiology*, 64(1): 128 –134.

O'Dor, R.K. 1993. Big squid, big currents and big fisheries. *In*: T. Okutani, R. O'Dor & T. Kubodera, eds. *Recent advances in cephalopods fisheries biology, Tokai. University Press, Tokyo*, 385–396.

O'Dor, R.K. 1998a. Can understanding squid life-history strategies and recruitment improve management? *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 193–206.

*__O'Dor, R.K.__ 1998b. Squid life-history strategies. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 233–254.

O'Dor, R.K. & N. Balch. 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. *NAFO Scientific Council Studies*, 9: 69–76.

O'Dor, R.K. & M.L. Coelho. 1993. Big squid, big currents, and big fisheries. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 385–396.

O'Dor, R.K. & E.G. Dawe. 1998. *Illex illecebrosus*. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 77–104.

O'Dor, R.K. & J.A. Hoar. 1998. Does geometry limit squid growth? *Council Meeting of the International Council for the Exploration of the Sea*, 18 pp.

*__O'Dor, R.K. & M.R. Lipinski.__ 1998. The genus *Illex* (Cephalopoda; Ommastrephidae): Characteristics, distribution and fisheries. In: Rodhouse, P.G., Dawe, E.G. & O'Dor, R.K. (eds) Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 1–12.

O'Dor, R.K. & M.J. Wells. 1978. Reproduction versus somatic growth, hormonal control in *Octopus vulgaris*. *Journal of Experimental Biology*, 77: 15–31.

O'Dor, R.K. & M.J. Wells. 1987. Energy and nutrient flow. *In*: P.R. Boyle, ed. *Cephalopod Life Cycles. Comparative Reviews*. Vol. 2: 85–108. London, Orlando, *Academic Press.*

O'Dor, R.K., N. Balch & N. Amaratunga. 1982. Laboratory observations of midwater spawning by *Illex illecebrosus*. *NAFO Science Council Studies*, 9: 69–76.

O'Dor, R.K., P. Helm. & N. Balch. 1985. Can *Rhynchoteuthions suspension* feed? (Mollusca: Cephalopoda). *Vie Milieu*, 33: 267–271.

O'Dor, R.K., P.G. Rodhouse & E.G. Dawe. 1997. Squid recruitment in the genus *Illex*. *In*: D.A. Hancock, D.C. Smith, A. Grant & J.P. Beumer, eds. Developing and sustaining world fisheries resources. The state of science and management. *CSIRO*, pp. 116–121.

O'Dor, R.K., R.D. Durward, E. Vessey & T, Amaratunga. 1980. Feeding and growth in captive squid, *Illex illecebrosus*, and the influence of food availablility on growth in the antural population. *ICNAF Selected Papers*, 6: 15–21.

O'Dor, R.K., S. Adamo, J.P. Aitken, Y. Andrade, J. Finn, R.T. Hanlon & G.D. Jackson. 2002. Currents as environmental constraints on the behavior, energetics and distribution of squid and cuttlefish. *Bulletin of Marine Science*, 71(2): 601–617.

O' Dor, R.K., J.A. Hoar, D.M. Webber, F.G. Carey, S. Tanaka, H.R. Martins & F.M. Porteiro. 1994. Squid (*Loligo forbesi*) performance and metabolic rates in nature. *Marine and Freshwater Behaviour and Physiology*, 25(1–39): 163–177.

O'Riordan, C.E. 1976. Marine fauna notes from the National Museum of Ireland – 2. *Irish Nature Journal*, 18(10): 305–307.

O'Shea, S. 1997. Giant squid in New Zealand waters. *Seafood New Zealand*, 5(10): 32–34.

O'Shea, S., K.S. Bolstad & P.A. Ritchie. 2004. First records of egg masses of *Nototodarus gouldi* McCoy, 1888 (Mollusca: Cephalopoda Ommastrephidae), with comments on egg-mass susceptibility to damage by fisheries trawl. *New Zealand Journal of Zoology,* 31(2): 161–166.

***O'Shea, S., G. Jackson & K.S. Bolstad.** 2007. The nomenclatural status, ontogeny and morphology of *Pholidoteuthis massyae* (Pfeffer, 1912), new comb. (Cephalopoda: Pholidoteuthidae). *Reviews in Fish Biology and Fisheries*, 17(2–3): 425–435.

O'Shea, S., C.C. Lu & M.C. Clarke. 2006. Description of paralarval *Architeuthis* and Onychoteuthidae squid (Cephalopoda: Teuthoidea) from New Zealand waters. Tasmania, *CIAC Meeting Abstracts*, p. 39.

O'Sullivan, D. 1980. Biology of Gould's Squid in Bass Strait Studied. *Australian Fisheries*, 39(12): 18–19.

O'Sullivan, D. & J.M. Cullen. 1983. Food of the squid *Nototodarus gouldi* in Bass Strait. *Australian Journal of Marine and Freshwater Research*, 34(2): 261–285.

O'Sullivan, D.B., G.W. Johnstone, K.R. Kerry & M.J. Imber. 1983. A mass stranding of squid *Martialia hyadesi* (Teuthoidea: Oegopsida) at Macquarie Island. *Paper and Proceedings of the Royal Society of Tasmania*, 117: 161–163.

Ochoa-Acuna, H. & J.M. Francis. 1995. Spring and summer prey of the Juan Fernandez fur seal, *Arctocephalus philippii*. *Canadian Journal of Zoology*, 73(8): 1444–1452.

***Odhner, N.H.** 1923. Die Cephalopoden. Further Zoological Results of the Swedish Antarctic Expedition 1901–1903, 1(4):1–7, 1 pl.

Oedblom, M.P., R. Williamson & M.B. Jones. 2000. Ionic currents in cardiac myocytes of squid, *Alloteuthis subulata*. *Journal of Comparative Physiology*, B, 170(1): 11–20.

Oehlenschlaeger, J. 1990. Heavy metal content in the mantle (edible part) and the intestines of cuttlefish (Cephalopoda). *Proceedings of the Food Science Advisory Board for the German Fisheries. 34 annual meeting*, 21: 105–115.

Oehlenschlaeger, J. 1991. Heavy metal content of deep frozen Californian squid. *Informationen fuer die Fischwirtschaft*, 38(2): 62–65.

Offredo, C., V. Ridoux & M.R. Clarke. 1985. Cephalopods in the diet of emperor and Adélie penguins in Adélie Land, Antarctica. *Marine Biology*, 86:199–202.

Ogawa, Y. & T. Sasaki. 1991. Catch fluctuation patterns of *Todarodes pacificus* (Steenstrup) in northern Japanese coastal waters of the Pacific Ocean. *Canadian Translation of Fisheries and Aquatic Science*, 5523: 90 pp.

Ogburn-Matthews, M. & D.M. Allen. 1993. Interactions among some dominant estuarine nekton species. *Estuaries*, 16(4): 840–850.

Ohizumi, H. & T. Kishiro. 2003. Stomach contents of a Cuvier's beaked whale (*Ziphius cavirostris*) stranded on the Central Pacific coast of Japan. *Aquatic Mammals*, 29(1): 99–103.

Ohizumi, H., T. Kuramochi, M. Amona & N. Miyazaki. 2000. Prey switching of Dall's porpoise *Phocoenoides dalli* with population decline of Japanese pilchard *Sardinops melanostictus* around Hokkaido, Japan. *Marine Ecology Progress Series*, 200: 265–275.

Oikawa, S., S.J. Song, T. Maeyama, T. Kishimoto, K. Tomura & H. Higuchi. 2003. Determination of trace elements in squid organs by inductively couple plasma mass spectrometry and neutron activation analysis. *Bunseki Kagaku*, 52(8): 551–557.

***Okada, Y.K.** 1927a. Cephalopodes japonais de collections de Museum. *Bulletin du Museum d'Histoire Naturelle*, 93–98: 172–179.

***Okada, Y.K.** 1927b. Contribution à l'etude des céphalopods lumineaux (notes préliminaires). I. Organes photogenes d'*Onychoteuthis*; établissement d'une nouvelle espèce: *Onychoteuthis borealijaponicus*. *Bulletin de l'Institut Oceanographique de Monaco*, 494: 1–7.

***Okada, Y.K.** 1927c. Contribution à l'etude des céphalopodes lumineaux (notes préliminaires). IV. *Ommastrephes volatilis* Sasaki est une forme lumineaux; établissement d'un nouveau genre: *Ornithoteuthis*. *Bulletin de l'Institut Océanographique de Monaco*, 494: 13–16.

Okamoto, Y. & S. Hayashi. 2003. Migration of the common squid, *Todarodes pacificus*, in Toyama Bay and adjacent waters, the Japan Sea, assess by release and recapture experiment in February and March. *Bulletin of Toyama Prefectural Fisheries Experiment Institute*, 14: 1–10.

***Okiyama, M.** 1969. A new species of *Gonatopsis* from the Japan Sea, with the record of a specimen referable to *Gonatopsis* sp. Okutani 1967 (Cephalopoda: Oegopsida: Gonatidae). *Publications of the Seto Marine Biological Laboratory*, 17(1): 19–32, 4 figs, 4 pls.

***Okiyama, M.** 1970. A record of the eight-armed squid, *Gonatopsis octopedatus* Sasaki, from the Japan Sea (Cephalopoda, Oegopsida, Gonatidae). *Bulletin of the Japan Sea Regional Fisheries Research Laboratory*, 22: 71–80.

Okiyama, M. 1993a. Kinds, abundance and distribution of the oceanic squids in the Sea of Japan. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 403–415.

Okiyama, M. 1993b. Why do gonatid squid *Berryteuthis magister* lose tentacles on maturation? *Bulletin of Japanese Society of Scientific Fishery*, 59(1): 61–65.

***Okiyama, M. & S. Kasahara.** 1975. Identification of the so-called common squid eggs collected in the Japan Sea and adjacent waters. *Bulletin of the Japan Sea National Fisheries Research Institute Niigata*, 26: 35–40.

Okutani, T. 1962. Diet of the common squid, *Ommastrephes sloani pacificus* landed around Ito Port, Shizuoka Prefecture. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 32: 41–47.

Okutani, T. 1965. Studies on early life history of decapodon Mollusca. I. A synoptic report on rhynchoteuthion larva of *Todarodes pacificus* Steenstrup. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 41: 23–29.

Okutani, T. 1968. Studies on early life history of decapodan Mollusca. III. Systematics and distribution of larvae of decapod cephalopods collected from the sea surface on the Pacific coast of Japan. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 55: 9–57.

***Okutani, T.** 1970. A small collection of gasteropod and decapod mollusks from the Seychelles Bank, Indian Ocean, by the training vessel Koyo-Maru in 1968. *Venus, Japanese Journal of Malacology*, 29: 123–130.

***Okutani, T.** 1973. Guide and keys to squid in Japan. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 74: 83–111.

***Okutani, T.** 1974a. Epipelagic decapod cephalopods collected by micronekton tows during the EASTROPAC Expeditions, 1967–1968 (systematic part). *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 80: 29–118.

Okutani, T. 1974b. Rare and interesting squid from Japan – 3. A cranchiid squid encased in gelatinous matter. *Venus*, 33(2): 87–90.

Okutani, T. 1975. A probable advanced stage of *Bathothauma lyromma* (Cephalopoda: Oegopsida: Cranchiidae). *Veliger*, 17(3): 243–246.

***Okutani, T.** 1976. Rare and interesting squid from Japan 5. A grand female of *Ancistrocheirus lesueuri*. *Venus*, 35(2): 73–81.

Okutani, T. 1977. Stock assessment of cephalopod resources fished in Japan. *FAO Fisheries Technical Paper, Rome*, 173: 62 pp.

*****Okutani, T.** 1980. Useful and latent Cuttlefish and Squids of the World. *National Cooperative Association of Squid Processors, Tokyo*, 66 p.

*****Okutani, T.** 1981. Two new species of the squid genus *Onykia* from the tropical Indian Ocean (Cephalopoda, Onychoteuthidae). *Bulletin of the National Science Museum Series-A Zoology*, 7(4): 155–163.

*****Okutani, T.** 1983a. A new species of an oceanic squid, *Moroteuthis pacifica* from the North Pacific (Cephalopoda: Onychoteuthidae). *Bulletin of the National Science Museum*, (series A) 9(3): 105–112, 10 figs, 1 pl.

*****Okutani, T.** 1983b. *Abralia marisarabica*, a new enoploteuthid squid from the Arabian Sea (Cephalopoda: Oegopsida). *Bulletin of the National Science Museum Series A Zoology*, 9(4): 161–168.

*****Okutani, T.** 1984. Life history of the oval squid, *Sepioteuthis lessoniana*. *Saibai Giken*, 13: 69–75 (In Japanese).

*****Okutani, T.** 1987. Juvenile morphology. *In*: P. R. Boyle, ed. *Cephalopod Life Cycles. Species Accounts*. Vol. 1, 201–216. London, *Academic Press*.

Okutani, T. 1988. Evidence of spawning of *Berryteuthis magister* in the northeastern Pacific (Cephalopoda: Gonatidae). *In*: T. Nemoto, W.G. Pearcy, eds. *The Biology of the Subarctic Pacific*, Part I, 26: 193–200.

*****Okutani, T.** 1990. Cuttlefish and squid of the world in colour. *National Cooperative Association of Squid Processors for the 30th Anniversary of its Foundation*, 185 pp., 50 pls.

*****Okutani, T.** 1995. Cuttlefish and squids of the world in color. *National Cooperative Association of Squid Processors, Tokyo*, 185 pp.

*****Okutani, T.** 1998. Biological significance and fisheries potential of large pelagic squids. *Japan Marine Fishery Resources Research Center, Tokyo*, 6 pp.

*****Okutani, T.** 2005. Cuttlefishes and squids of the world. *National Cooperative Association of Squid Processors, Tokyo*, 253 pp.

*****Okutani, T. & M.R. Clarke.** 1992. Family Gonatidae, Hoyle 1886. *In* M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 139–156.

*****Okutani, T. & T. Kubodera.** 1987. *Berryteuthis magister nipponensis* Okutani & Kubodera, n. sbsp. *In*: T. Okutani, M. Tagawa & H. Horikawa, eds. Cephalopods from continental shelf and slope around Japan. *Tokyo: Japan Fisheries Resource Conservation Association*, 132–133.

Okutani, T. & T. Kubota. 1972. Rare and interesting squid from Japan. I. *Joubiniteuthis portieri* (Joubin, 1912), the first occurrence from the Pacific (Cephalopoda: Oegopsida). *Venus, Kyoto*, 31(1): 35–40.

Okutani, T. & T. Kubota. 1976. Cephalopods eaten by lancetfish, *Alepisaurus ferox* Lowe, in Suruga Bay, Japan. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 84: 1–9.

*****Okutani, T. & M. Kuroiwa.** 1985. The first occurrence of *Nototodarus* (Cephalopoda: Ommastrephidae) from off Chile, Southeast Pacific (Preliminary Report). *Venus*, 44(2): 95–102.

Okutani, T. & J.A. McGowan. 1969. Systematics distribution, and abundance of the epiplanktonic squid (Cephalopoda: Decapoda) larvae of the California Current April, 1954–March, 1957. *Bulletin of Scripps Institute of Oceanography*, 14: 1–90.

Okutani, T. & M. Murata. 1983. A review of the biology of the oceanic squid *Onychoteuthis borealijaponica*. *Memoirs of the National Museum of Victoria*, 44: 189–195.

*****Okutani, T. & T. Nemoto.** 1964. Squids as the food of sperm whales in the Bering Sea and Alaskan Gulf. *Scientific Reports of the Whales Research Institute*, 18: 111–121, 5 pls.

Okutani T. & Y. Satake. 1978. Squids in the diet of 38 sperm whales caught in the Pacific off northern Honshu, Japan, February 1977. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 93: 13–27.

*****Okutani, T. & K. Tsuchiya.** 1987. *Abralia similis*, a new enoploteuthid squid from the northwest Pacific (Cephalopoda, Oegopsida). *Bulletin of the National Science Museum,* Tokyo, (series A)13(4): 141–150, 15 figs.

*****Okutani, T. & K. Tsukada.** 1988. Squids eaten by lancetfish and tunas in the tropical Indo-Pacific Oceans. *Journal of the Tokyo University of Fisheries*, 75: 1–44.

Okutani, T. & I. Tung. 1978. Reviews of the biology of commercially important squids in Japanese and adjacent waters. I. *Symplectoteuthis oualaniensis* (Lesson). *Veliger*, 21: 87–94.

*****Okutani, T. & K. Uemura.** 1973. Rare and interesting squid from Japan 2. A new species of the genus *Nototodarus* from Japan (Oegopsida: Ommastrephidae). *Venus*, 32(2): 39–49.

*****Okutani, T., T. Kubodera & K. Jefferts.** 1988. Diversity, distribution and ecology of gonatid squids in the subarctic Pacific: a review. *The Biology of the Subarctic-Pacific – Part 1*, 26: 159–192.

*****Okutani, T., I. Nakamura & K. Seki.** 1995. An unusual egg-brooding behavior of an oceanic squid in the Okhotsk Sea. *Venus, Japanese Journal of Malacolgia*, 54(3): 237–239.

*****Okutani, T., R.K. O'Dor & T. Kubodera** (eds). 1993. Recent advances in cephalopod fisheries biology. *Tokai University Press*, 752 pp.

*****Okutani, T., M. Tagawa & H. Horikawa.** 1987. Cephalopods from continental shelf and slope around Japan. *Japan Fisheries Resource Conservation Association*, 194 pp.

*****Okutani, T., A. Wakatsuki & T. Kubota.** 1976a. Further notes on decapod cephalopods collected by Shirasu boat seines operated in Suruga Bay, Japan, and discrimination of juveniles of two loliginid species. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 86: 59–70.

*****Okutani, T., H. Hamada, H. Mochizuki & T. Kubota.** 1975. A survey on decapod cephalopods collected by Shirasu boat seines operated in Suruga Bay, Japan, with special reference to discrimination of juveniles of two loliginid species. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 82: 41–56.

Okutani, T., Y. Satake, S. Ohsumi & T. Kawakami. 1976b. Squids eaten by sperm whales caught off Joban District, Japan, during January–February, 1976. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 87: 67–113.

*****Oliveira, H.P. de**. 1940. Sobre dois cefalopodos da Guanabara. *Boletim do Ministerio da Agricoltura*, 29(19): 29–35.

Olson, R.J., M.H. Roman-Verdesoto & G.L. Macias-Pita. 2006. Bycatch of jumbo squid *Dosidicus gigas* in the tuna purse-seine fishery of the eastern Pacific Ocean and predatory behaviour during capture. *Fisheries Research*, 79(1–2): 48–55.

Olyott, L.J.H., A.J. Booth & W.H.H. Sauer. 2000. The use of a GIS to understand the spatial and temporal biology of the chokka squid *Loligo vulgaris reynaudii* on the southern coast of South Africa. 10th Southern African Marine Science Symposium SAMSS 2000. *Land, Sea and People in the New Millennium, Abstracts*, 2000: 1.

Olyott, L.J.H., W.H.H. Sauer & A.J. Booth. 2007. Spatial patterns in the biology of the chokka squid, *Loligo reynaudii* on the Agulhas Bank, South Africa. *Reviews in Fish Biology and Fisheries*, 17(2–3): 159–172.

Omoto S., A. Kajita & H. Shiraishi. 1998. The marketing and price formation of diamond squid *Thysanoteuthis rhombus* in Japan. *In*: T. Okutani, ed. Large Pelagic Squids. *Japan Marine Fishery Resource Research Center, Tokyo*, pp. 199–205.

Oordt, G.J. van. 1938. The spermatheca of *Loligo vulgaris*. 1. Structure of the spermatheca and function of its unicellular glands. *Quarterly Journal of Microscopical Science*, 80: 593–599.

Oosthuizen, A., M.J. Roberts & W.H.H. Sauer. 2002a. Temperature effects on the embryonic development and hatching success of the squid *Loligo vulgaris reynaudii*. *Bulletin of Marine Science*, 71(2): 619–632.

Oosthuizen, A., M.J. Roberts & W.H.H. Sauer. 2002b. Early post-cleavage stages and abnormalities identified in the embryonic development of chokka squid eggs *Loligo vulgaris reynaudii*. *South African Journal of Marine Science*, 24: 379–382.

Oozeki, Y. & H. Saito. 2004. Progresses and achievements of GLOBEC research projects in Japan. *PICES 13th Annual Meeting Book of Abstracts*, p. 133.

*****Orbigny, A. d'.** 1826. Tableau methodique de la Classe de Céphalopodes. *Annales des Sciences Naturelles, Paris*, (series 1)7: 95–169, 245–314, 8 pls.

*****Orbigny, A. d'.** [1834]1835–1843[1847]. Mollusques. *In*: *Voyage dans l'Amerique Meridionale*, 5(3): 1–758, Atlas of 85 pls. [See Sherborn and Griffin (1934) for publication dates of sections].

Orbigny, A. d'. 1845–1847. Mollusques vivants et fossiles ou description de toutes les espèces de Coquilles et de Mollusques. 605 pp., atlas of 36 pls. Paris.

Oremland, M.S., M. Vecchione, G. Waring, E. Shea & R. Gibbons. 2006. Cephalopod prey fields in relation to sperm, pilot, and beaked whale sightings off Bear Seamount and Georges Bank in 2002. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 27.

Orlov, A.M. 1996. Role of fishes in predator diets of the Pacific slope of the northern Kuril Islands and southeastern Kamchatka. *American Fisheries Society*, 14: 828 pp.

Orlov, A.M. 2007. Some data on the distribution and biology of the boreal clubhook squid *Moroteuthis robusta* (Verrill, 1876) (Onychoteuthidae, Teuthida) in the Northwest Pacific. *In*: N.H. Landman *et al*., eds. *Cephalopods Present and Past: New Insights and Fresh Perspectives*, 423–433.

Orlov, A.M. & A.A. Abramov. 2001. Age, rate of sexual maturation and feeding of the shortraker rockfish, *Sebastes borealis* (Scorpaenidae) in the northwestern Pacific Ocean. *Journal of Ichthyology*, 41(4): 279–288.

Orr, P.A., C.G.J. Michielsens & D.J. Agnew. 2006. A baysian delury model for *Loligo gahi* from Falkland Islands waters. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 55.

Orsi Relini, L. & F. Garibaldi. 1992. Feeding of the pilot whale (*Globicephala melas*) in the Ligurian Sea. A preliminary note. *European Research on Cetacean*, 6: 142–145.

Orsi Relini, L. & F. Garibaldi. 2005. Mesopelagic cephalopods biodiversity in the cetacean sanctuary as a result of direct sampling and observations on the diet of the Cuvier's beaked whale, *Ziphius cavirostris*. Biologia-Marina-Mediterranea, 12(1): 106–115 (Diversità dei cefalopodi mesopelagici del Santuario de Cetacei in base a campionamenti diretti e osservazioni sull'alimentazione dello zifio, *Ziphius cavirostris*).

Orsi Relini, L. & M. Relini. 1993. The stomach content of some *Delphinus delphis* L. from the Ligurian Sea. *European Research on Cetaceans*, 7: 199–202.

Orsi Relini, L., M. Capello & R. Poggi. 1994. The stomach content of some bottlenose dolphins (*Tursiops truncatus*) from the Ligurian Sea. *European Research on Cetaceans*, 8: 192–195.

Orsi Relini, L., L. Tunesi, A. Peirano & G. Relini. 1985. Otter trawling in Ligurian coastal waters: 2. Distribution and incidence in the catches of young specimens. *Oebalia*, 11(N.S, no. 2): 509–519.

Orsi Relini, L., C. Cima, G. Palandri, M. Relini & F. Garibaldi. 1999. Alimentazione del tonno giovanile nell'ecosistema del largo del mar Ligure. *Biologia Marina Mediterranea*, 6 (2): 295–302.

***Ortmann, A.S.** 1888. Japanishe Cephalopoden. *Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere*, 3: 639–670.

Ortmann, A.S. 1891. Cephalopoden von Ceylon. *Zoologische Jahrbücher*, 5: 669–678.

Osaka, M. & M. Murata. 1983. Stock assessment of cephalopod resources in the northwestern Pacific. *FAO Fisheries Technical Paper*, 231: 55–144.

Otano, D. 2004. A squid fishery in Kauai. *Pacific Islands Fishery News*, Winter issue: 3.

Otero, H.O., S.I. Bezzi, M.A. Renzi & G. Verazay. 1982. Atlas de los recursos pesqueros demersales del Mar Argentino. *Contributión de l'Instituto Nacional de Investigación y Desarrollo Pesquero*, 423: 248 pp.

Overholtz, W.J. & G.T. Waring. 1991. Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the mid-Atlantic Bight during spring 1989. *Fishery Bulletin*, 89(4): 723–728.

Overholtz, W.J., J.S. Link & L.E. Suslowicz. 1998. Consumption and harvest of pelagic fishes and squids in the Gulf of Maine-Georges Bank ecosystem. *Ecosystem Approaches for Fisheries Management University of Alaska Sea Grant*, 16: 163–186.

***Overholtz, W.J., J.S. Link & L.E. Suslowicz.** 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparison. *ICES Journal of Marine Science*, 57: 1147–1159.

***Owen, R.** 1836. Descriptions of some new or rare Cephalopoda, collected by Mr. George Bennett, Corr. Memb. Z.S. *Proceedings of the Zoological Society of London*, 37:19–24.

***Owen, R.** 1881. Descriptions of some new and rare Cephalopoda (Part II). *Transactions of the Zoological Society of London*, 11(5):131–170, 4 figs, 13 pls.

Ozturk, B., A. Salman, A.A. Ozturk & A. Tonay. 2007. Cephalopod remains in the diet of striped dolphins (*Stenella coeruleoalba*) and Risso's dophins (*Grampus griseus*) in the Eastern Mediterranean Sea. *Vie et milieu*, 57(1/2): 57–63.

Paarup, T., J. Sanchez, A. Moral, H. Christensen, M. Bisgaard & L. Gram. 2002. Sensory, chemical and bacteriological changes during storage of iced squid (*Todaropsis eblanae*). *Journal of Applied Microbiology*, 92(5): 941–950.

Packard, A. 1991. Cephalopods as individuals. *Bulletin of Marine Science*, 49(1–2): 666.

Page, B., J. McKenzie & S.D. Goldsworthy. 2005. Dietary resource partitioning among sympatric New Zealand and Australian fur seals. *Marine Ecology Progress Series*, 293: 283–302.

Paiva, M.P., A.C.C. Santos & L.H.A. Moreira. 2002. Distribution and abundance of squids and octopuses in Rio de Janeiro state (Brazil). *Boletim Técnico-Científico do Cepene*, 10(1): 239–254.

Palacio, F.J. 1977. A study of the coastal cephalopods from Brazil with a review of Brazilian zoogeography. *Ph.D. Dissertation, University of Miami*, 311 pp.

Palm, H.W., T. Walter, G. Schwerdtfeger & L.W. Reimer. 1997. *Nybelinia poche*, 1926 (Cestoda: Trypanorhyncha) from the Mozambique coast, description of *N. beveridgei* sp. Nov. and systematic consideration of the genus. *South African Journal of Marine Science*, 18: 273–285.

Panetta, P. 1975. Osservazioni ecologiche sui cefalopodi della costa Salentina (Golfo di Taranto). *Bollettino Pesca Piscicicoltura Idrobiologia*, 29(2): 187–196.

Panetta, P., G. D'onghia, A. Tursi & E. Cecere. 1986. Il ruolo dei Molluschi Cefalopodi nella valutazione delle risorse marine dello Jonio (campagne di pesca 1985). *Nova Thalassia*, 8: 523–527.

Parfenjuk, A.V., A.E. Filippov & A.S. Shchetinnikov. 1983. Feeding behaviour of squids, *Sthenoteuthis oualaniensis* and *Dosidicus gigas*. *In*: Ya.I. Starobogatov & K.N. Nesis, eds. Taxonomy and Ecology of Cephalopods. Leningrad: *Zoological Institute of Academy of the Sciences USSR Publication*, pp. 113–114 (In Russian).

Parfeniuk, A.V., Y.M. Froerman & A.N. Golub. 1992. Particularidades de la distribucion de los juveniles del calamar (*Illex argentinus*) en el area de la depression argentina. *Frente Maritmo*, 12(A): 105–112.

Park, Y.C., M. Yoda & Y. Hiyama. 2002. Stock assessment for swordtip squid, *Loligo edulis*, in the East China Sea and the Southwest Sea of Japan. *Fisheries Science*, 68(suppl. 1): 89–92.

***Parry, M.** 2006. Feeding behavior of two ommastrephid squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* off Hawaii. *Marine Ecology Progress Series*, 318: 229–235.

Pascoe, P.L. 1986. Size data and stomach contents of common dolphins, *Delphinus delphis*, near Plymouth. *Journal of the Marine Biological Association of United Kingdom*, 66(2): 319–322.

Pascoe, P.L., M.C. Mickiewicz & H.P. Castello. 1990. Cephalopod remains from the stomach of a sperm whale stranded off Patagonia. *Marine Biology*, 104(1): 1–4.

Pascual, S. & F.G. Hochberg. 1996. Marine parasites as biological tags of cephalopod hosts. *Parasitology Today*, 12: 324–327.

Pascual, S., C. Arias & A. Guerra. 1996. First record of the trypanorhynchidean parasite *Nybelinia lingualis* Cuvier, 1817 in the squid *Todaropsis eblanae* (Cephalopoda: Ommastrephidae). *Scientia Marina Barcelona*, 60(4): 553–555.

Pascual, S., C. Gestal & E. Abollo. 1997. Effect of *Pennella* sp. (Copepoda, Pennellidae) on the condition of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda, Ommastrephidae. *Bulletin of the European Association of Fish Pathology*, 17(3/4): 91–95.

Pascual, S., A.F. González & A. Guerra. 1998a. Parasites and cephalopod fisheries uncertainty: towards a water fall understanding. *Reviews in Fish Biology and Fisheries*, 17(2–3): 139–144.

Pascual, S., A.F. González & A. Guerra. 1998b. Effect of parasitism on the productivity of the ommastrephid stocks in Galician waters (NW Spain: economic loss). *Iberus 1998*, 16(2): 95–98.

Pascual, S., A.F. González & A. Guerra. 2005. The recruitment of gill-infesting copepods as a categorical predictor of size-at-age data in squid populations. *ICES Journal of Marine Science,* 62(4): 629–633.

Pascual, S., A.F. González, C. Arias & A. Guerra. 1996. Biotic relationships of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in the Northeast Atlantic: evidence from parasites. *Sarsia*, 81: 265–274.

Pascual, S., A.F. González, C. Arias & A. Guerra. 1999. Larval nisakis simplex B (Nematoda: Ascaridoidea) of short-finned squid (Cephalopoda: Ommastrephidae) in north-west Spain. *Journal of the Marine Biological Association of United Kingdom*, 79(1): 65–72.

Pascual, S., M.A. Vega, F.J. Rocha & A. Guerra. 2002. First Report of an Endoparasitic Epicaridean Isopod Infecting Cephalopods. *Journal of Wildlife Diseases*, 38(2): 473–477.

Pascual, S., A.F. Gonzaalez, C. Gestal, E. Abollo & A. Guerra. 1998. What makes a cephalopod a suitable host for parasites? The case of Galician waters. *Copenhagen Denmark ICES*, 7 pp.

***Passarella, K.C. & T.L. Hopkins.** 1992 [1991]. Species composition and food habits of the micronektonic cephalopod assemblage in the eastern Gulf of Mexico. *Bulletin of Marine Science*, 49(1–2): 638–659.

Pastorelli, A.M., R. Vaccarella & V. De Zio. 1995. Distribuzione dei cefalopodi commerciali nel Basso Adriatico. *Biologia Marina Mediterranea,* 2: 510–502.

Paulij, W.P., P.M.J. Herman, E.J. Van Hannen & J.M. Denuce. 1990. The impact of photoperiodicity on hatching of *Loligo vulgaris* and *Loligo forbesi*. *Journal of the Marine Biological Association of the United Kingdom*, 70: 597–610.

Pauly, D. 1998. Why squid, though not fish, may be better understood by pretending they are. *In*: A.I. Payne, M.R. Lipiński, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 47–58.

Payne, A.G., D.J. Agnew & G.J. Pierce (Guest Editors). 2006. Trends and assessment of cephalopod fisheries. Proceedings of the CEPHSTOCK Cephalopod Assessment Workshop. *Fisheries Research*, 78(1): 1–106.

Payne, A.I.L. & K.L. Cochrane. 1995. How management and science are trying to develop fisheries policy in South Africa. *Copenhagen Denmark ICES*, 16 pp.

Payne, A.I., M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld. 1998: Editors. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 1–469.

Pearcy, W.G. 2002. Marine nekton off Oregon and the 1997–98 El Niño. *Progress in Oceanography*, 54(1–4): 399–403.

***Pearcy, W.G. & G.L. Voss.** 1963. A new species of gonatid squid from the northeastern Pacific. *Proceedings of the Biological Society of Washington*, 76:105–112, 2 figs.

Pecl, G.T. 2000. Comparative life history of tropical and temperate *Sepioteuthis* squids in Australian waters. *Ph.D. thesis, James Cook University, Australia.*

Pecl, G.T. 2001. Flexible reproductive strategies in the tropical and temperate *Sepioteuthis* squids. *Marine Biology*, 138: 93–101.

Pecl, G.T. 2002. Effects of hatching season on the growth rate, reproductive-somatic investment and spawning biology of *Sepioteuthis australis* in the temperate waters of southern Australia. *Bulletin of Marine Science*, 71(2): 1135.

Pecl, G.T. 2004.The in situ relationships between season of hatching, growth and condition in the southern calamary, *Sepioteuthis australis*. *Marine and Freshwater Rresearch*, 55(4): 429–438.

***Pecl, G.T. & N.A. Moltschaniwskyj.** 2006. Life history of a short-lived squid (*Sepioteuthis australis*): resource allocation as a function of size, growth, maturation, and hatching season. *ICES Journal of Marine Science*, 63: 995–1004.

Pecl, G.T., M.A. Steer & K.E. Hodgson. 2004a. The role of hatchling size in generating the intrinsic size-at-age variability of cephalopods: extending the Forsythe Hypothesis. *Marine and Freshwater Research*, 55(4): 387–394.

Pecl, G.T., N.A. Moltschaniwskyj, S.R. Tracey & A.R. Jordan. 2004b. Inter-annual plasticity of squid life history and population structure: ecological and management implications. *Oecologia*, 139(4): 515–524.

***Pecl, G.T., S.R. Tracey, J.M. Semmens & G.D. Jackson.** 2007. Use of acoustic telemetry for spatial management of southern calamari *Sepioteuthis australis*, a highly mobile inshore squid species. *Marine Ecology Progress Series*, 328: 1–15.

Pecquerie, L., L. Drapeau, P. Freon, J.C. Coetzee, R.W. Leslie & M.H. Griffiths. 2004. Distribution patterns of key fish species of the southern Benguela ecosystem: An approach combining fishery-dependent and fishery-independent data. *African Journal of Marine Science*, 26: 115–139.

Pelczarski, W. 1990. Food of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) from the open waters of the Central Atlantic. *Reports of the Sea Fisheries Institute. Gdynia*, 22: 85–106.

Pena-Cayetano, J.A. 1995. New resources – Peru. 3rd International Cephalopod Trade Conference, Venice, Italy. *Proceedings London UK. Agra Europe*, 5 pp.

Peng, C.Y & S.Y. Su. 1993. Chemical composition of giant squid, *Dosidicus gigas*, caught from Peru. *Journal Taiwan Fisheries Research*, 1(2): 67–71.

Pereira, J.M.F. 1993. Squid fishing trials with trawl nets off the Portuguese coast. *Copenhagen Denmark ICES*, 17 pp.

Pereira, J.M.F., M.M. Cunha & A. Moreno. 1995. Os cefalópodes e o seu habitat: substratos preferenciais. 8º Congresso do Algarve. 7 a 9 de Abril de 1995. Volume de Comunicações: 829–837.

Pereira, J.M.F., M.M. da Cunha & A. Moreno. 1997. Fish and cephalopods associated with the squid *Loligo vulgaris* Lamarck, 1798 in Portuguese waters. *In*: J. Ros & A. Guerra, eds. *Ecology of Marine Molluscs*, 61(suppl. 2): 87–97.

Pereira, J.M.F., A. Moreno & M.M. Cunha. 1998. Western European squid distribution: A review. *Copenhagen Denmark ICES*, 20 pp.

Pereira, J., R. Rosa, A. Moreno, M. Henriques, J. Sendao & T.C. Borges. 2005. First recorded specimen of the giant squid *Architeuthis* sp. in Portugal. *Journal of the Marine Biological Association of the United Kingdom*, 85(1): 175–176.

Perera, N.M.P. 1975. Taxonomic study of the cephalopods, particularly the Teuthoidea (Squid) and Sepioidea (Cuttlefish) in the water around Sri Lanka. *Bulletin of the Fisheries Research Station, Sri Lanka*, 26: 45–60.

Perez, J.A.A. 2002. Biomass dynamics of the squid *Loligo plei* and the development of a small-scale seasonal fishery off southern Brazil.

Perez, J.A.A. & M. Haimovici. 1993. Cephalopods from the continental slope off southern Brazil. *Atlantica Rio Grande*, 15(1): 49–72.

Perez, J.A.A. & R.K. O'Dor. 1998. The impact of environmental gradients on the early life inshore migration of the short-finned squid *Illex illecebrosus*. *In* A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 293–303.

Perez, J.A.A. & R.K. O'Dor. 2000. Critical transitions in early life histories of short-finned squid, *Illex illecebrosus* as reconstructed from gladius growth. *Journal of Mariane Biological Association of the United Kingdom*, 80(3): 509–514.

Perez, J.A.A. & P.R. Pezzuto. 1998. Valuable shellfish species in the by-catch of shrimp fishery in southern Brazil: Spatial and temporal patterns. *Journal of Shellfish Research*, 17(1): 303–309.

Perez, J.A.A. & P.R. Pezzuto. 2006. Trawl fishing on slope grounds off southeastern and southern Brazill: trends of the national fleet between 2001 and 2003. *Boletim do Instituto de Pesca Sao Paulo*, 32(2): 127–150.

***Perez, J.A.A. & E.G. Vidal.** 1997. Morfologia da desova de *Lolliguncula brevis* (Cephalopoda: Teuthoidea) no litoral catarinense: evidências para um empasse sistemático. *XV Encontro Brasileiro de Malacologia*. 21 a 25 de julho, 1997. *Florianópolis*, SC. p. 49.

Perez, J.A.A., D.C. Aguiar & U.C. Oliveira. 1999. Estrutura e dinamica de pesca artesanal de lulas (Mollusco: Cephalopoda) en Santa Catarina. *Anais do XII Congresso Brasileiro de Engenharia de Pesca, Olinda*, 2: 954–967.

***Perez, J.A.A., D.C. Aguiar de & U.C. Oliveira.** 2002. Biology and population dynamics of long-finned squid *Loligo plei* (Cephalopoda: Loliginidae) in southern Brazilian waters. *Fisheries Research*, 58: 267–279.

Perez, J.A.A., D.C. Aguiar de & J.A.T. dos Santos. 2006. Gladius and statolith as tools for age and growth studies of the squid *Loligo plei* (Teuthida: Loliginidae) off Southern Brazil. *Brazilian Archives of Biology and Technology*, 49(5): 747–755.

Perez, J.A.A., R.S. Martins & R.A. Santos. 2004. Cefalopodes capturados pela pesca comercial de talude no sudeste e sul do Brasil. *Notas-Tecnicas-de-FACIMAR*, 8: 65–74.

Perez, J.A.A., R.K. O'Dor, P. Beck & E.G. Dawe. 1996. Evaluation of gladius dorsal surface structure for age and growth studies of the short-finned squid, *Illex illecebrosus* (Teuthoidea: Ommastrephidae). *Canadian Journal of Fisheries and Aquatic Science*, 53(12): 2837–2846.

Perez-Gandaras, G. & A. Guerra. 1978. Nueva cita de *Architeuthis* (Cephalopoda: Teuthoidea): Descripcion y alimentacion. *Investigacion Pesquera*, 42(2): 401–414.

Perez-Gandaras, G. & A. Guerra. 1989. *Architeuthis* de Sudafrica: nuevas citas y consideraciones biologicas. *Scientia Marina, Barcelona*, 53(1): 113–116.

Perez-Losada, M., A. Guerra & A. Sanjuan. 1999. Allozyme differentiation in the cuttlefish *Sepia officinalis* (Mollusca: Cehpalopoda) from the NE Atlantic and Mediterranean. *Journal of Heredity*, 83: 280–289.

Peristeraki, P., G. Tserpes & E. Lefkaditou. 2005. What cephalopod remains from *Xiphias gladius* stomachs can imply about predator-prey interactions in the Mediterranean Sea? *Journal of Fish Biology*, 66:1–6.

Peristeraki, P., E. Lefkaditou, G. Karamitros & G. Tserpes. 2003. Cephalopod remains from the stomachs of swordfish (*Xiphias gladius* L., 1758) caught in the S. Aegean Sea. *7th Hellenic Symposium on Oceanography and Fisheries*. NCMR p. 180.

Perlov, A.S. 1975. The diet of fur seals in the Kuril Islands area. *Ekologiya*, 4: 106–108.

Pernice, M., D. Destoumieux-Garzón, J. Peduzzi, S. Rebuffat & R. Boucher-Rodoni. 2007. Identification of a *Vibrio* strain producing antimicrobial agents in the excretory organs of *Nautilus polpilius* (Cephalopoda: Nautiloidea). *Reviews in Fish Biology and Fisheries*, 17(2–3): 197–205.

Pertierra, J.P. & P. Sanchez. 2005. Distribution of four cephalopod species along the Catalan coast (NW Mediterranean) using GIS techniques. *Phuket Marine Biological Center Research Bulletin*, 66: 283–289.

Perugini, M., M. Cavaliere, A. Giammarino, P. Mazzone, V. Olivieri & M. Amorena. 2004. Levels of polychlorinated biphenyls and organochlorine pesticides in some edible marine organisms from the Central Adriatic Sea. *Chemosphere*, 57(5): 391–400.

Perugini, M., P. Visciano, M. Manera, G. Turno, A. Lucisano & M. Amorena. 2007. Polycyclic aromatic hydrocarbons in marine organisms from the Adriatic Sea, Italy. *Journal of Agricultural and Food Chemistry*, 55(5): 2049–2054.

Petrie, L. 1992. Oceanographic and biological data relating to short-finned squid (*Illex illecebrosus*), southern Florida, January 1986. *Canadian Data Report – Hydrography and Ocean Science*, 111: 54 pp.

***Pfeffer, G.** 1884. Die Cephalopoden des Hamburger Naturhistorischen Museums. *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*, 8(1): 1–30, 37 figs.

***Pfeffer, G.** 1900. Synopsis der oegopsiden Cephalopoden. *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 17(2): 147–198.

***Pfeffer, G.** 1908a. Teuthologische Bemerkungen. *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 25:289–295.

***Pfeffer, G.** 1908b. Die Cephalopoden. *Nordisches Plankton*, 2(part 9)(4): 9–116, 120 figs.

***Pfeffer, G.** 1912. Die Cephalopoden der Plankton-Expedition. Zugleich eine monographische übersicht der Oegopsiden Cephalopoden. *Ergebnisse der Plankton-Expedition der Humboldt-stiftung*, 2:1–815, 48 pls. (The Cephalopoda of the plankton expedition. *Results of the plankton expedition of the Humboldt Foundation*, Vol. 2 F.a.: 618 pp., 48 pls) [English translation (1993)].

Phillips, K.L., G.D. Jackson & P.D. Nichols. 2001. Predation of myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analysis. *Marine Ecology Progress Series*, 215: 179–189.

Phillips, K.L., G.D. Jackson & P.D. Nichols. 2003a. Temporal variations in the diet of the squid *Moroteuthis ingens* at Macquarie Island: Stomach contents and fatty acid analyses. *Marine Ecology Progress Series*, 256: 135–149.

Phillips, K.L., P.D. Nichols & G.D. Jackson. 2002. Lipid and fatty acid composition of the mantle and digestive gland of four Southern Ocean squid species: implications for food-web studies. *Antarctic Science*, 14(3): 212–220.

Phillips, K.L., P.D. Nichols & G.D. Jackson. 2003a. Dietary variation of the squid *Moroteuthis ingens* at four sites in the Southern Ocean: stomach contents, lipid and fatty acid profiles. *Journal of the Marine Biological Association of the United Kingdom*, 83(3): 523–534.

Phillips, K.L., P.D. Nichols & G.D. Jackson. 2003c. Size-related dietary changes observed in the squid *Moroteuthis ingens* at the Falkland Islands: stomach contents and fatty-acid analyses. *Polar Biology*, 26(7): 474–485.

***Piatkowski, U.** 1989. Macroplankton communities in Antarctic surface waters: spatial changes related to hydrography. *Marine Ecology Progress Series*, 55: 251–259.

Piatkowski, U. 1998. Modern target sampling techniques provide new insights into the biology of early life stages of pelagic cephalopods. *Biologia Marina Mediterranea*, 5(1): 260–272.

***Piatkowski, U.** 2008. Psychroteuthidae Thiele 1920. *Psychroteuthis glacialis* Thiele 1920. Version 28 April 2008 (under construction). http://tolweb.org/Psychroteuthis_glacialis/19783/2008.04.28 in The Tree of Life Web Project, http://tolweb.org/

Piatkowski, U. & R. Diekmann. 2005. A short note on the cephalopods sampled in the Angola Basin during the DIVA–1 expedition. *Organisms-Diversity-and-Evolution*, 5: 227–230 (Supplement 1).

Piatkowski, U. & W. Hagen. (1994). Distribution and lipid composition of early life stages of the cranchid squid *Galiteuthis glacialis* (Chun) in the Weddell Sea, Antarctica. *Antarctic Science*, 6: 235–239.

Piatkowski, U. & V. Hernández-García. 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. *Marine Ecology Progress Series*, 183: 281–294.

Piatkowski, U. & K. Putz. 1994. Squid diet of emperor penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica during late summer. *Antarctic Science,* 6(2): 241–247.

Piatkowski, U. & D.F. Vergani. 2002. The cephalopod prey of southern elephant seals (*Mirounga leonina*) from Stranger Point, King George Island, Antarctica. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. *Bulletin of Marine Science*, 71(2): 1136–1137.

***Piatkowski, U. & W. Welsch.** 1992 [1991]. On the distribution of pelagic cephalopods in the Arabian Sea. *Bulletin of Marine Science*, 49(1–2): 186–198 [Date on title page is 1991; actually published in 1992].

Piatkowski, U. & K. Wieland. 1991. The Boreoatlantic gonate squid *Gonatus fabricii*: occurrence off West Greenland in summer and autumn 1989 and 1990. *ICES Council Meeting*, 1991/K: 55.

Piatkowski, U. & K. Wieland. 1993. The Boreoatlantic gonate squid *Gonatus fabricii*: distribution and size off West Greenland in summer 1989 and in summer and autumn 1990. *Aquatic Living Resources*, 6(2): 109–114.

***Piatkowski, U., V. Hernández-García & M.R. Clarke.** 1998. On the biology of the european flying squid *Todarodes sagittatus* (Lamarck, 1798) (Cephalopoda, Ommastrephidae) in the central eastern Atlantic. *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 375–383.

***Piatkowski, U., G.J. Pierce & M. Morais da Cunha.** 2001a. Impact of cephalopods in the food chain and their interactions with the environment and fisheries: an overview. *Fisheries Research*, 52: 5–10.

Piatkowski, U., K. Putz & H. Heinemann. 2001b. Cephalopod prey of king penguins (*Aptenodytes patagonicus*) breeding at Volunteer Beach, Falkland Islands, during austral winter 1996. *Fisheries Research*, 52: 79–90.

Piatkowski U, P.G. Rodhouse & G. Duhamel. 1991. Occurrence of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Kerguelen Islands in the Indian Ocean sector of the Southern Ocean. *Polar Biology*, 11: 273–275.

***Piatkowski, U., D.F. Vergani & Z.B. Stanganelli.** 2002. Changes in the cephalopod diet of southern elephant seal females at King George Island, during El Niño–La Niña events. *Journal of the Marine Biological Association of the United Kingdom*, 82(5): 913–916.

Piatkowski, U., M. Vecchione & R.E. Young. 2006. Cephalopod diversity along the northern mid-Atlantic Ridge. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 95.

Piatkowski, U., W. Welsch & A. Röpke. 1993. Distribution patterns of the early life stages of pelagic cephalopods in three geographically different regions of the Arabian Sea. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology. Tokai University Press*, 417–431.

Piatkowski, U., M. White & W. Dimmler. (1990) Micronekton of the Weddell Sea: distribution and abundance. *In* W. Arntz, W. Ernst & I. Hempel, eds. The expedition ANTARKTIS VII/4 (Epos leg 3) and VII/5 of RV "Polarstern" in 1989. *Ber Polarforsch*, 68: 73–81.

***Piatkowski, U., P.G. Rodhouse, M.G. White, D.G. Bone & C. Symon.** 1994. Nekton community of the Scotia Sea as sampled by the RMT 25 during austral summer. *Marine Ecology Progress Series*, 112(1–2): 13–28.

Pichon, D., V. Gaia, M. Norman & R. Boucher-Rodoni. 2005a. Phylogenetic diversity of epibiotic bacteria in the accessory nidamental glands of squids (Cephaslopoda: Loliginidae and Idiosepiidae). *Marine Biology*, 147(6): 1323–1332.

***Pichon, D., S. Grigioni, F. Jocelyne & R. Boucher-Rodoni.** 2005b. Symbiotic associations between cephalopods and the *Roseobacter* bacteria strain. *Phuket Marine Biological Center Resaerch Bulletin*, 66: 243–248, 1 fig.

Pierce, G.F. & A. Guerra. 1994 Stock assessment methods used for cephalopod fisheries. *Fishery Research*, 21(1–2): 255–285.

Pierce, G.J. 1995. Stock assessment with a thermometer: Correlation between sea surface temperature and landings of squid (*Loligo forbesi*) in Scotland. *Copenhagen Denmark ICES*, 8 pp.

Pierce, G.J. & P.R. Boyle. 2003. Empirical modelling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. *Fisheries Research*, 59: 305–326.

Pierce, G.J. & M.B. Santos. 1996. Trophic interactions of squid *Loligo forbesi* in Scottish waters. *In*: S.P.R. Greenstreet & M.L. Tasker, eds. Aquatic predators and their prey. *Fishing News Books*, pp. 58–64.

Pierce, G.J., P.R. Boyle & L.C. Hastie. 1992a. The life history of *Loligo forbesi* in the Northeast Atlantic. *Copenhagen Denmark ICES*, 18 pp.

Pierce, G.J., J. Wang & P.R. Boyle. 2002. Cephalopod fishery patterns in the UK and adjacent waters. *Bulletin of Marine Science*, 71(2): 1137.

Pierce, G.J., N. Bailey, Y. Stradoudakis & A. Newton. 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. *ICES Journal of Marine Science*, 55: 14–33.

Pierce, G.J., P.R. Boyle, L.C. Hastie & F.G. Howard. 1992b. The Scottish fishery for *Loligo forbesi*: Current trends. *Copenhagen Denmark ICES*, 1992. 27 pp.

Pierce, G.J., P.R. Boyle, L.C. Hastie & L. Key. 1993a. Population ecology of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Copenhagen Denmark ICES*, 29 pp.

Pierce, G.J., P.R. Boyle, L.C. Hastie & L. Key. 1994a. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fisheries Research*, 21: 17–41.

Pierce, G.J., P.R. Boyle, L.C. Hastie & M.B. Santos. 1994b. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the Northeast Atlantic. *Fisheries Research*, 21(1–2): 149–163.

Pierce, G.J., P.R. Boyle, L.C. Hastie & A.M. Shanks. 1994c. Distribution and abundance of the fished population of *Loligo forbesi* in UK waters: analysis of fishery data. *Fisheries Research*, 21: 193–216.

Pierce, G.J., A. Miller, P.M. Thompson & J.R.G. Hislop. 1991. Prey remains in gray seal (*Halichoerus grypus*) feces from the Moray Firth, north-east Scotland. *Journal of Zoology*, 224: 337–341.

Pierce, G.J., G. Stowasser, L.C. Hastie & P. Bustamante. 2008a. Geographic, seasonal and ontogenetic variation in cadmium and mercury concentrations in squid (Cephalopoda: Teuthoidea) from UK waters. *Ecotoxicology and Environmental Safety*, 70(3): 422–432.

Pierce, G.J., L.C. Hastie, P.R. Boyle, E. Mucklow & A. Linnane. 1993b. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. *Copenhagen Denmark ICES*, 13 pp.

*****Pierce, G.J., L.C. Hastie, A. Guerra, R.S. Thorpe, F.G. Howard & P.R. Boyle.** 1994d. Morphometric variation in *Loligo forbesi* and *Loligo vulgaris*: Regional, seasonal, sex, maturity and worker differences. *Fisheries Research*, 21(1–2): 127–148.

Pierce, G.J., M.A. Collins, M.M. Cunha, A. Guerra, U. Piatkowski, F. Porteiro & J.P. Robin. 1995b. Correlation analysis of inter-annual variation in cephalopod landings from European waters. *ICES Council Meeting., 1995/K: 22.*

Pierce, G.J., L.N. Key, P.R. Boyle, K.J. Siegert, J.M. Goncalves, F.M. Porteiro & H.R. Martins. 1999. RNA concentration and the RNA to protein ratio in cephalopod tissues: sources of variation and relationship with growth rate. *Journal of Experimental Marine Biology and Ecology*, 237(2): 185–201.

Pierce, G.J., C.D. MacLeod, G. Stowasser, T. Valinassab, M.B. Santos, J. Wang & I. Tuck. 2006. The protection for future breeding stocks – modelling spawning areas of the squid *Loligo forbesi*. *Tasmania, CIAC Meeting*, p. 63.

Pierce, G.J., J. Wang, X. Zheng, J.M. Bellido, P.R. Boyle, V. Denis & J.P. Robin. 2001. A cephalopod fishery GIS for the Northeast Atlantic: development and application. *International Journal of Geographical Information Science*, 15: 763–784.

Pierce, G.J., R.S. Thorpe, L.C. Hastie, A.S. Brierley, A. Guerra, P.R. Boyle, R. Jamieson & P. Avila. 1994e. Geographic variation in *Loligo forbesi* in the Northeast Atlantic Ocean: Analysis of morphometric data and tests of causal hypotheses. *Marine Biology*, 119: 541–547.

*****Pierce, G.J., V.D. Valavanis, A. Guerra, P. Jereb L. Orsi-Relini, J.M. Bellido, I. Katara, U. Piatkowski, J. Pereira, E. Balguerias, I. Sobrino, E. Lefkaditou, J. Wang, M. Santurtun, P.R. Boyle, L. Hastie, C.D. Macleod, J. Smith, M. Via, A.F. Gonzalez & A. Zuur.** 2008b. A review of cephalopod-environment interactions in European Seas. *Hydrobiologia*, 612: 49–70.

Pierce, S.K., G.N. Smith, T.K. Maugel & E. Clark. 1995a. On the giant Octopus (*Octopus giganteus*) and the Bermuda blob: homage to A.E. Verrill. *Biology Bulletin*, 188: 219–230.

Pinchukov, M.A. 1983. Spatial isolation of the intraspecific groups of *Sthenoteuthis oualaniensis* (Lesson). *In*: Ya.I. Starobogatov & K.N. Nesis, eds. Taxonomy and Ecology of Cephalopods. *Leningrad: Zoological Institute of the Academy of Sciences USSR Publication*, pp. 91–92 (In Russian).

Pinchukov, M.A. 1989. Oceanic squids. *In*: N.V. Parin & N.P. Novikov, eds. Biological Resources of the Indian Ocean. *Moscow: Nauka Publication*, pp. 186–194 (In Russian).

Pinchukov, M.A. 2002. Vertical migration and distribution of the purple-back squid in the Indian Ocean. *In*: B.G. Ivanov & Ch.M. Nigmatullin, eds. *VI All-Russian Conference on Commercial Invertebrates* (3–6 September 2002, Kaliningrad-Lesnoe). Theses of Reports. *Moscow: VNIRO Publication*, pp. 161–164 (In Russian).

Pinchukov, M.A. & L.M. Makarova. 1984. Feeding and helminth fauna of the demersal squid *Doryteuthis singhalensis* in the western part of the Indian Ocean. *Malacological Review*, 17: 130.

***Pineda, S.E., A. Aubone & N.E. Brunetti.** 1996. Identificacion y morfometria comparada de las mandibulas de *Loligo gahi* y *Loligo sanpaulensis* (Cephalopoda, Loliginidae) del Atlantico sudoccidental. *Revista de Investigación y Desarrollo Pesquero*, 10: 85–99.

***Pineda, S.E., N.E. Brunetti & N. Scarlato.** 1998a. *Calamares loliginidos* (Cephalopoda, Loliginidae) . *In*: E.E. Boschi, ed. The Argentine Sea and its fisheries resources. Vol 2. Molluscs of interest for fisheries. Culture and reproductive strategies of bivalves and echinoids. *Mar del Plata, Argentina, INIDEP: Instituto Nacional de Investigacion y Desarrollo Pesquero*, 13–36.

***Pineda, S.E., D.R. Hernandez & N.E. Brunetti.** 1998b. Statolith comparison of two south-west Atlantic loliginid squid: *Loligo sanpaulensis* and *Loligo gahi*. *In*: A.I.L. Payne, M.R. Lipinski & M.A.C. Roeleveld, eds. Cephalopod Biodiversity, Ecology and Evolution. *South African Journal of Marine Science*, 20: 347–354.

***Pineda, S.E., D.R. Hernandez, N.E. Brunetti & B. Jerez.** 2002. Morphological identification of two southwest Atlantic loliginid squids: *Loligo gahi* and *Loligo sanpaulensis*. *Revista de Investigación y Desarrollo Pesquero*, 15: 67–84.

Pitman, R.L., W.A. Walker, W.T. Everett & J.P. Gallo-Reynoso. 2004. Population status, foods and foraging of Laysan albatrosses *Phoebastria immutabilis* nesting on Guadalupe Island, Mexico. *Marine Ornithology*, 32(2): 159–165.

Podesta, G.P. 1990. Migratory pattern of the Argentina hake *Merluccius hubbsi* and oceanic processes in the southwestern Atlantic Ocean. *Fishery Bulletin*, 88: 167–177.

Polezhaev, A.N. 1986. Oceanic squids of the southern part of the Pacific Ocean. *Zoologicheskij Zhurnal*, 65 (7): 994–1002 (In Russian with English abstract).

Pomeroy, C. 1998. The human dimension: The missing link in California's fishery management? *In*: O.R. Magoon, H. Converse, B. Baird & M. Miller Henson, eds. Taking a Look at California's Ocean Resources: An Agenda for the Future. *American Society of Civil Engineers,* Reston, VA USA, 1: 856 pp.

Pomeroy, C. & M. Fitzsimmons. 1998. Information needs for effective management of the California market squid fishery: The role of social science research. *Reports of California Cooperative Oceanic Fisheries Investigations*, 39: 108–116.

Pon, J.P.S. & P.A. Gandini. 2007. Bycatch of the piked dogfish *Squalus acanthias* Linne, 1758 (*Chondrichthyes squalidae*) in semi-pelagic longline fisheries at Patagonian Shelf. *Investigaciones marinas*, 35(1): 85–88.

Porteiro, F.M. 1992. The present status of squid fishery in the Azores archipelago. *Copenhagen Denmark ICES*, 11 pp.

Porteiro, F.M. 1994. The present status of the squid fishery (*Loligo forbesi*) in the Azores Archipelago. *Fisheries Research*, 21(1–2): 243–253

Porteiro, F.M. & H.R. Martins. 1988. Some observations on the behaviour of adult *Loligo forbesi* in captivity. *Copenhagen Denmark ICES*, 15 pp.

Porteiro, F. & H.R. Martins. 1992. First finding of natural laid eggs from *Loligo forbesi* Steenstrup, 1856 (Mollusca: Cephalopoda) in the Azores. *Arquipelago*, 10: 119–120.

Porteiro, F.M. & H.R. Martins. 1994. Biology of *Loligo forbesi* Steenstrup, 1856 (Mollusca: Cephalopoda) in the Azores: sample composition and maturation of squid caught by jigging. *Fisheries Research*, 21: 103–114.

Porteiro, F.M., H.R. Martins & R.T. Hanlon. 1990. Some observations on the behaviour of adult squids, *Loligo forbesi*, in captivity. *Journal of the Marine Biological Association of the United Kingdom,* 70: 459–472.

Porteiro, F.M., Goncalves, J.M., Cardigos, F. & Martins, H.R. 1995a. The Azorean squid *Loligo forbesi* (Cephalopoda: Loliginidae) in captivity: reproductive behaviour. *Copenhagen Denmark ICES*, 9 pp.

Porteiro, F.M., J.M. Goncalves, F. Cardigos, P. Martins & H.R. Martins. 1995b. The Azorean squid *Loligo forbesi* (Cephalopoda: Loliginidae) in captivity: feeding and growth. *Copenhagen Denmark ICES*, 12 pp.

Portela, J.M. & M. Rasero. 1998. Daily feeding pattern of Patagonian squid *Loligo gahi* in Falkland-Malvinas Islands waters. *Copenhagen Denmark ICES*, 11 pp.

Portela, J., M. Sacau, J. Wang, G.J. Pierce, M.B. Santos & X. Cardoso. 2005. Variability in the abundance of the Argentine squid *Illex argentinus* in relation to environmental conditions on the high seas of the Patagonian Shelf. *ICES Council Meeting documents Copenhagen*, No. 2005/O: 16.

Portela, J., M. Sacau, X. Cardoso, J.R. Fuertes, E. Ulloa, V. Tato & M. Otero. 2005. Analysis of the fishing strategy of the Spanish bottom trawl feet operating on the high seas off the SW Atlantic. *ICES Council Meeting Documents. Copenhagen*. No 2005.

Portela, J., A. Arkhipkin, S. Hill, E. Ulloa, B. Santos, V. Tato, J.M. Bellido, D. Middleton, D. Agnew & J. Wang. 2002. Overview of the Spanish fisheries in the Patagonian Shelf. *ICES Council Meeting Documents*.

Portman, A. & A.M. Bidder. 1928. Yolk absorption in *Loligo* and the function of the embryonic liver and pancreas. *Quarterly Journal of Microscopical Science*, 72: 301–324.

Pörtner, H.O., D.M. Webber, R.G. Boutilier & R.K. O'Dor. 1991. Acid-base regulation in exercising squid (*Illex illecebrosus*, *Loligo pealei*). *American Journal of Physiology*, 261(1): R239–R246.

Pörtner, H.O. & S. Zielinski. 1998. Environmental constraints and the physiology of performance in squids. *In* A.I.L. Payne, M.R. Lipinski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod Biodiversity, Ecology and Evolution. *South African Journal of Marine Science*, 20: 207–221.

Posada, C. & C.B. Garcia. 2006. Diet of *Elagatis bipinnulata* (Quoy y Gaimard) (Carangidae) from Taganga Bay and Tayrona Natural National Park, Colombia, Caribbean Sea. Proceedings of the Gulf and Caribbean. *Fisheries Institute*, 57: 1030–1031.

***Posselt, H.I.** 1891. *Todarodes sagittatus* (Lmk.) Stp., En anatomisk studie med Bemaerkinger om Slaegtskabsforholdet mellem Ommatostrephfamiliens Genera. *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobenhavn*, 1890: 301–359.

Potelov, V., K.T. Nilssen, V. Svetochev & T. Haug. 1997. Feeding habits of harp *Phoca groenlandica* and hood seals *Cystophora cristata* during molt (April to June) in the Greenland Sea. *NAMMCO*, SC/5/ME/8.

Potelov, V., K.T. Nilssen, V. Svetochev & T. Haug. 2000. Feeding habits of harp (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) during late winter, spring and early summer in the Greenland Sea. *North Atlantic Marine Mammal Commission*, 2: 40–49.

Powell, E.N., A.J. Bonner & E.A. Bochenek. 2003a. Vessel time allocation in the US *Illex illecebrosus* fishery. *Fisheries Research (Amsterdam)*, 61(1–3): 35–55.

Powell, E.N., S.E. King & A.J. Bonner. 2005. Determinants of temporal trends in size in vessel-based reporting in the USA *Illex illecebrosus* fishery. *Journal of Applied Ichthyology*, 21(3): 184–197.

Powell, E.N., A.J. Bonner, R. Mann & S.E. Banta. 2003b. Evaluation of real-time catch and effort reporting in the US *Illex illecebrosus* fishery. *Journal of Northwest Atlantic Fishery Science*, 32: 39–55.

Powell, E.N., A.J. Bonner, B. Muller & E.A. Bochenek. 2004. Assessment of the effectiveness of scup bycatch-reduction regulations in the *Loligo* squid fishery. *Journal of Environmental Management*, 71(2): 155–167.

Prafulla, V., L. Francis & P.T. Lakshmanan. 2000. Effect of different methods of icing on the quality of squid and cuttlefish during storage. *Fishery Technology Society of Fisheries Technologists India Kochi*, 37(2): 81–88.

Prafulla, V., L. Francis & P.T. Lakshmanan. 2001. Concentrations of trace metals in the squids, *Loligo duvauceli* and *Doryteuthis sibogae* caught from the southwest coast of India. *Asian Fisheries Science*, 14(4): 399–410.

Prenski, L.B. & V. Angelescu. 1993. Ecologia trofica de la merluza comun (*Merluccius herbbsi*) del mar Argentino. Parte 3. Consumo annual de alimento a nivel poblacional y su relacion con la explotacion de las pesquerias multiespecificas. *Inidep Documento Cientifico 1*, Mar del Plata, Republica Argentina, xiv + 118 pp.

Preti, A., S.E. Smith & D.A. Ramon. 2001. Feeding habits of the common thresher shark (*Alopias vulpinus*) sampled from the California-based drift gill net fishery, 1998–1999. *Reports of California Cooperative Oceanic Fisheries Investigations*, 42: 145–152.

Preti, A., S.E. Smith & D.A. Ramon. 2005. Diet differences in the thresher shark (*Alopias vulpinus*) during transition from a warm-water regime to a cool-water regime off California-Oregon, 1998–2000. *Cooperative Oceanic Fisheries Investigations*, 45: 118–125.

Preuss, T. & W.F. Gilly. 2000. Role of prey-capture experience in the development of the escape response in the squid *Loligo opalescens*: a physiological correlate in an identified neuron. *Journal of Experimental Biology*, 203(3): 559–565.

Prinngennies, D. & J.M. Jorgensen. 1994. Morphology of the luminous organ of the squid *Loligo duvaucelii* d'Orbigny, 1839. *Acta Zoologica, Stokholm*, 75: 305–309.

***Prinngennies, D., M. Murdjani, S. Sastrodihardjo & N.R. Nganro.** 2000. A first attempt at culturing the squid *Loligo duvaucelii* Orbigny, 1835 in Indonesia. Pp. 87–188, *In*: J. Hylleberg, ed. Proceedings of the 10th International Congress and Workshop of the Tropical Marine Mollusc Programme (TMMP), 20–30 October 1999, 21(1).

Prinngennies, D., S. Sastrodihardjo, N.R. Nganro & I.N. Aryantha. 2001. Bacterial symbionts in the luminous organ of the squid, *Loligo duvauceli*, and cuttlefish, *Sepia* sp. In: J. Hylleberg, ed., Proceedings of the 11th International Congress and Workshop of the Tropical Marine Mollusc Programme (TMMP), 28 September–8 October 2000, 25: 145–148.

***Prosch, V.** 1847. Nogle nye Cephalopoder, beskrevne og Anatomisk undersogte. *Kongelige Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk*, (series 5)1[1849]:53–72, 7 figs [Separates, 20 pp., dated 1847].

Pshenichnov, L.K. 1994. Some peculiarities in the Patagonian toothfish *Dissostichus eleginoides* (Notothenidae) biology in the area of the Kerguelen Islands (Sub-Antarctica, Indian Ocean). *In*: V.N. Yakovlev, ed. *Main results of YugNIRO complex research in the Azov Black Seas Region and the World Ocean in 1993, Kerch, Yugoslavia NIRO*, 40: 78–83.

Puetz, K., R.I. Ingham, J.I. Smith & J.I. Croxall. 2001. Population trends, breeding success and diet composition of gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rockhopper *Eudyptes chrysocome* penguins in the Falkland Islands. *A review. Polar Biology*, 24(11): 793–807.

Pulcini, M., R. Carlini & M. Wurtz. 1992. Stomach contents of striped dolphins, *Stenella coeruleoalba*, (Meyen, 1933) from the south-central Tyrrhenian coast. European Research on Cetaceans. *In* P.G.H. Evans, ed. Proc. of 6th conf. of European Cetacean Society, Sandefjord, 6: 194–195.

Pusineri, C., V. Magnin, L. Meynier, J. Spitz, S. Hassani & V. Ridoux. 2007. Food and feeding ecology of the common dolphin (*Delphinus delphis*) in the oceanic northeast Atlantic and comparison with its diet in neritic areas. *Marine Mammal Science*, 23(1): 30–47.

Qian, W., X. Chen & M. Sun. 2005. Comparison of illumination distribution underwater between two kinds of fish aggregating lamps. *Journal of Fishery Sciences of China*, 12(2): 173–178.

Qiu, S., X. Wang, Y. Ge & W. Cai. 1995. Distribution and migration of the common squid *Todarodes pacificus* in the Yellow Sea. *Chinese Journal of Oceanology and Limnology*,13(1): 78–85.

Qiu, X. 1986. Studies on the biological characteristics of squid (*Loligo japonica*) and its resources in the Yellow Sea. *Mar. Fisheries Research*, (7): 109–119.

Quetglas, A. & B. Morales-Nin. 2004. Age and growth of the ommastrephid squid *Todarodes sagittatus* western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 84: 421–426.

***Quetglas, A., A. Carbonell & P. Sanchez.** 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (North Western Mediterranean). Biological aspects of some deep-sea species. *Estuarine and Coastal Shelf Science*, 50(6): 739–749.

***Quetglas, A., F. Alemany, A. Carbonell & P. Sanchez.** 1999a. First record of *Cranchia scabra* Leach, 1817 (Cephalopoda: Cranchiidae) in the Mediterranean Sea. *Bollettino Malacologico*, 35(1–4): 1–2.

***Quetglas, A., F. Alemany, A. Carbonell, P. Merella & P. Sanchez.** 1998. Some aspects of the biology of *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) from the Balearic Sea (Western Mediterranean). *Scientia Marina*, 62(1–2): 73–82.

Quetglas, A., F. Alemany, A. Carbonell, P. Merella & P. Sanchez. 1999b. Diet of the European flying squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) in the Balearic Sea (western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, 79(3): 479–486.

*__Quetglas, A., K. Fliti, E. Massuti, W. Refes, B. Guijarro & S. Zaghdoudi.__ 2006. First record of *Taningia danae* (Cephalopoda: Octopoteuthidae) in the Mediterranean Sea. *Scientia Marina (Barcelona)*, 70(1): 153–155.

*__Quoy, J.R. & J.P. Gaimard.__ 1824–1826. Zoologie. *In*: Louis de Freycinet. Voyage autour du Monde....execute sur les corvettes de S.M. L'Uranie et la Physicienne, pendant les annees 1817, 1818, 1819, et 1820. 712 pp., atlas of 96 pls. Paris. [See Sherborn and Woodward (1901:392) for dates of publication].

*__Quoy, J.R. & J.P. Gaimard.__ 1832. Voyage de decouvertes de l'Astrolabe pendant les annees 1826–1827–1828–1829. *Zoologie*, 2(1): 1–320, Atlas of 93 pls [1833] [77, pl. 4 fig. 1].

Radchenko, V.I. 1992. The role of squids in the pelagic ecosystem of the Bering Sea. *Okeanologiya (Russian Journal of Oceanology)*, 32(6): 1093–1101 (In Russian).

Ragonese, S. & M.L. Bianchini. 1990. Oceanic squid jigging in the Sicilian Channel: Potential and drawbacks. *Quaderni dell'Istituto di Idrobiologia e Acquicoltura 'G. Brunelli'*, 10: 65–79.

Ragonese, S. & Jereb, P. 1986. *Loligo forbesi* Steenstrup 1856 (Cephalopoda: Loliginidae) nel versante Siciliano del Mare Pelagico (Canale di Sicilia): nota preliminare sulla Distribuzione, Composizione per Taglia e Biologia Riproduttiva. *Nova Thalassia*, 8(Suppl. 3): 529–535.

Ragonese S. & P. Jereb. 1990. Sulla teutofauna di interesse commerciale del Canale di Sicilia. *Oebalia*, 16(2): 745–748.

Ragonese, S. & P. Jereb. 1992. Length-weight relationships of *Illex coindetii* Verany, 1839 (Mollusca: Cephalopoda) in the Sicilian Channel. *Oebalia*, Vol. XVIII, N.S., 17–24.

Rahim, S.V.M.A. & M.R. Chandran. 1984a Studies on the reproductive biology of the warm water squid *Loligo duvaucelii* D'Orbigny. 1. Functional morphology of male reproductive system. *Journal of the Marine Biological Association of India, 26(1–2): 71–79.*

Rahim, S.V.M.A. & M.R. Chandran. 1984b. Studies on the reproductive biology of the warm water squid *Loligo duvaucelii* D'Orbigny. 2. Histology of the testis. *Journal of the Marine Biological Association of India*, 26(1–2): 80–82.

Rahim, S.V.M.A. & M.R. Chandran. 1995. The reproductive biology of the warm water squid *Loligo duvauceli* D' Orbigny: 3. Formation of spermatophore. *Journal of the Marine Biological Association of India*, 36(1–2): 267–275.

Railko, P.P. 1979 Distribution and biology of the Kommander squid *Berryteuthis magister* (Cephalopoda, Gonatidae) in the Sea of Japan. *USSR Academy of Sciences Zoological Institute Sixth Meeting on the Investigations of Molluscs*, 1979: 182–183 [in Russian].

Railko, P.P., Y.A. Fedorets, V.D. Didenko & N.E. Kravchenko. 1996. Estimation of age and growth of the squid *Berryteuthis magister* from the western Bering Sea. *Ecology of Nekton, Nektobenthos and Plankton of the far eastern seas. TINRO*, 119: 224–233.

Rajabipour, F., T. Valinasab & S. Gilkolaei. 2001. Identification of different species of squids in Oman Sea (Iranian waters). *Iranian Journal of Fisheries Sciences*, 3(2): 63–72.

Rajabipour, F. & N. Mashaii. 2002. The Indian squid, *Loligo duvauceli*, Orbigny 1848, as a trawl by-catch in offshore fisheries in Iranian waters of Oman Sea. *Southern African Marine Science Symposium (SAMSS 2002).*

Rajagopalsamy, C.B.T., G.I. Jasmine, G. Sugumar & P. Jeyachandran. 2002. Quality characteristics of freeze dried Indian white squid (*Loligo duvauceli* Orbigny). *Journal of Food Science and Technology (Mysore)*, 39(4): 410–412.

Raksakulthai, R. & N. Haard. 1988. Contribution of cathepsin C to the fermentation of fish sauce prepared from capelin (*Mallotus villosus*) and squid hepatopancreas. *Twelfth Annual Conference of Tropical and Subtropical Fisheries Technological Society of the Americas*, Florida University, pp. 658–670.

Raksakulthai, R. & N.F. Haard. 2001. Purification and characterization of a carboxypeptidase from squid hepatopancreas (*Illex illecbrosus*). *Journal of Agricultural and Food Chemistry*, 49(10): 5019–5030.

Raksakulthai, R., M. Rosenberg & N.F. Haard. 2002. Accelerated cheddar cheese ripening with an aminopeptidase fraction from squid hepatopancreas. *Journal of Food Science*, 67(3): [np] Apr.

Ramachandran, A. 1987. Cephalopod resources, potential and utilisation in India. *Seafood Export Journal*, 19: 22–26.

Ramirez, R. & T.A. Klett. 1985. Size composition of the giant squid catch from the Gulf of California during 1981. *Transactions CIBCASIO*, 10: 124–137.

*__Rancurel, P.__ 1970. The stomach contents of *Alepisaurus ferox* in the southwest Pacific (Cephalopoda). *Cahiers ORSTOM, Séries Océanographique*, 8(4): 3–88.

Rancurel, P. 1971. *Mastigoteuthis grimaldii* (Joubin, 1895) a little known member of the Chiroteuthidae from the tropical Atlantic (Cephalopoda-Oegopsida). *Cahiers ORSTOM Séries Océanographique*, 9(2): 124–145.

***Rancurel, P.** 1972. *Mastigoteuthis inermis*, n.sp. of Chiroteuthidae from Gulf of Guinea. *Bulletin of Society of Zoology*, 97(1): 25–34.

***Rancurel, P.** 1973a. *Mastigoteuthis hjorti* Chun 1913, description of three specimens from the Gulf of Guinea (Cephalopoda-Oegopsida). *Cahiers ORSTOM Séries Océanographique*, 11(1): 27–32.

Rancurel, P. 1973b. On some cephalopod mandibles from the stomach of a tiger-shark. *Cahiers ORSTOM Séries Océanographique*, 11(3): 359–366.

Rancurel, P. 1976a. Note sur les Cephalopodes des contenus stomacaux de *Thunnus albacores* (Bonnaterre) dans le sud-ouest Pacifique. *Cahiers O.R.S.T.O.M. series Océanographique*, 14(1): 71–80.

***Rancurel, P.** 1976b. Presence dans le sud-ouest Pacifique du calmar geant *Ommastrephes caroli* Furtado, 1887 (Cephalopoda, Oegopsida) et description du male. *Cahiers ORSTOM Séries Océanographique*, 14 (1): 81–96.

***Rancurel, P. & T. Okutani.** 1990. A new species of squid genus *Onychoteuthis* from the southwest Pacific. *Venus Japanese Journal of Malacology*, 49(1): 25–30.

Randall, R.M., B.M. Randall & E.W. Klingelhoeffer. 1981. Species diversity and size ranges of cephalopods in the diet of jackass penguins from Algoa Bay, South Africa. *South African Journal of Zoology*, 16(3): 163–166.

Rang, M.S. 1837. Documents pour servir a l'histoire naturelle des Cephalopodes crypyobranches. *Magasin de Zoologie*, (Cl.V.): 1–77.

Rao, G.S. 1988. Biology of inshore squid *Loligo duvaucelii* Orbigny, with a note on its fishery off Mangalore. *Indian Journal of Fisheries*, 35: 121–130.

Rao, K.V. 1954. Biology and fishery of the Palk-bay squid, *Sepioteuthis arctipinnis* Gould. *Indian Journal of Fisheries*, 1: 37–66.

Rao, K.V. 1973. Distribution pattern of the major exploited marine fisheries resources of India. Proceedings of the Symposium on Living Resources of the Seas around India, Central Marine Fisheries Research Institute, CMFRI, 1968. *CMFRI Special Publication*, 18–101.

Rasero, M. 1994. Relatioship between cephalopod abundance and upwelling: the case of *Todaropsis eblanae* in Galician waters (NW Spain). *ICES Council Meeting*, 1994/K:20, 3pp.

Rasero, M. & B.G. Castro. 1995. Signs of prey-size selectivity in the feeding behaviour of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae). *ICES Copenhagen Denmark*, 7 pp.

Rasero, M. & J.M. Portela. 1996. Occurence of mated females of *Loligo gahi* (Cephalopoda: Loliginidae) in the trawling fishery around the Falkland Islands: Implications for the fishery and the life cycle. *ICES Council Meetings Documents*.

Rasero, M. & J.M. Portela. 1998. Relationships between mating and sexual maturation of *Loligo gahi* females in Falkland waters. *Journal of the Marine Biological Association of the United Kingdom*, 78: 673–676.

Rasero, M., A.F. Gonzalez & A. Guerra. 1993. First record of *Ancistroteuthis lichtensteini* (Cephalopoda, Onychoteuthidae) in the European Atlantic waters. *Scientia Marina Barcelona*, 57(1): 91–94.

Rasero, M., A.F. Gonzalez & A. Guerra. 1995. Spawning pattern and fecundity of the ommastrephid squid *Todaropsis eblanae* in northeastern Atlantic waters. *ICES Copenhagen Denmark*, 18 pp.

***Rasero, M., A.F. Gonzalez, B.G. Castro & A. Guerra.** 1996. Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Illex coindetii* (Cephalopoda: Ommastrephidae) in Galician waters. *Journal of the Marine Biological Association of the United Kingdom*, 76: 73–87.

Rasero, M., E. Roman, J.M. Portela & J.A. Cardoso. 2001. A contribution to the knowledge of the cephalopod fauna of Svalbard Islands. *Theme Session on the Response of Cephalopod Populations and Fisheries to Changing Environment and Ecosystems – ICES.*

Rathjen, W.F. 1983. Present status of North American squid fisheries. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Proceedings of the workshop on the biology and resource potential of cephalopods. Memoirs of National Museum Victoria*, 44: 255–260.

***Rathjen, W.F.** 1984. Squid fishing techniques. *Gulf and South Atlantic Fisheries Development Foundation*, 15 pp.

*__Rathjen, W.F.__ 1992 [1991]. Cephalopod capture methods: an overview. *Bulletin of Marine Science*, 49: 494–505.

Rathjen, W.F. & G.L. Voss. 1987. The cephalopod fisheries: a review. *In*: P.R. Boyle, ed. *Cephalopod Life Cycles, Vol. II Comparative Reviews, Academic Press, London*, pp. 253–275.

*__Rathke, H.__ 1833. Perothis, ein neues genus der Cephalopoden. Mémoires présentes a l'Academie Imperiale des Sciences de St. Petersbourg par divers Savans, 2(1/2):149–175, 18 figs in 2 pls. [Separate date, 1833; volume date, 1835].

Raya, C.P. 2001. Determinación de la edad y estudio del crecimiento del choco (*Sepia hierredda* Rang, 1837), el calamar (*Loligo vulgaris* Lamarck, 1798) y el pulpo (*Octopus vulgaris* Cuvier, 1797) de la costa Noroccidental Africana. Ph.D.. Thesis, Universidad de La Laguna, 192 pp.

Raya, C.P., E. Balguerias, M.M. Fernández-Nuñez & G.J. Pierce. 1995. Maturation pattern and recruitment of the squid *Loligo vulgaris* from north west African coast. *ICES Copenhagen Denmark*, 11 pp.

Raya, C.P., E. Balguerias, M.M. Fernández-Núñez & G.J. Pierce. 1999. On the reproduction and age of the squid *Loligo vulgaris* from the Saharan Bank (northwest African coast). *Journal of the Marine Biological Association of the United Kingdom*, 79: 111–120.

Ré, M.E., P.J. Baron & J.C. Beron. 1996. *Architeuthis* sp. Steenstrup 1857 (Mollusca, Cephalopoda) from Bustamante Bay, Argentine Patagonia. *Naturalia Patagonica Ciencias Biologicas*, 4(1–2): 161–165.

Ré, M.E., P.J. Baron & L. Kuba. 2002. *Ommastrephes bartramii* (Le Sueur, 1821) and *Todarodes filippovae* Adam, 1975 (Cephalopoda, Ommastrephidae): Coastal records in Argentina. *Bulletin of Marine Science*, 71(2): 1095–1098.

Ré, M.E., P.J. Baron, J.C. Beron, A.E. Gosztonyi, L. Kuba, M.A. Monsalve & N.H. Sardella. 1998. A giant squid *Architeuthis* sp. (Mollusca, Cephalopoda) stranded on the Patagonian shore of Argentina. *In*: Payne, A.I., M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 109–122.

Recksiek, C.W. 1978. California's market squid. *Pacific Discovery, California Academy of Science, San Francisco*, 31(6): 19–27.

Recksier, C.W. & J. Kashiwada. 1979. Distribution of larval squid, *Loligo opalescens*, in various nearshore locations. *Reports of California Cooperative Oceanic Fisheries Investigations*, 20: 31–34.

*__Rees, W.J. & G.E. Maul.__ 1956. The cephalopoda of Madeira. Records and distribution. *Bulletin of the British Museum (Natural History), Zoology*, 3(6): 257–281.

*__Rehder, H.A.__ 1945. A new genus and species of squids from the Philippines. *Proceedings of the Biological Society of Washington*, 58:21–26, 1 pl.

*__Reichow, D. & M.J. Smith.__ 1999. Highly variable microsatellites in the California market squid *Loligo opalescens*. *Marine Biotechnology*, 1(4): 403–406.

*__Reichow, D. & M.J. Smith.__ 2001. Microsatellites reveal high levels of gene flow among populations of the California squid *Loligo opalescens*. *Molecular Ecology*, 10(5): 1101–1109.

Reid, S.B., J. Hirota, R.E. Young & L.E. Hallacher. 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Marine Biology*, 109: 427–440.

Reijnders, P., S. Brasseur, J. van der Toorn, P. van der Wolf, I. Boyd, J. Harwood, D. Lavigne & L. Lowry. 1993. Seals, fur seals, sea lions and walrus. *Gland*, Switzerland, IUCN.

Reiss, C.S., M.R. Maxwell, J.R. Hunter & A. Henry. 2005. Investigating environmental effects on population dynamics of *Loligo opalescens* in the southern California Bight. *Reports of California Cooperative Oceanic Fisheries Investigations*, 45: 87–97.

Relini G. & L. Orsi Relini. 1984. The role of cephalopods in the inshore trawl fishing of the Ligurian Sea. *Oebalia*, 10: 37–58.

Relini, G., C. De Rossi, T. Piano & A. Zamboni. 2002. Osservazioni sui cefalopodi dei fondi strascicabili liguri. *Biologia Marina Mediterranea*, 9(1): 792–795.

*__Ren, Y.P., B.D. Xu, Z.J. Ye & Y.G. Liu.__ 2005. Preliminary study on community structure of fishery resources during spring and autumn in the coastal waters of Qingdao. *Periodical of Ocean University of China*, 35(5): 792–798.

Replinger, S.E. & J.B. Wood. 2007. A preliminary investigation of the use of subcutaneous tagging in Caribbean reef squid *Sepioteuthis sepioidea* (Cephalopoda: Loliginidae). *Fisheries Research (Amsterdam)*, 84(3): 308–313.

Restuccia, V. & S. Ragonese. 1986. Cefalopodi dei fondali strascicabili della Sicilia nord occidentale. Nota preliminare. *Nova Thalassia*, 8(Suppl.3): 543–549.

Reunreng, A. 2005. Performance of simple large-scale cephalopod culture system in Thailand. *Phuket Marine Biological Center Research Bulletin*, No. 66: 337–350, 2 figs.

Rey, I., O. Soriano, B.A. Dorda, A.F. Gonzalez, F. Rocha & A. Guerra. 2006. First Cytochrome C Oxidase I and 16S RNA genes partial sequences and phylogenetic relationships in the hooked giant squid *Taningia danae*. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 95.

***Reynaud, A.** 1831. L'Onychotheute de Fleury, pages 61–62, pl. 17. In: R.P. Lesson, Centurie Zoologique ou choix d'animaux rares, nouveaux ou imparfaitement connus. 244 pp., Paris: F.G. Levrault.

Reznik, Y.I. 1983. General morphology of reproductive system in *Berryteuthis magister*. In: Systematics and Ecology of Cephalopod Mollusks. *Leningrad, Nauka press*, p. 64–66.

Ria, M., C. Rustighi, M. Casotti, R. Silvestri & R. Baino. 2005. Note sulla distribuzione e biologia di *Loligo vulgaris* e *Loligo forbesi* nelle acque toscane. *Biologia Marina Mediterranea*, 12: 575–579.

Ribeiro, P. & J.P. Andrade. 2000. Feeding dynamics of swordfish (*Xiphias gladius*) in the Azores area. *Collective Volume of Scientific Papers ICCAT*, 51(1): 1642–1657.

***Riddell, D.J.** 1985. The Enoploteuthidae (Cephalopoda: Oegopsida) of the New Zealand region. *Fisheries Research Bulletin*, 27: 52 pp.

Ringelstein, J, C. Pusineri, S. Hassani, L. Meynier, R. Nicolas & V. Ridoux. 2006. Food and feeding ecology of the striped dolphin, *Stenella coeruleoalba*, in the oceanic waters of the north-east Atlantic. *Journal of the Mrine Biological Association of the United Kingdom*, 86(4): 909–918.

***Risso, A**. 1854. Mollusques Céphalopodes vivants observés dans les parage mediterraneen du Comte de Nice. 81 pp., 33 pls, Nice.

Ritchie, J. 1920. Shoals of squids in the Firth of Forth. *Scottish. Naturalist*, 101–102: 93–94.

Rivard, D., L.C. Hendrickson & F.M. Serchuk. 1998. Yield estimates for short-finned squid (*Illex illecebrosus*) in SA 3–4 from research vessel survey relative biomass indices. *Science Council Research Document NAFO*, 98/75, 4 pp.

Robaina, G. 1993. Reproductive potential, time and space distribution of the spawning of the tropical squid, *Sepioteuthis sepioidea* at Mochima Bay, Venezuela. *Memorias de la Sociedad de Ciencias Naturales "La Salle"*, 53(139): 5–21.

***Robaina, G. & J.F. Voglar.** 1986. Sexual maturation of the *Sepioteuthis sepioidea* (Blainville, 1823) females (Cephalopoda, Loliginidae) in Venezuelan coast. *Investigaciones Pesqueras, Barcelona*, 50: 57–68 [In Spanish].

Roberts, M.J. 1998. The influence of the environment on chokka squid *Loligo vulgaris reynaudii* spawning aggregations: Steps towards a quantified model. *South African Journal of Marine Science*, 20: 267–284.

Roberts, M.J. 2001. Chokka squid abundance maybe linked to changes in the Agulhas bank ecosystem during spawning and the early life cycle. *Copenhagen Denmark ICES*, C.M./K:028.

Roberts, M.J. 2005. Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. *ICES Journal of Marine Science*, 62(1): 33–55.

Roberts, M.J. & N. Downey. 2006. Determining the influence of bottom turbidity and upwelling on chokka squid spawning behaviour. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 96.

Roberts, M.J. & W.H.H. Sauer. 1994. Environment: the key to understanding the South African chokka squid *Loligo vulgaris reynaudii* life cycle and fishery. *Antarctic Science*, 6(2): 249–258.

Roberts, M.J. & M. van den Berg. 2002 Recruitment variability of chokka squid (*Loligo vulgaris reynaudii*) – role of currents on the Agulhas Bank (South Africa) in paralarvae distribution and food abundance. *Bulletin of Marine Science*, 71(2): 691–710.

Roberts, M.J., M. Barange, M.R. Lipinski & M.R. Prowse. 2002. Direct hydroacoustic observations of chokka squid *Loligo vulgaris reynaudii* spawning activity in deep water. *South African Journal of Marine Science*, 24: 387–393.

Roberts, M.J., P. Rodhouse, R. O'Dor & Y. Sakurai. 1998. A global perspective of environmental research on squid. *ICES Copenhagen*, 22 pp.

Roberts, P.E. 1978. New Zealand squid resources. *In*: G. Habib & P.E. Roberts, eds. Proceedings of the Pelagic Fisheries Conference, July 1977. *New Zealand Fisheries Research Division Occasional Publication*, No. 15. pp. 90–93.

Roberts, P.E. 1979. Prospects and problems for New Zealand's demersal fisheries. Squid. *In*: R.D. Elder & J.L. Taylor, eds. Proceedings of the Demersal Fisheries Conference, October 1978. *Fisheries Research Division Occasional Publication*, No. 19. pp. 35–41.

***Roberts, P.E.** 1983. The Biology of jig-caught arrow squid (*Nototodarus* spp.) in New Zealand waters. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Memoirs of the National Museum of Victoria, Australia*, 44: 297–303.

Roberts, S.M. 2003. Examination of the stomach contents from a Mediterranean sperm whale found south of Crete, Greece. *Journal of the Marine Biological Association of the United Kingdom*, 83(3): 667–670.

Robertson, G., R. Williams, K. Green & L. Robertson. 1994. Diet composition of emperor penguin chicks *Apenodytes forsteri* at two Mawson Coast colonies, *Antarctica. IBIS*, 136(1): 19–31.

Robin, J.P. & E. Boucaud Camou. 1993. Proportion of the squid *Loligo forbesi* and *Loligo vulgaris* in French landings of the channel bottom trawl fishery: Sampling scheme of the Port-en-Bessin landings and preliminary results. *Copenhagen Denmark ICES*, 9 pp.

Robin, J.P. & E. Boucaud Camou. 1995. Squid catch composition in the English Channel bottom trawl fishery: proportion of *Loligo forbesi* and *Loligo vulgaris* in the landings and length-frequencies of both species during the 1993–1994 period. *ICES Council Meeting., 1995/K: 36, 9 pp.*

Robin, J.P., V. Denis & A. Carpentier. 1998. Distribution and abundance indexes of East English Channel squid populations: comparison of commercial trawlers LPUE and CGFS research cruise data. *Copenhagen Denmark ICES*, 12 pp.

***Robin, J.P., V. Denis, J. Royer & L. Challier.** 2002. Recruitment, growth and reproduction in *Todaropsis eblanae* (Ball, 1841), in the area fished by French Atlantic trawlers. *Bulletin of Marine Science*, 71: 711–724.

Robison, B.H. & L.D. Zeidberg. 2006. Invasive range expansion by the jumbo squid, *Dosidicus gigas*, in the eastern North Pacific: ecological impact in Monterey Bay. *EOS, Transactions, American Geophysical Union*, 87(36).

***Robson, G.C.** 1924. Preliminary report on the Cephalopoda (Decapoda) procured by the S.S. "Pickle." *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*, 3:1–14.

***Robson, G.C.** 1925. On *Mesonychoteuthis*, a new genus of oegopsid Cephalopoda. *Annals and Magazine Natural History*, (series 9) 16: 272–277, 2 figs.

***Robson, G.C.** 1926a. The Cephalopoda obtained by the S.S. Pickle. Supplementary Report. *Union of South Africa, Fisheries and Marine Biological Survey.* Report 4 (1925) (special report 8): 1–6, 2 figs.

***Robson, G.C.** 1926b. Notes on the Cephalopoda II.B. On a new Species of *Sepioteuthis* from Tobago. *Annals and Magazine of Natural History (Series 9)*, 18: 352–356.

***Robson, G.C.** 1928. Céphalopodes des mers d'Indiochine. *Service Océanographique des Peches de l'Indochine, Station Maritime de Cauda*, 10: 1–53, 31 figs.

***Robson, G.C.** 1948. The Cephalopoda Decapoda of the "Arcturus" Oceanographic Expedition, 1925. *Zoologica, Scientific Contributions of the New York Zoological Society*, 33(3):115–132, 18 figs.

Rocha, F. 1994. Aspectos biológicos y ecológicos de *Loligo vulgaris* y *Loligo forbesi* (Cephalopoda: Loliginidae) en las costas de Galicia. Ph.D.. Thesis. Universidad de Oviedo. 240 pp.

Rocha, F. & A. Guerra. 1995. Flexible reproductive patterns in the squids *Loligo vulgaris* and *Loligo forbesi*. *Copenhagen Denmark ICES*, 13 pp.

Rocha, F. & A. Guerra. 1996. Signs of an extended and intermittent terminal spawning in the squids *Loligo vulgaris* Lamarck and *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae). *Journal of Experimental Marine Biology and Ecology*, 207(1–2): 177–189.

Rocha, F. & A. Guerra. 1999. Age and growth of two sympatric squid *Loligo vulgaris* and *Loligo forbesi*, in Galician waters (north-west Spain). *Journal of the Marine Biological Association of the United Kingdom*, 79: 697–707.

Rocha, F. & M.A. Vega. 2003. Overview of cephalopod fisheries in Chilean waters. *Fisheries Research*, 60(1): 151–159.

***Rocha, F., A. Guerra & A.F. González.** 2001. A review of reproductive strategies in cephalopods. *Biological Reviews*, 76: 291–304.

Rocha V.F., T.O. Poblete & N.N. Bahamonde. 1991. Cephalopods in gastric contents of *Merluccius australis polylepis* Ginsburg and *Macruronus magellanicus* Lonnberg. *Investigación Pesquera, Santiago,*, 36: 51–65.

Rocha, F., B.G. Castro, M.S. Gil & A. Guerra. 1993. The diet of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in the Galician waters (NW Spain). *Copenhagen Denmark ICES*, 14 pp.

Rocha, F., B.G. Castro, M.S. Gil & A. Guerra. 1994. The diets of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Northwestern Spanish Atlantic waters. *Sarsia*, 79: 119–126.

Rocha, F., L. Fuentes, A. Guerra & M.C. Sainza. (1998). Cephalopodos de Somalia. *Iberus*, 16: 129–142.

Rocha, F., A. Guerra, R. Prego & U. Piatkowski. 1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). *Journal of Plankton Research*, 21(1): 21–33.

***Rochebrune, A.T. de.** 1884. Etude monographique sur la famille des Loligopsidae. *Bulletin de la Societe Philomathique de Paris*, (series 7) 8(1): 7–28, 2 pl.

***Rochebrune, A. & J. Mabill.** 1889. Mollusques. Mission Scientifiques du Cap Horn, 1882–83, 6(Zoologie): H1–H129, 8 pls.

Rodhouse, P.G. 1986. Distribution of the early-life phase of the Antarctic squid *Galiteuthis glacialis* in relation to the hydrology of the Southern Ocean in the sector 15°E to 30°E. *Marine Biology*, 91: 353–357.

***Rodhouse, P.G.** 1988. Distribution of the neoteuthid squid *Alluroteuthis antarcticus* Odhner in the Atlantic sector of the Southern Ocean. *Malacologia*, 29(1): 267–274.

***Rodhouse, P.G.** 1989. Pelagic cephalopods caught by nets during the Antarctic research cruises of the “Polarstern” and “Walther Herwig”, 1985–1987. *Polarstern*, 39(1): 111–121.

Rodhouse, P.G. 1990. Cephalopod fauna of the Scotia Sea at South Georgia: potential for commercial exploitation andpossible consequences. *In*: K. R. Kerry & G. Hempel, eds. Antarctic ecosystems. Ecological change and conservation. *Berlin, Springer–Verlag*, pp. 289–298.

Rodhouse, P.G. 1991. A preliminary assessment of the stock of the Ommastrephid squid *Martialia hyadesi* in the Scotia sea based on data from predators. Scientific Committee CCAMLR, pp. 479–480.

***Rodhouse, P.G.** 1992[1991]. Population structure of *Martialia hyadesi* (Cephalopoda: Ommastrephidae) at the Antarctic Polar Front and the Patagonian shelf, South Atlantic. *Bulletin of Marine Science*, 49(1–2): 404–418.

Rodhouse, P.G. 1995. Southwest Atlantic squid resources. 3. *International Cephalopod Trade Conference ‘Squid’94 Venice’*.

***Rodhouse, P.G.** 1998. *Todarodes flippovae* in the Southern Ocean: an appraisal for exploitation and management. In: Okutani T (Ed.) Large pelagic squids. *Japan Marine Fishery Resources Research Center, Tokyo*, pp. 207–215.

Rodhouse, P.G. 2001. Managing and forecasting squid fisheries in variable environments. *Fisheries Research*, 54(1): 3–8.

Rodhouse, P.G. 2005. World Squid Resources. Review of the state of world marine fishery resources. *FAO Fisheries Technical Paper*, 457: 175–187.

***Rodhouse, P.G. & M.R. Clarke.** 1985. Growth and distribution of young *Mesonychoteuthis hamiltoni* Robson (Mollusca: Cephalopoda): an Antarctic squid. *Vie et Milieu*, 35(3–4): 223–230.

Rodhouse, P.G. & E.M.C. Hatfield. 1990. Age determination in squid using statolith growth increments. *Fisheries Research*, 8: 323–334.

Rodhouse, P.G. & E.M.C. Hatfield. 1990. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea, Ommastrephidae). *Phil. Trnas. R. Soc. Lond. B*, 329: 229–241.

Rodhouse, P.G. & E.M.C. Hatfield. 1992. Production of soma and gonad in maturing male *Illex argentinus* (Mollusca: Cephalopoda). *Journal of the Marine Biological Association of the United Kingdom*, 72: 293–300.

Rodhouse, P.G. & C.C. Lu. 1998. Chiroteuthis veranyi from the Atlantic sector of the Southern Ocean (Cephalopoda: Chiroteuthidae). *In* A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 311–322.

Rodhouse, P.G. & Ch.M. Nigmatullin. 1996. Role as consumers, *In*: M.R. Clarke, ed. The role of cephalopods in the world’s oceans. *Philosophical Transactions of the Royal Society of London*, 351: 1003–1022.

***Rodhouse, P.G. & U. Piatkowski.** 1995. Fine-scale distribution of juvenile cephalopods in the Scotia Sea and adaptive allometry of the brachial crown. *Marine Biology*, 124(1): 111–117.

Rodhouse, P.G. & P.A. Prince. 1993. Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. *Polar Biology*, 13(6): 373–376.

Rodhouse, P.G. & M.G. White. 1995. Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. *Biological Bulletin*, 189(2): 77–80.

***Rodhouse, P.G., E.G. Dawe & R.K. O'Dor (eds).** 1998a. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376:

***Rodhouse, P.G., C.D. Elvidge & P.N. Trathan.** 2001. Remote sensing of the global light-fishing fleet, an analysis of interactions with oceanography, other fisheries and predators. *Advances in Marine Biology*, 39: 261–303.

Rodhouse, P.G., E.J. Murphy & M.L. Coelho. 1998b. Impact of fishing on life histories. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 255–268.

***Rodhouse, P.G., U. Piatkowski & C.C. Lu (eds).** 1994. Southern Oceans Cephalopods: Life Cycles and Populations. *Antarctic Science, Special Issue*, 6(2): 287 pp.

***Rodhouse, P.G., C. Symon & E.M.C. Hatfield.** 1992a. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Marine Ecology Progress Series*, 89(2–3): 183–195.

Rodhouse, P.G., R.C. Swinfen & A.W.A. Murray. 1988. Life cycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata*. *Marine Ecology Progress Series*, 45: 245–253.

Rodhouse, P.G., M.G. White & M.R.R. Jones. 1992b Trophic relations of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. *Marine Biology*, 114(3): 415–421.

Rodhouse, P.G., J. Barton, E.M.C. Hatfield & C. Symon. 1995. *Illex argentinus*: life cycle, population structure and fishery. *ICES Marine Science Symposium*, 199: 425–432.

Rodhouse, P.G., O. Olsson, P. Anker-Nilssen & A.W.A. Murray. 1998c. Cephalopod predation by the king penguin (*Aptenodytes patagonicus*) from South Georgia. *Marine Ecology Progress Series*, 168: 13–19.

Rodhouse, P.G., P.A. Prince, M.R. Clarke & A.W.A. Murray. 1990. Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Marine Biology*, 104(3): 353–362.

***Rodhouse, P.G., T.R. Arnbom, M.A. Fedak, J. Yeatman & A.W.A. Murray.** 1992c. Cephalopod prey of the southern elephant seal, *Mirounga leoninia* L. *Canadian Journal of Zoology*, 70(5): 1007–1015.

***Rodhouse, P.G., C.M. Waluda, E. Morales-Bojorquez & A. Hernandez-Herrera.** 2006. Fishery biology of the Humboldt squid, *Dosidicus gigas*, in the Eastern Pacific Ocean. *Fisheries Research*, 79(1–2): 13–15.

Rodhouse, P.G., P.A. Prince, P.N. Trathan, E.M.C. Hatfield, J.L. Watkins, D.G. Bone, E.J. Murphy & M.G. White. 1996. Cephalopods and mesoscale oceanography at the Antarctic Polar Front – satellite tracked predators locate pelagic trophic interactions. *Marine Ecology Progress Series*, 136: 37–50.

Rodriguez-Navarro, A., A. Guerra, C.S. Romanek, F. Rocha & A.F. Gonzalez. 2006. Life history of the giant squid *Architeuthis* as revealed from stable isotope and trace elements signatures recorded in its beak. *Cephalopod International Advisory Council Symposium 2006*, Abstract. p. 97.

Roel, B.A. & A.I.L. Payne. 1998. Management of the South African chokka squid jig fishery under uncertainty regarding trends in resource abundance. *Copenhagen Denmark ICE*S, 13 pp.

Roel, B.A., K.L. Cochrane & D.S. Butterworth. 1998. Investigation on the effects of different levels of effort and of the closed season in the jig fishery for chokka squid *Loligo vulgaris reynaudii*. *South African Journal of Marine Science*, 19: 501–512.

Roel, B.A. & G. Maharaj. 1999. Fishing effort and fishing capacity in the chokka squid jig fishery off South Africa. *Copenhagen Denmark ICES*, 10 pp.

Roel, B.A., K.L. Cochrane & J.G. Field. 2000. Investigation into the declining trend in chokka squid *Loligo vulgaris reynaudii* catches made by South African trawlers. *South African Journal of Marine Science*, 22: 121–135.

Roel, B.A. & D.S. Butterworth. 2000. Assessment of the South African chokka squid *Loligo vulgaris reynaudii*. Is disturbance of aggregations by the recent jig fishery having a negative impact on recruitment? *Fisheries Research*, 48(3): 213–228.

Roeleveld, M.A. 1982. Interpretation of tentacular club structure in *Sthenoteuthis oualaniensis* (Lesson, 1830) and *Ommastrephes bartramii* (Lesueur, 1821) (Cephalopoda: Ommastrephidae). *Annals of the South African Museum*, 89(4): 249–264.

***Roeleveld, M.A.** 1988. Generic interrelationships within the Ommastrephidae (Cephalopoda). *In* M.R. Clarke & E.R. Trueman, eds. *The Mollusca*, 12: Paleontology and Neontology of Cephalopods. *Academic Press, New York*, pp. 277–291.

***Roeleveld, M.A.** 1989. The occurrence of two species of squid *Todarodes* in the Benguela system. *South African Journal of Science*, 85: 659–663.

***Roeleveld, M.A.** 1995. Systematics and evolution of *Todarodes* and *Martialia* (Cephalopoda: Ommastrephidae) revisited. *Abstracts of the American Malacological Meeting, Hilo, Hawaii*, 1995, p. 39.

***Roeleveld, M.A.** 1998. The status and importance of cephalopod systematics in southern Africa. *In* A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld: Editors, Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 1–16.

***Roeleveld, M.A.C.** 2000. Giant squid beaks: implications for systematics. *Journal of the Marine Biological Association of the United Kingdom*, 80(1): 185–187.

Roeleveld, M.A.C. 2002. Tentacle morphology of the giant squid *Architeuthis* from the North Atlantic and Pacific Oceans. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(2): 725–737.

***Roeleveld, M.A.C. & C.J. Augustine.** 2005. Description of a new species of *Uroteuthis* (*Photololigo*) from the Mozambique Channel. *Phuket Marine Biological Center Research Bulletin*, 66: 97–107.

Roeleveld, M.A.C. & J. Knudsen. 1980. Japetus Steenstrup: On the merman (called the sea monk) caught in the Øresund in the time of King Christian III. *Zoological Museum of University of Copenhagen*, 6(17): 293–332.

***Roeleveld, M.A.C. & M.R. Lipinski.** 1991. The giant squid *Architeuthis* in southern African waters. *Journal of Zoology, London*, 224: 4331–477.

***Roeleveld, M.A.C., M.R. Lipinski, C.J. Augustyn & B.A. Stewart.** 1992. The distribution and abundance of cephalopds on the continental slope of the eastern South Atlantic. *In*: A.I.S Payne, K.H. Brink, K.H. Mann & R. Hilborn, eds. Benguela Trophic Functioning. *South African Journal of Marine Science*, 12: 739–752.

Rogers-Bennet, L. 2000. Review of some California fisheries for 1999: market squid, dungeness crab, sea urchin, prawn, abalone, groundfish, swordfish and shark, ocean salmon, nearshore finfish, Pacific sardine, Pacific herring, Pacific mackerel, reduction, white seabass and recreational. *Reports of California Cooperative Oceanic Fisheries Investigations*, 41: 8–26.

Roongrati, M. 1998. Re-examination of *Loligo sumatrensis* d'Orbigny, 1835 along the eastern coast of the Gulf of Thailand. *Thai Marine Fisheries Research Bulletin*, 6: 11–16.

Roongratri, M. & S. Fujiwara. 1992 Some biological aspects of Indian squid, *Loligo duvauceli*, along the eastern coast of the Gulf of Thailand. *Thai Marine Fisheries Research Bulletin*, 3: 45–53.

***Roper, C.F.E**. 1963. Observation on bioluminescence in *Ommastrephes pteropus* (Steenstrup, 1855), with notes on its occurrence in the family Ommastrephidae (Mollusca: Cephalopoda). *Bulletin of Marine Science*, 13(2): 343–353.

***Roper, C.F.E.** 1964. *Enoploteuthis anapsis*, a new species of enoploteuthid squid (Cephalopoda: Oegopsida) from the Atlantic Ocean. *Bulletin of Marine Science of the Gulf and Caribbean*, 14(1): 140–148, 2 figs.

Roper, C.F.E. 1965. A note on egg deposition by *Doryteuthis plei* (Blainville, 1823) and its comparison with other North American loliginid squids. *Bulletin of Marine Science Gulf and Caribbean*, 15: 589–598.

***Roper, C.F.E.** 1966. A study of the genus *Enoploteuthis* (Cephalopoda: Oegopsida) in the Atlantic Ocean with a redescription of the type species *E. leptura* (Leach, 1817). *Dana Report*, 66: 1–46, 24 figs.

***Roper, C.F.E.** 1968. Preliminary descriptions of two new species of the bathypelagic squid *Bathyteuthis* (Cephalopoda: Oegopsida). *Proceedings of the Biological Society of Washington*, 81: 161–172.

***Roper, C.F.E.** 1969. Systematics and zoogeography of the worldwide bathypelagic squid *Bathyteuthis* (Cephalopoda: Oegopsida). *US National Museum Bulletin*, 291: 210 pp., 12 pls.

***Roper, C.F.E.** 1978. Cephalopods. *In*: FAO species identification sheets for fishery purposes. Western central Atlantic (fishing area 31), *In* W. Fischer, ed. *Rome, FAO*, Vol. 6: pag. var.

Roper, C.F.E. 1981. Cephalopods of the Southern Ocean region: potential resources and bibliography. *Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS)*, Vol. II: 99–105.

***Roper, C.F.E.** 1983. An overview of cephalopod systematics: status, problems and recommendations. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. Proceedings of the workshop on the biology and resource potential of cephalopods. *Memoirs of National Museum Victoria*, 44: 13–27.

Roper, C.F.E. 1992a. Architeuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. Larval and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 99–101.

Roper, C.F.E. 1992b. Neoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. Larval and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 101–103.

***Roper, C.F.E.** 1998a. Architeuthidae Pfeffer 1900. *Architeuthis*, giant squid. Tree of Life, Version 01, Jan. 1998. http://Tolweb.Org/Architeuthis 19408/1998.01.01.

Roper, C.F.E. 1998b. Tracking the giant squid: mythology and science meet beneath the sea. *Wings*, 21(1): 12–17.

Roper, C.F.E. 1998c. The hunt for the giant squid. Special report: oceanography. *Science Year 1999. World Book* Chicago, pp. 86–101.

***Roper, C.F.E.** 1998d. Bathyteuthidae Pfeffer 1900. *Bathyteuthis* Hoyle 1885. in The Tree of Life Web Project, http://tolweb.org/

Roper, C.F.E. 2000. The quest for the giant squid. *Muse*, 4(2): 10–19.

Roper, C.F.E. 2006. Search for the giant squid. *Explorers Journal*, 84(2): 28–37.

Roper, C.F.E. & K.J. Boss. 1982. The giant squid. *Scientific American*, 246(4): 96–105.

Roper, C.F.E. & W.L. Brundage Jr. 1972. Cirrate octopods with associated deep-sea organisms: new biological data based on deep benthic photographs (Cephalopoda). *Smithsonian Contributions to Zoology*, 121: 1–46.

Roper, C.F.E. & M.R. Clarke. 1992g. Joubiniteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 179–180.

Roper, C.F.E. & C.C. Lu. 1979. Rhynchoteuthion larvae of ammastrephid squids of the western North Atlantic, with the first description of larvae and juveniles of *Illex illecebrosus*. *Proceedings of the Biological Society of Washington*, 91(4): 1039–1059.

***Roper, C.F.E. & C.C. Lu.** 1989. Systematic status of *Lepidoteuthis*, *Pholidoteuthis* and *Tetronychoteuthis* (Cephalopoda: Oegopsida). *Proceedings of the Biological Society of Washington*, 102(3): 805–807.

***Roper, C.F.E. & C.C. Lu.** 1990. Comparative morphology and function of dermal structures in oceanic squids (Cephalopoda). *Smithsonian Contributions to Zoology*, 493: 40 pp.

***Roper, C.F.E. & K.M. Mangold.** 1998. Systematic and distributional relationships of *Illex coindetii* to the genus *Illex* (Cephalopoda; Ommastrephidae). *In*: P.G. Rodhouse, E.G. Dawe & R.K. O’Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 13–26.

***Roper, C.F.E. & W. Rathjen.** 1991. World-wide squid fisheries: a summary of landings and capture techniques. *Journal of Cephalopod Biology*, 2(1): 51–63.

Roper, C.F.E. & M.J. Sweeney. 1981. Cephalopods. *In:* W. Fischer, G. Bianchi & W.B. Scott, eds. *FAO species identification sheets for fishery purposes. Eastern central Atlantic, fishing areas 34, 47 (in part).* Canada Funds-in-Trust. Ottawa, Dept. Fisheries and Oceans Canada, by arrangement with FAO. Vol. 6: pag. var.

Roper, C.F.E. & M.J. Sweeney. 1983. Techniques for fixation and preservation of cephalopods. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg: Editors. Proceedings of the workshop on the biology and resource potential of cephalopods. *Memoirs of National Museum Victoria*, 44: 28–47.

***Roper, C.F.E. & M.J. Sweeney.** 1992a. Bathyteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 93–95.

Roper, C.F.E. & M.J. Sweeney. 1992b. Psychroteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 95–97.

***Roper, C.F.E. & M.J. Sweeney.** 1992c. Brachioteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 157–159.

Roper, C.F.E. & M.J. Sweeney. 1992d. Batoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 171–172.

Roper, C.F.E. & M.J. Sweeney. 1992e. Chiroteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 173–175.

Roper, C.F.E. & M.J. Sweeney. 1992f. Mastigoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 175–178.

***Roper, C.F.E. & M. Vecchione.** 1993. A geographic and taxonomic review of *Taningia danae* Joubin, 1931 (Cephalopoda: Octopoteuthidae), with new records and observations on bioluminescence. *In* T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 441–456.

***Roper, C.F.E. & M. Vecchione.** 1996. In situ observations on *Brachioteuthis beanii* Verrill: paired behavior, probably mating (Cephalopoda, Oegopsida). *American Malacological Bulletin*, 13(1/2): 55–60.

***Roper, C.F.E. & M. Vecchione.** 1997. In situ observations test hypotheses of functional morphology in *Mastigoteuthis* (Cephalopoda, Oegopsida). *In* S.v. Boletsky, P. Fioroni & A. Guerra, eds. *Proceedings of the Second International Symposium on Functional Morphology of Cephalopods, Vigo (Spain), 6–8 Sep 1995*, Banyuls sur Mer, France, Laboratoire Arago, 47(2): 87–93.

***Roper, C.F.E. & M. Vecchione.** 2001. *Pickfordiateuthis bayeri*, a new species of squid (Cephalopoda: Loliginidae) from the western North Atlantic Ocean discovered by submersible. *Bulletin of the Biological Society of Washington*, 10: 301–310.

***Roper, C.F.E. & G.L. Voss.** 1983. Guidelines for taxonomic descriptions of cephalopod species. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. Proceedings of the workshop on the biology and resource potential of cephalopods. *Memoirs of National Museum Victoria*, 49–63.

***Roper, C.F.E. & R.E. Young.** 1967. A review of the Valbyteuthidae and an evaluation of its relationship with the Chiroteuthidae (Cephalopoda: Oegopsida). *Proceedings of the US National Museum*, 123(3612): 1–9.

***Roper, C.F.E. & R.E. Young.** 1968. The family Promachoteuthidae (Cephalopoda: Oegopsida). I. A re-evaluation of its systematic position based on new material from Antarctic and adjacent waters. *Antarctic Research Series*, 11: 203–214.

***Roper, C.F.E. & R.E. Young.** 1972. First records of juvenile giant squid, *Architeuthis* (Cephalopoda: Oegopsida). *Proceedings of the Biological Society of Washington*, 85(16): 205–222.

***Roper, C.F.E. & R.E. Young.** 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology*, 209: 1–51.

***Roper, C.F.E. & R.E. Young.** 1998. *Chiroteuthis* Orbigny, 1841. Version 01 January 1998 (under construction). http://tolweb.org/Chiroteuthis/19462/1998.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Roper, C.F.E. & R.E. Young.** 1999a. *Chiroteuthis veranyi* (Ferussac, 1835). Version 01 January 1999 (under construction). http://tolweb.org/Chiroteuthis_veranyi/19479/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Roper, C.F.E. & R.E. Young.** 1999b. *Chiroteuthis calyx* Young, 1972. Version 01 January 1999 (under construction). http://tolweb.org/Chiroteuthis_calyx/19474/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Roper, C.F.E. & R.E. Young.** 1999c. *Chiroteuthis joubini* Voss, 1967. Version 01 January 1999 (under construction). http://tolweb.org/Chiroteuthis_joubini/19475/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Roper, C.F.E. & R.E. Young.** 1999d. *Chiroteuthis mega* (Joubin, 1932). Version 01 January 1999 (under construction). http://tolweb.org/Chiroteuthis_mega/19476/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Roper, C.F.E. & R.E. Young.** 1999e. *Chiroteuthis picteti* Joubin, 1894. Version 01 January 1999 (under construction). http://tolweb.org/Chiroteuthis_picteti/19477/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Roper, C.F.E. & R.E. Young.** 1999f. *Chiroteuthis spoeli* Salcedo-Vargas, 1996. Version 01 January 1999 (under construction). http://tolweb.org/Chiroteuthis_spoeli/19478/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

Roper, C.F.E. & R.E. Young. 2002. *Architeuthis*, Tree of Life Project. http://tolweb.org.

Roper, C.F.E., C.C. Lu & F.G. Hochberg. 1983. Biology and resources potential of cephalopods. *Memoirs of the National Museum of Victoria*, 44: 311 pp.

***Roper, C.F.E., C.C. Lu & K. Mangold.** 1969a. A new species of *Illex* from the Western Atlantic and distributional aspects of other *Illex* species Cephalopoda: Oegopsida). *Proceedings of Biological Society of Washington*, 82: 295–322.

***Roper, C.F.E., C.C. Lu & M. Vecchione.** 1998. A revision of the systematics and distribution of *Illex* Species (Cephalopoda: Ommastrephidae). *Smithsonian Contributions to Zoology*, 586: 405–423.

***Roper, C.F.E., M.J. Sweeney & M.R. Clarke.** 1985. FAO species identification sheets for fishery purposes. Food and Agriculture Organization of the United Nations, Rome, Vol. 1, pp. 117–205.

***Roper, C.F.E., M.J. Sweeney & F.G. Hochberg.** 1995. Cefalopodos. *In*: W. Fisher, F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter & V.H. Niem, eds. Guia FAO para la identificacion de especies para los fines del la pesca. Pacifico centro-oriental, Vol. I. Plantas e invertebrados. FAO, Rome, pp. 305–353 [in Spanish].

***Roper C.F.E., M.J. Sweeney & C.E. Nauen.** 1984. FAO species catalogue. Vol. 3. Cephalopoda of the world. An annotated and illustrated catalogue of species of interest to fisheries. *FAO Fisheries Synopsis., (125)(3): 277 pp.*

***Roper, C.F.E., R.E. Young & G.L. Voss.** 1969b. An illustrated key to the families of the order Teuthoidea (Cephalopoda). *Smithsonian Contribution to Zoology*, 3: 32 pp.

Rosa, R., J. Pereira & M.L. Nunes. 2005. Biochemical composition of cephalopods with different life strategies, with special reference to a giant squid, *Architeuthis* sp. *Marine Biology*, 146(4): 739–751.

Rosa, R., P.R. Costa, N. Bandarra & M.L. Nunes. 2005. Changes in tissue biochemical composition and energy reserves associated with sexual maturation in the Ommastrephid squids *Illex coindetii* and *Todaropsis eblanae*. *Biological Bulletin*, 208(2): 100–113.

Rosas-Alayola, J., A. Hernandez-Herrera, F. Galvan-Magan, L.A. Abitia-Cardenas & A.F. Muhlia-Melo. 2002. Diet composition of sailfish (*Istiophorus platypterus*) from the southern Gulf of California, Mexico. *Fisheries Research*, 57(2): 185–195.

Rosenberg A.A., K.F. Wiborg & I.M. Bech. 1981. Growth of *Todarodes sagittatus* (Lamarck) (Cephalopoda, Ommastrephidae) from the northeast Atlantic, based on counts of statolith growth rings. *Sarsia*, 66 (1): 53–57.

Rosenberg, A.A., G.P. Kirkwood, J.A. Crombie & J.R. Beddington. 1990. The assessment of stocks of annual squid species. *Fisheries Research*, 8: 335–349.

Ross, B. 1990. Greek cephalopod market, 1990. *NTIS Order No.: PB91–110395/GAR*, 26 pp.

Rowe, V.L. & K. Mangold. 1975. The effect of starvation on sexual maturation in *Illex illecebrosus* (Lesueur) (Cephalopoda: Teuthoidea). *Journal of Experimental Marine Biology and Ecology*, 17(2): 157–163.

Rowell, T.W. 1985. Synopsis of the special session on squids, September 1984. *NAFO Scientific Council Studies*, 9: 7–9.

Rowell, T.W. & R.W. Trites. 1985. Distribution of larval and juvenile *Illex* (Mollusca: Cephalopoda) in the Blake Plateau region (Northwest Atlantic). *In*: K.M. Mangold & S.v. Boletsky, eds. *Biology and Distribution of Early Juvenile Cephalopods*, 35(3–4): 149–161.

Royer, J., P. Peries & J.P. Robin. 2002 Stock assessments of English Channel loliginid squids: updated depletion methods and new analytical methods. *ICES Journal of Marine Science*, 59(3): 445–457.

Rozengart, E.V. & N.E. Basova. 2006. Comparative enzymology of cholinesterases is based in the biochemical method of taxonomy in squids. *Zhurnal Evolyutsionnoi Biokhimii fiziologii*, 41(6): 490–499.

Rozengart, E.V., N.E. Basova & A.A. Suvorov. 2006. The study of reversible inhibition mechanism on the action of thiophosphonates against different cholinesterases by the data of comparative inhibitor specificity. *Doklady-Akademii Nauk*, 411(2): 262–266.

Rubio, R.J. & C.C. Salazar. 1991. Fishery prospection of the giant squid (*Dosidicus gigas*) aboard the Japanese vessel Shinko Maru 2. *Informe Instituto del Mar del Peru*, 103: 3–32.

Ruby, G. & J. Knudsen. 1972. Cephalopoda from the eastern Mediterranean. *Israel Journal of Zoology*, 21: 83–97.

Ruiz-Capillas, C., A. Moral, J. Morales & P. Montero. 2002a. Characterisation of non-protein nitrogen in the cephalopds volaodr (*Illex coindetii*), pota (*Todaraopsis eblanae*) and octopus (*Eledone cirrhosa*). *Food Chemistry*, 76(2): 165–172.

Ruiz-Capillas, C., A. Moral, J. Morales & P. Montero. 2002b. Preservation of shelf life of Pota and Octopus in chilled storage under controlled atmospheres. *Journal of Food Protection*, 65(1): 140–145.

Ruiz-Capillas, C., A. Moral, J. Morales & P. Montero. 2003. Characterization and functionality of frozen muscle protein in Volador (*Illex coindetii*), Pota (*Todaropsis eblanae*), and Octopus (*Eledone cirrhosa*). *Journal of Food Science*, 68(7): 2164–2168.

Ruiz-Cooley, R.I., U. Markaida, D. Gendron & S. Aguiniga. 2006. Stable isotopes in jumbo squid (*Dosidicus gigas*) beaks to estimate its trophic position: comparison between stomach contents and stable isotopes. *Journal of the Marine Biological Association of the United Kingdom*, 86(2): 437–445.

Ruiz-Cooley, R.I., D. Gendron, S. Aguiniga, S. Mesnick & J.D. Carriquiry. 2004. Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. *Marine Ecology Progress Series*, 277: 275–283.

***Rüppell, E.** 1844. Intorno ad alcuni cefalopodi del mare di Messina: lettera del Dr. Eduardo Ruppell di Frankfort sul Meno al Prof. Anastasio Cocco. *Giornale del Gabinetto Letterario di Messina*, 5(27–28): 129–135.

***Rüppell, E. & F.S. Leuckart.** 1828. Neue wirbellose thiere des rothen Meeres. *In*: Atlas zu der reise im nordlichen Afrika, von Eduard Ruppell, 1826–1828, *Frankfurt am Main*, 47 pp., 12 pls.

***Russell, E.S.** 1909. Preliminary notice on the Cephalopoda collected by the Fishery Cruiser Goldseeker 1903–1908. *Annals and Magazine of Natural History*, (series 8)3: 446–455.

Rustad, D. 1952. Biological notes from the biological station. *Univ Bergen Arb. 1951, naturv. R.*, 1–11 (in Clarke).

Sabirov, R.M. 1995. Spermatophorogenesis and reproductive strategy in males of ommastrephid squids (Cephalopoda: Ommastrephidae). *Thesis, Kazan*, 198 p.

Sabirov, R.M. & V.P. Zalygalin. 2002. Ontogenetic and evolutionary patterns of the male reproductive system function in the squid family Ommastrephidae. *Bulletin of Marine Science*, 71(2): 1138.

Sabirov, R.M., A.I. Arkhipkin, V.Yu. Tsygankov & A.S. Schetinnikov. 1987. Egg-laying and embryonic development of the diamond-shaped squid *Thysanoteuthis rhombus* (Oegopsida, Thysanoteuthidae). *Zoologicheskij Zhurnal*, 66(8): 1155–1163.

Sacarrão, G.F. 1956–57. Os cefalópodos da costa de Portugal (fauna local). *Naturália*, 6: 147–158.

Sacau, M., J. Wang, A.I. Arkhipkin, J. Portela, G.J. Pierce, P. Brickle & X. Cardoso. 2004. The spatio-temporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the Spanish bottom-trawl fishery in the southwest Atlantic. ICES Council Meeting Documents Copenhagen. No. 2004.

Sacau, M., G.J. Pierce, J. Wang, A.I. Arkhipkin, J. Portela, P. Brickle, M.B. Santos, A.F. Zuur & X. Cardoso. 2006. The spatio-temporal pattern of Argentine shortfin squid *Illex argentinus* abundance in the southwest Atlantic. *Aquatic Living Resources*, 18(4): 361–372.

Saibil, H.R. 1984. A light-stimulated increase of cyclic GMP in squid photoreceptors. *FEBS Letters*, 168(2): 213–216.

Said, M.Z.M., A.W.A. Rashid, A.K.M.Mohsin & M.A. Ambak. 1987. An evaluation and estimation of non-fish resources in the southwestern part of the South China Sea. *In*: A.K.M. Mohsin, R.A. Rahman, M.A. Ambak, eds. Ekspedisi Matahari ' 86: A study on the offshore waters of the Malaysian EEZ, 4: 133–146.

Saito, K. 1994. Distribution of paralarvae of *Ommastrephes bartramii* and *Eucleoteuthis luminosa* in the eastern waters off Ogasawara Islands. *Bulletin of Hokkaido National Fisheries Research Institute*, 58: 15–23.

***Saito, R., T. Kawakami, M. Hamabe & Y. Matsushita.** 1974. A preliminary note on the ecology of the ommastriphid squid *Nototodarus sloani sloani* (Gray) in New Zealand waters 3. Studies on the catch by jigs by the Hoyo-Maru No. 51 in 1971 and 1972. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 79: 35–38.

Saitoh, K., M. Takagaki & Y. Yamashita. 2003. Detection of Japanese flounder-specific DNA from gut contents of potential predators in the field. *Fisheries Science*, 69(3): 473–477.

Sakaguchi, K. & S. Takayanagi. 2001. Factors causing differences in body size of Japanese common squid, *Todarodes pacificus*, in the Sea of Japan off Hokkaido in 1996 and 1997. *Science Report Hokkaido Fisheries Experimental Station*, 59: 25–30.

Sakai, M., N. Brunetti, M. Ivanovic, B. Elena & K. Nakamura. 2004. Interpretation of statolith microstructure in reared hatchling paralarvae of the squid *Illex argentinus*. *Marine and Freshwater Research*, 55(4): 403–413.

Sakai, K., K. Mori, S. Miyanaga, J. Yamamoto & Y. Sakurai. 2006. Estimated winter spawning areas of Japanese common squid, *Todarodes, pacificus* in the East China Sea. Cephalopod International Advisory Council Symposium 2006, Abstract.

Sakai, M., N. Brunetti, J. Bower, B. Elena, T. Goto, T. Ichii, M. Ivanovic, Y. Sakurai, T. Wakabayashi & A. Yatsu. 2006. Upper-beak growth increments in ommastrephid paralarvae. Cephalopod International Advisory Council Symposium 2006, Abstract.

***Sakurai, Y. & M.J. Kishi.** 2007. Prediction of life strategy and stock fluctuation of the Japanese common squid, *Todarodes pacificus*, related to climate change during the 21st century. *The Changing North Pacific: Previous Patterns, Future Projections and Ecosystem Impacts*, p. 6.

Sakurai, Y., J.R. Bower & Y. Ikeda. 2003. Reproductive characteristics of the ommastrephid squid *Todarodes pacificus*. *Report of the working group on modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids*, pp. 105–116.

Sakurai, Y., S. Miyanaga & J. Yamamoto. 2004. Why do ommastrephid squids increase in abundance during warm regimes? *PICES 13th Annual Meeting Book of Abstracts*, p. 26.

Sakurai, Y., Y. Ikeda, M. Shimizu & K. Shimazaki. 1993. Feeding and growth of captive adult Japanese common squid *Todarodes pacificus*, measuring initial body size by cold anesthesia. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology*, 467–476.

Sakurai, Y., S. Miyanaga, J. Yamamoto & K. Mori. 2006b. How environmental factors affect the stock size of ommastrephid squid, *Todarodes pacificus* – a possible scenario. *Climate Variability and Ecosystem Impacts on the North Pacific: A Basin-Scale Synthesis*, p. 62.

Sakurai, Y., J.R. Bower, Y. Nakamura, S. Yamamota & K. Watanabe. 1996. Effect of temperature on development and survival of *Todarodes pacificus* embryos and paralarvae. *American Malacological Bulletin*, 13: 89–95.

Sakurai, Y., H. Kiyofuji, S. Saitoh, T. Goto & Y. Hiyama. 2000. Changes in inferred spawning sites of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. *ICES Journal Marine Science*, 57: 24–30.

Sakurai, Y., G. Lima, J. Yamamoto, H. Nakao & K. Itoh. 2002a. Effects of low temperature and cold shock on the embryonic development of *Loligo bleekeri* (Cephalopoda: Loliginidae). *Bulletin of Marine Science*, 71(2): 1138–1139.

Sakurai, Y., J. Yamamoto, K. Mori, T. Goto & H. Kidokoro. 2006a. Can we explain and predict stock fluctuations of Japanese common squid, *Todarodes pacificus*, related to climatic regime shifts? *PICES XV. Book of Abstracts*, p. 83.

Sakurai, Y., H. Kiyofuji, S. Saitoh, J. Yamamoto, T. Goto, K. Mori & T. Kinoshita. 2002b. Stock fluctuations of the Japanese common squid, *Todarodes pacificus*, related to recent climate changes. *Fisheries Science*, 68(Supplement I): 226–229.

Sakurai, Y., R.E. Young, J. Hirota, K. Mangold, M. Vecchione, M.R. Clarke & J. Bower. 1995. Artificial fertilization and development through hatching in the oceanic squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* (Cephalopoda: Ommastrephidae). *Veliger*, 38(3): 185–191.

Salat, J., J. Font & A. Cruzado. 1978. Datos oceanográficos frente a Barcelona (1975–1976). *Datos Informativos, Instituto de Investigaciones Pesqueras*, 5: 73 pp.

***Salcedo-Vargas, M.A.** 1995. Systematic value of the ultrastructure of the sucker surface in the squid family Mastigoteuthidae (Mollusca: Cephalopoda). *Contributions to Zoology*, 65(2): 65–77.

***Salcedo-Vargas, M.A.** 1996. Cephalopods from the Netherlands Indian Ocean Programme (NIOP) – I. *Chiroteuthis spoeli* n. spec. and *Chiroteuthis picteti somaliensis* n. subspec. *Beaufortia*, 46(2): 11–26.

***Salcedo-Vargas, M.A.** 1997. Cephalopods from the Netherlands Indian Ocean Programme (NIOP) – II. Mastigoteutid lineage and related forms. *Beaufortia*, 47: 91–108.

***Salcedo-Vargas, M.A.** 1999. An asperoteuthid squid (Mollusca: Cephalopoda: Chiroteuthidae) from New Zealand misidentified as *Architeuthis*. *Mitteilungen aus dem Museum fur Naturkunde in Berlin, Zoologische Reihe*, 75: 47–49.

***Salcedo-Vargas, M.A. & J. Guerrero-Kommritz.** 2000. Three new cephalopods from the Atlantic Ocean. *Mitteilungen aus dem Hamburgischen Zoologische Museum und Institut Hamburg*, 97: 31–44.

Salcedo-Vargas, M.A. & J. Guerrero-Kommritz. 2001. New data on juvenile stages of lepidoteuthid families (Mollusca: Cephalopoda). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut,* 98: 23–30.

***Salcedo-Vargas, M.A. & T. Okutani.** 1994. New classification of the squid family Mastigoteuthidae (Cephalopoda: Oegopsida). *Venus Japanese Journal of Malacology*, 53(2): 119–127.

Salcedo-Vargas, M.A. & R.E. Young. 1996. Mastigoteuthis, general systematics. Tree of Life Project, http://tolweb.org.

***Salcedo-Vargas, M.A. & R.E. Young.** 2001a. *Chtenopteryx canariensis* Salcedo-Vargas and Guerrero-Kommritz 2000. Dark combfin squid. Version 31 October 2001 (under construction). http://tolweb.org/Chtenopteryx_canariensis/19439/2001.10.31 in The Tree of Life Web Project, http://tolweb.org/

***Salcedo-Vargas, M.A. & R.E. Young.** 2001b. *Discoteuthis*sp. A. Version 01 January 2001 (under construction). http://tolweb.org/Discoteuthis_sp._A/19627/2001.01.01 in The Tree of Life Web Project, http://tolweb.org/

Salcedo-Vargas, M.A. & R.E. Young. 2007. *Mastigoteuthis* tyroi Salcedo-Vargas, 1997. Version 19 November 2007 (under construction). http://tolweb.org/Mastigoteuthis_tyroi/19526/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

***Salman, A.** 2002. New report of the loliginid squid *Sepioteuthis lessoniana* Lesson 1830 in the Mediterranean. *Israel Journal of Zoology*, 48: 249–250.

Salman, A. 2004. The role of cephalopods in the diet of swordfish (*Xiphias gladius* Linnaeus, 1758) in the Aegean Sea (Eastern Mediterranean). *Bulletin of Marine Science*, 74(1): 21–29.

Salman, A. & T. Katagan. 2002. Lesseppsian immigrant cephalopods of the Mediterranean Sea. Workshop on Lessepsian Migration, 20–21 July 2002, *Gokceada, Turkey*, 4 pp.

Salman, A. & V. Laptikhovsky. 2002. First occurrence of egg masses of *Loligo forbesi* (Cephalopoda: Loliginidae) in deep waters of the Aegean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 82: 925–926.

Salman, A., T. Katagan & H.A. Benli. 1997. Bottom trawl teuthofauna of the Aegean Sea. *Archives of Fisheries Marine Research*, 45(2): 183–196.

***Salman, A., T. Katagan & H.A. Benli.** 2003. Vertical distribution and abundance of juvenile cephalopods in the Aegean Sea. *Scientia Marina*, 67(2): 167–176.

Salman, A., T. Katagan & S.V. Boletzky. 1999. New Cephalopod Molluscs in the Eastern Mediterranean: Previously unnoted species or Lessepsian migrants? *Vie et Milieu*, 49 (1): 11–17.

Salman, Y., A. Salman & S. Ozkizilcik. 2007. The Fatty Acid Profile of the Marine Cephalopod: *Loligo vulgaris*. *Israeli Journal of Aquaculture/Bamidgeh*, 59(3): 133–136.

Samuel, V.D. & J. Patterson. 2002. Intercapsular embryonic development of the big fin squid *Sepioteuthis lessoniana* (Loliginidae). *Indian Journal of Marine Sciences*, 31(2): 150–152.

San Miguel, A. 1977. Feeding habits of the Dolphin, *Tursiops truncatus*. *Revista de Parque Zoológico de Barcelona*, 28: 12–13.

***Sanchez, P.** 1981. Cefalopodos capturados durante la campaña “Benguela I” en el SW africano. *Resultados de Expediciones Cientificas*, 9: 29-35.

***Sanchez, P.** 1982. Algunos aspectos biologicos de la pota (*Todarodes sagittatus*, Lamarck) de las aguas de Namibia. *Collection of Scientific Papers of the International commission for the Southeast Atlantic Fisheries*, 9(II): 319–322.

Sanchez, P. 1984. Determinacion de la edad y de los parametros del crecimiento de *Illex coindetii* (Verany, 1837) en el mar Catalan (Mediterraneo Occidental). *Investigacion Pesquera*, 48: 59–70.

Sanchez, P. 1986a Bathymetric distribution and abundance of some cephalopods in the Catalan Sea, northeast Spain. *Investigacion Pesquera (Barcelona)*, 50: 237–246.

Sanchez, P. 1986b. Donneés preliminaires sur la biologie de trois especes de Cephalopodes de la Mer Catalane. *Rapp. Comm. Int. Mer Medit.*, 30: 247.

***Sanchez, P.** 1988. Systematics and distribution of the cephalopodos of Namibia. *Monografias de Zoologia Marina*, 3: 205–366.

Sanchez, P. 1995. Age and growth of *Illex coindetii*. *ICES Marine Science Symposium*, 199: 441–444.

***Sanchez, P.** 2003. Cephalopods from off the Pacific coast of Mexico: biological aspects of the most abundant species. *Scientia Marina*, 67(1): 81–90.

Sanchez, P. & M. Gonzalez. 2006. Modelling catch and climatic variables in *Loligo vulgaris* and *Sepia officinalis* fisheries in two Spanish Mediterranean ports. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 99.

Sanchez, P. & A. Guerra. 1994. Bathymetric distribution and aspects of the life history of the loliginid squid *Loligo vulgaris* (Mollusca: Cephalopoda) in the Catalan sea (NW Mediterranean). *Iberus*, 12(2): 1–12.

Sanchez, P. & P. Martin. 1993. Population dynamics of the exploited cephalopod species of the Catalan Sea (NW Mediterranean). *Scientia Marina*, 57 (2–3): 153–159.

***Sanchez, P. & B. Moli.** 1984. The cephalopods of the Namibian coast (SE Atlantic). *Res. Exped. Cient. B/O Cornide De Saavedra*, 12:3–22.

***Sanchez, P. & B. Moli.** 1985. An annotated list of cephalopod larvae collected off the Mediterranean coast of Spain, 1976–1981. *Vie et Milieu*, 35(3–4): 171–173.

Sanchez, P., M. Baeta & R. Allue. 2006. Biology and population dynamics of *Loligo vulgaris* in Catalan waters. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 99.

Sanchez, P., P. Belcari & P. Sartor. 1998a. Composition and spatial distribution of cephalopods in two northwestern Mediterranean areas. *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 17–24.

***Sanchez, G., H.M. Perry, C.B. Trigg, M. Vecchione, C. Roper & P.M. Biesiot.** 1996. Morphometry of juvenile and subadult *Loligo pealei* and *L. plei* from the northern Gulf of Mexico. *Fishery Bulletin*, 94(3): 535–550.

***Sanchez, P., A.F. Gonzalez, P. Jereb, V.V. Laptikhovsky, K.M. Mangold, Ch.M. Nigmatullin & S. Ragonese.** 1998b. *Illex coindetii*. *In*: *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 59–76.

Sanchez, P., P. Sartor, L. Recasens, A. Ligas, J. Martin, S. De Ranieri & M. Demestre. 2007. Trawl catch composition during different fishing intensity periods in two Mediterranean demersal fishing grounds. *Scientia Marina*, 71(2): 765–773.

Sanchez-Alonso, I., M. Careche & A.J. Borderias. 2007. Method for producing a functional protein concentrate from giant squid (*Dosidicus gigas*) muscle. *Food Chemistry*, 100(1): 48–54.

Sanchez-Brambila, G.Y., G. Alvarez-Manilla, F. Soto-Cordova, B.G. Lyons & R. Pecheco-Aguilar. 2004. Identification and characterization of the off-flavor in mantle muscle of jumbo squid (*Dosidicus gigas*) from the Gulf of California. *Journal of Aquatic Food Product Technology*, 13(1): 55–67.

Sands, C.J., S.N. Jarman & G.D. Jackson. 2003. Genetic differentiation in the squid *Moroteuthis ingens* inferred from RAPD analysis. *Polar Biology*, 26(3): 166–170.

Santos, M.B., M.R. Clarke & G.J. Pierce. 2001a. Assessing the importance of cephalopods in the diet of marine mammals and other top predators: problems and solutions. *Fisheries Research*, 52: 121–139.

Santos, M.B, V. Martin, M. Arbelo, A. Fernandez & G.J. Pierce. 2007. Insights into the diet of beaked whales from the atypical mass stranding in the Canary Islands in September 2002. *Journal of the Marine Biological Association of the United Kingdom*, 87(1): 243–251.

Santos, M.B., G.J. Pierce, A. Lopez, A. Barreiro & A. Guerra. 1996a. Diets of small cetaceans stranded in NW Spain 1994–95. *Copenhagen Denmark ICES*, 6 pp.

Santos, M.B., G.J. Pierce, H.M. Ross, R.J. Reid & B. Wilson. 1994. Diets of small cetaceans from the Scottish coast. *Copenhagen Denmark ICES*, 16 pp.

Santos, M.B., G.J. Pierce, R. Fernández, A. López, J.A. Martínez & E.N. Ieno. 2005a.Variability in the diet of bottlenose dolphins (*Tursiops truncatus*) in Galician waters and relationship with their prey abundance. *ICES Council Meeting*, 2005/R: 29.

Santos, M.B., G.J. Pierce, E.N. Ieno, M. Addink, C. Smeenk & C.C. Kinze. 2005b. Harbour porpoise (*Phocoena phocoena*) feeding ecology in the eastern North Sea. *ICES Council Meeting*, 2005/R:15.

Santos, M.B., G.J. Pierce, A. Lopez, R.J. Reid, V. Ridoux & E. Mente. 2006. Pygmy sperm whales *Kogia breviceps* in the northeast Atlantic: New information on stomach contents and strandings. *Marine Mammal Science*, 22(3): 600–616.

Santos, M.B., G.J. Pierce, R.J. Reid, I.A.P. Patterson, H.M. Ross & E. Mente. 2001b. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom*, 81(1): 873–878.

Santos, M.B., G.J. Pierce, T.J. Carter, S. Hoskins, H.M. Ross, R.J. Reid & C. Mckenzie. 1996b. Stomach contents of sperm whales stranded in the North Sea. *Copenhagen Denmark ICES*, 5 pp.

Santos, M.B., G.J. Pierce, J. Herman, A. Lopez, A. Guerra, E. Mente & M.R. Clarke. 2001c. Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): a review with new information on the diet of this species. *Journal of the Marine Biological Association of the United Kingdom*, 81(4): 687–694.

Santos, M.B., G.J. Pierce, C. Smeenk, M.J. Addink, C.C. Kinze, S. Tougaard & J. Herman. 2001d. Stomach contents of northern bottlenose whales *Hyperoodon ampullatus* stranded in the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, 81: 143–150.

Santos, M.B., G.J. Pierce, J.A. Learmonth, R.J. Reid, H.M. Ross, I.A.P. Patterson, D.G. Reid & D. Beare. 2004a. Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. *Marine Mammal Science*, 20: 1–27.

***Santos, M.B., J.G. Pierce, P.R. Boyle, R.J. Reid, H.M. Ross, I.A.P. Patterson, C.C. Kinze, S. Tougaard & R. Lick.** 1999. Stomach contents of sperm whales *Pyseter macrocephalus* stranded in the North Sea 1990–1996. *Marine Ecology Progress Series*, 183: 281–294.

Santos, M.B., G.J. Pierce, A. López, J.A. Martínez, R. Fernández, E. Ieno, F. Porteiro, P. Carrera & M. Meixide. 2004b. Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991–2003 and relationship with prey abundance. *ICES Council Meeting*, 2004/Q:09.

Santos, M.B., G.J. Pierce, A. López, J.A. Martínez, M.T. Fernández, E. Ieno, E. Mente, C. Porteiro, P. Carrera. & M. Meixide. 2004c. Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991 – 2003 and relationship with prey abundance. *ICES*, 2004 Q:09.

Santos, M.B., G.J. Pierce, M. Garcia-Hartmann, C. Smeenk, M.J. Addink, T. Kuiken, I.A.P. Pattersen, R.J. Reid, C. Lordan, E. Rogan & E. Mente. 2002. Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the northeast Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 82(3): 501–507.

Santos, R.A. 1992. Relacoes troficas de *Illex argentinus* (Castellanos, 1960) (Teuthoidea: Ommastrephidae), no sul do Brasil. Tesis de Maestrado. *Fundacao Universidade do Rio Grande*, 85 pp.

Santos, R.A. & M. Haimovici. 1997. Reproductive biology of the winter-spring spawners of *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil. *Scientia Marina*, 61: 53–64.

Santos, R.A. & M. Haimovici. 1998a. Trophic relationships of the long-finned squid *Loligo sanpaulensis* on the southern Brazilian shelf. *In*: A.I.L. Payne, M.R. Lipinski & M.A.C. Roeleveld, EDS. Cephalopod Biodiversity, Ecology and Evolution. *South African Journal of Marine Science*, 20: 81–91.

Santos, R.A. & M. Haimovici. 1998b. Cephalopods in the diet of marine mammals stranded or incidentally caught along Southeast and Southern Brazil (21° to 34° S). *Copenhagen Denmark ICES*, 15 pp.

Santos, R.A. & M. Haimovici. 2001. Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21° to 34°S). *Fisheries Research, Amsterdam*, 2(1–2): 99–112.

***Santos, R.A. & M. Haimovici.** 2002. Cephalopods in the trophic relations off southern Brazil. *Bulletin of Marine Science. Special Issue: Cephalopod Biomass and Production. [Part II.]*. 71: 753–770.

Sartor, P., P. Belcari, A. Carbonell, M. Gonzalez, A. Quetglas & P. Sanchez. 1998. The importance of cephalopods to trawl fisheries in the western Mediterranean Sea. *In*: A.I.L. Payne, M.R. Lipinski & M.A.C. Roeleveld, eds. Cephalopod Biodiversity, Ecology and Evolution. *South African Journal of Marine Science*, 20: 67–72.

Sarvaiya, R.T. 1991. Prospect for export of dried squid from India. *Seafood Export Journal*, 23: 6–8.

***Sasaki, M.** 1914. Notes on the Japanese Myopsida. *Annotationes Zoologicae Japonenses*, 8(5): 587–529.

Sasaki, M. 1915a. On a new species of oegopsid from the Bay of Toyama, *Gonatus septemdentatus*. *Transactions of the Sapporo Natural History Society*, 5(3): 185–189.

***Sasaki, M.** 1915b. On three interesting new oegopsids from the Bay of Sagami. *Journal of the College of Agriculture, Tohoku Imperial University, Sapporo*, 6(6): 131–150, 4 figs, 1 pl.

***Sasaki, M.** 1916. Notes on oegopsid cephalopods found in Japan. *Annotationes Zoologicae Japonenses*, 9(2): 89–120, 1 pl.

***Sasaki, M.** 1920. Report on cephalopods collected during 1906 by the United States Bureau of Fisheries steamer "Albatross" in the northwestern Pacific. *Proceedings of the United States National Museum*, 57(2310): 163–203, 4 pls.

Sasaki, M. 1921. On the life history of an economic cuttlefish of Japan, *Ommastrephes sloani pacificus*. Translation, *Wagner Free Institute of Science of Philadelphia*, 9: 1–25.

***Sasaki, M.** 1923. On a new eight-armed squid from Hokkaido, *Gonatopsis borealis* n. sp. *Annotationes Zoologicae Japonenses*, 10: 203–207, 1 fig.

***Sasaki, M.** 1929. A monograph of the dibranchiate cephalopods of the Japanese and Adjacent Waters. *Journal of the College of Agriculture, Hokkaido Imperial University*, 20: 1–357.

Sato, T. & H. Hatanaka. 1983. A review of assessment of Japanese distant-water fisheries for cephalopods. *In*: J.F. Caddy, ed. "Advances in assessment of world cephalopod resources". *FAO*, Rome, Italy, 231: 145–180.

Sauer, W.H.H. 1995a. The impact of fishing on chokka squid *Loligo vulgaris* reynaudii concentrations on inshore spawning grounds in the south-eastern cape, South Africa. *South African Journal of Marine Science*, 16: 185–193.

Sauer, W.H.H. 1995b. South Africa's Tsitsikamma National Park as a protected breeding area for the commercially exploited chokka squid *Loligo vulgaris reynaudii*. *South African Journal of Marine Science*, 16: 365–371.

Sauer, W.H.H. 1998. A bottomless pit of 'white gold' in the Eastern Cape, South Africa: Sex education and the common squid. African Fishes and Fisheries Diversity and Utilisation. *In* L. Coetzee, J. Gon & C. Kulongowski, eds. *Grahamstown South Africa Fisa*, Paradi, p. 168.

Sauer, W.H.H. & M.R. Lipinski. 1990. Histological validation of morphological stages of sexual maturity in chokker squid *Loligo vulgaris reynaudii* D'Orb (Cephalopoda: Loliginidae). *South African Journal of Marine Science*, 9: 189–200.

Sauer, W.H.H. & M.R. Lipinski. 1991. Food of squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) on their spawning grounds off the eastern Cape, South Africa. *South African Journal of Marine Science*, 10: 193–201.

Sauer, W.H.H. & Y. Melo. 2000. Birth control measures in squid. 10th Southern African Marine Science Symposium SAMSS 2000. *Land, Sea and People in the New Millennium Abstracts.*

Sauer, W.H.H. & M.J. Smale. 1991. Predation patterns on the inshore spawning grounds of the squid *Loligo vulgaris reynaudii* (Cephalopoda Loliginidae), off the eastern Cape, South Africa. *South African Journal of Marine Science*, 11: 513–523.

Sauer, W.H.H. & M.J. Smale. 1993. Spawning behaviour of *Loligo vulgaris reynaudii* in shallow waters of the south eastern Cape, South Africa. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology*, 489–498.

Sauer, W.H.H., W.S. Goschen & A.S. Koorts. 1991. A preliminary investigation of the effect of sea temperature fluctuations on squid catches in the inshore areas of the eastern Cape. *South African Journal of Marine Science*, 11: 467–473.

Sauer, W.H.H., M.R. Lipinski & C.J. Augustyn. 2000. Movement of the squid *Loligo vulgaris reynaudii*. *Fisheries Reserch*, 45: 283–289.

Sauer, W.H.H., Y.C. Melo & W. de Wet. 1999. Fecundity of the chokka squid *Loligo vulgaris reynaudii* on the southeastern coast of South Africa. *Marine Biology*, 135(2): 315–319.

Sauer, W.H.H., M.J. Smale & M.R. Lipinski. 1992. The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape Coast, South Africa. *Marine Biology*, 114(1): 97–107.

Sauer, W.H.H., C. McCarthy, M.J. Smale & A.S. Koorts. 1993. An investigation of the egg distribution of the chokka squid, *Loligo vulgaris reynaudii*, in Krom Bay, South Africa. *Bulletin of Marine Science*, 53(3): 1066–1077.

Sauer, W.H.H., M.J. Roberts, M.R. Lipinski, M.J. Smale, R.T. Hanlon, D.M. Webber & R.K. O'Dor. 1997. Choreography of the squid's "nuptial dance". *Biological Bulletinof the MarineBiological Laboratory of Woods Hole*, 192(2): 203–207.

Savinykh, V.F. 1993. Feeding of the Pacific pomfret, Brama japonica. *Journal of Ichthyology*, 33(5): 644–650.

Savinykh, V.F. 1999. Nektonic community of the epipelagial zone of the Californian convergence region in winter. *Journal of Ichthyology*, 39(1): 29–42.

Savinykh, V.F. 2006. The micronekton community of the epi- and mesopelagic layers of the Kuroshio current zone. *PICES 14th Annual Meeting, Book of Abstracts*, p. 59.

Savinykh, V.F., N.S. Kosenok & M.A. Zuev. 2005. Distribution and feeding of Japanese flying squid in the subarctic boundary zone. *PICES 14th Annual Meeting Book of Abstracts*, p. 123.

Savinykh, V.F., G.A. Shevtsov, K.A. Karyakin, E.V. Slobodskoi & Yu.V. Novikov. 2003. Yearly variability of migrations in nekton fishes and squids in the Pacific waters of the South Kuril Isles. *Journal of Icthyology*, 43(9): 729–740.

Sawada, K. 2006. Estimation of target strength and mantle length, and behavioural observation of squids using in situ acoustic-optical system. *Cephalopod International Advisory Council Symposium 2006, Abstract*, p. 29.

Scandol, J.P., T.J. Underwood & M.K. Broadhurst. 2006. Experiments in gear configuration to reduce by-catch in an estuarine squid-trawl fishery. *Fishery Bulletin*, 104(4): 533–541.

Scharenberg, A. 1997. Developmental aspects of embryonic integument in *Alloteuthis media* (Cephalopoda, Loliginidae): A scanning electron microscopical study. *In*: S.v. Boletzky, P. Fioroni & A. Guerra, eds. *Functional Morphology of Cephalopods*. Banyuls sur Mer France, Laboratoire Arago, 47(2): 149–153.

Schmidtberg, H. 1997. The structure of suckers of newly hatched *Sepia officinalis*, *Loligo vulgaris* and *Octopus vulgaris*. *In*: S.v. Boletzky, P. Fioroni & A. Guerra, eds. *Functional Morphology of Cephalopods*. Banyuls sur Mer, France, Laboratoire Arago, 47(2): 155–159.

Schoen, P.J., W.H.H. Sauer & M.J. Roberts. 2002. Environmental influences on spawning aggregations and jig catches of chokka squid *Loligo vulgaris reynaudii*: a `black box' approach. *Bulletin of Marine Science*, 71(2): 783–800.

***Seapy, R.R. & R.E. Young.** 1986. Concealment in epipelagic pterotracheid heteropods (Gastropoda) and cranchiid squids (Cephalopoda). *Journal of Zology*, (A), 210(1): 137–147.

Segawa, S. 1987. Life history of the oval squid *Sepioteuthis lessoniana* in Kominato and adjacent waters of central Honshu, Japan. *Journal of the Tokyo University of Fisheries*, 74: 67–105.

Segawa, S. 1990. Food consumption, food conversion and growth rates of the oval squid *Sepioteuthis lessoniana* by laboratory experiments. *Bulletin of the Japanese Society of Scientific Fishery*, 56(2): 217–222.

Segawa, S. 1991. Body size and oxygen consumption rate of the oval squid *Sepioteuthis lessoniana*. *Bulletin of the Japanese Society of Scientific Fishery,* 57(9): 1651–1656.

Segawa, S. 1995. Effect of temperature on oxygen consumption of juvenile oval squid *Sepioteuthis lessoniana*. *Fishery Science*, 61(5): 743–746.

***Segawa, S., S. Hirayama & T. Okutani.** 1993a. Is *Sepioteuthis lessoniana* in Okinawa a single species? *In*: T. Okutani, R. K. O'Dor & T. Kubodera, eds. Recent Advances in Cephalopod. *Fisheries Biology. Tokyo*, pp. 513–521.

***Segawa, S., W.T. Yang, H.J. Marthy & R.T. Hanlon.** 1988. Illustrated embryonic stages of the Eastern Atlantic squid *Loligo forbesi*. *The Veliger*, 30: 230–243.

Segawa, S., T. Izuka, T. Tamashiro & T. Okutani. 1993b. A note on mating and egg deposition by *Sepioteuthis lessoniana* in Ishigaki Island, Okinawa, southwestern Japan. *Venus, Japanese Journal of Malacology*, 52: 101–108.

Seibel, B.A. 2007. On the depth and scale of metabolic rate variation: scaling of oxygen consumption rates and enzymatic activity in the class Cephalopoda (Mollusca). *Journal of Experimental Biology*, 210(1): 1–11.

Seibel, B.A. & D.B. Carlini. 2001. Metabolism of pelagic cephalopods as a function of habitat depth: a re-analysis using phylogenetically independent contrasts. *Biological Bulletin*, 201: 1–5.

***Seibel, B.A., F.G. Hochberg & D.B. Carlini.** 2000a. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): deep-sea spawning and post-spawning egg care. *Marine Biology*, 137: 519–526.

*__Seibel, B.A., B.H. Robison & S.H.D. Haddock.__ 2005. Post-spawning egg care by a squid. *Nature*, 438: 929.

*__Seibel, B.A., E.V. Thuesen & J.J. Childress.__ 2000b. Light-limitation on predator-prey interactions: consequences for metabolism and locomotion of deep-sea cephalopods. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 198(2): 284–298.

*__Seibel, B.A., E.V. Thuesen, J.J. Childress & L.A. Gorodezky.__ 1997. Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. *Biological Bulletin*, 192(2): 262–278.

*__Seibel, B.A., S.K. Goffredi, E.V. Thuesen, J.J. Childress & B.H. Robison.__ 2004. Ammonium content and buoyancy in midwater cephalopods. *Journal of Experimental Marine Biology and Ecology*, 313(2): 375–387.

Seidou, M., M. Sugahara, H. Uchiyama, K. Hiraki, T. Hamanaka, M. Michinomae, K. Yoshihara & Y. Kito. 1990. On the three visual pigments in the retina of the firefly squid, *Watasenia scintillans*. *Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology*, 166(3): 769–773.

Seki, M. 1993. Trophic relationships of *Ommastrephes bartramii* during winter migrations to subtropical waters north of the Hawaiian Islands. *In* T. Okutani, R.K. O'Dor, T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology.* Tokyo. *Tokai University Press*, 523–529.

Sekiguchi, K. 1995. Occurrence, behavior and feeding habits of harbor porpoises (*Phocoena phocoena*) at Pajaro Dunes, Monterey Bay, California. *Aquatic Mammals*, 21(2): 91–103.

Sekiguchi, K., N.T.W. Klages & P.B. Best. 1992. Comparative analysis of the diets of smaller odontocete cetaceans along the coast of southern Africa. *South African Journal of Marine Science*, 12: 843–861.

Sekiguchi, K.N., T.W. Klages & P.B. Best. 1996. The diet of strap-toothed whales (*Mesoplodon layardii*). *Journal of Zoology*, 239(3): 453–463.

Sekiguchi, K., N. Klages, K. Findlay & P.B. Best. 1993. Feeding habits and possible movements of southern bottlenose whales (*Hyperoodon planifrons*). Proceedings of NIPR Symposium. *Polar Biology*, 6: 84–97.

Selman K. & J.M. Arnold. 1977. An ultrastructural and cytochemical analysis of Oogenesis in the squid *Loligo pealei*. *Journal of Morphology*, 152: 381–400.

Selvaraj, P., G.I. Jasmine & P. Jeyachandran. 1991. Effect of ascorbic acid dip treatment on frozen storage of squid (*Loligo duvaucelii*, Orbigny). *Fisheries Technology, Society of fisheries Technology, Kochi*, 28(2): 117–121.

Semmens, J.M. 2002. Changes in the digestive gland of the loliginid squid *Sepioteuthis lessoniana* (Lesson 1830) associated with feeding. *Journal of Experimental Marine Biology and Ecology*, 274(1): 19–39.

Semmens, J.M. & G.D. Jackson. 2005. Evaluation of biochemical indices for assessing growth and condition of the deepwater squid *Moroteuthis ingens*. *Marine Ecology Progress Series*, 289: 25–223.

Semmens, J.M. & N.A. Moltschaniwskyj. 2000. An examination of variable growth in the loliginid squid *Sepioteuthis lessoniana*: A whole animal and reductionist approach. *Marine Ecology Progress Series*, 193: 135–141.

Semmens, J.M., G.T. Pecl, B.M. Gillanders, C.M. Waluda, E.K. Shea, D. Jouffre, T. Ichii, K. Zumholz, O.N. Katugin, S.C. Leporati & P.W. Shaw. 2007. Approaches to resolving cephalopod movement and migration patterns. *Reviews in Fish Biology and Fisheries*, 17(2–3): 401–423.

Sen, H. 2004a. A preliminary study on the effects of salinity on egg development of European squid (*Loligo vulgaris* Lamarck, 1798). *The Israeli Journal of Aquaculture/Bamidgeh*, 56(2): 93–99.

Sen, H. 2004b. Effects of photoperiodicity on development and incubation of squid (*Loligo vulgaris* Lamarck, 1798) eggs. *Journal of Fisheries & Aquatic Sciences*, 21(3–4): 211–214.

Sen, H. 2005. Incubation of European Squid (*Loligo vulgaris* Lamarck, 1798) eggs at different salinities. *Aquaculture Research*, 36: 876–881.

Sendao, S.J., I. Goncalves & T.C. Borges. 2002. By-catch and discards of cephalopods in the fisheries of the South Portuguese coast. *Bulletin of Marine Science*, 71(2): 1139.

Sennikov, A.M. & T.E. Bliznichenko. 1985. Spatial-temporal structure of feeding concentrations of the squid *Todarodes sagittatus* (Lamarck) in the Barents Sea. *ICES Council Meeting1985/K3*, 1–13.

Sennikov, A.M., S.G. Mukhin & T.E. Bliznichenko. 1989. Distribution and trophic importance of juvenile squid (*Gonatus fabricii* Lichtenstein) in the Norwegian and Barents Seas in 1986–1988. *Copenhagen Denmark ICES*, 18 pp.

Sennikov, A.M., B.P. Shimko, S.G. Mukhin & T.E. Bliznichenko. 1985. Biology and distribution of the winter-spawning group of the European flying squid *Todarodes sagittatus* (Lamarck)in the northern Atlantic. *In*: B.G. Ivanov, ed. Resources and fishery perspectives of squids of the world ocean. *Moscow, VNIRO Press*, 29–37 (in Russian, English Abstract)

Shabalin, V.N. 1993. Causes of catching effect in a light jigger longline squid fishery under condition of acoustic stimulation. *Commercial Fishery Technology*, 1993: 163–177.

Shannon, L.V., R.J.M. Crawford, D.E. Pollock, L. Hutchings, A.J. Boyd, J. Taunton-Clark, A. Badenhorst, R. Melville-Smith, C.J. Augustyn, K.L. Cochrane, I. Hampton, G. Nelson, D.W. Japp & R.J.Q. Tarr. 1992. The 1980s. A decade of change in the Benguela ecosystem. *In*: A.I.L. Payne, K.H. Brink, K.H. Mann & R. Hilborn, eds. “Benguela trophic functioning”. *South African Journal of Marine Science*, 12: 271–296.

Shao, Q., W. Ma, Z. Chen, Z. You & W. Wang. 2005. Relationship between Kuroshio meander pattern and *Ommastrephes bartramii* CPUE in northwest Pacific Ocean. *Oceanologia et limnologia sinica*, 36(2): 111–122.

Sharifuddin B.A.O., E. Danakusumah, C. Rani, E. Siswanto & A.R. Hade. 2000. Incubation period and hatching rate of bigfin squid, *Sepioteuthis lessoniana*, in 24 to 38 ppt salinity. *Special publication, Phuket Marine Biological Center*, 25(pt. 1): 139–143.

Shashar, N. & R.T. Hanlon. 1997. Squids (*Loligo pealei* and *Euprymna scolopes*) can exhibit polarized light patterns produced by their skin. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 193(2): 207–208.

Shashar, N., R.T. Hanlon & A.M. de Petz. 1998. Polarization vision helps detect transparent prey. *Nature*, 393(6682): 222–223.

Shaw, P.W. 1997. Polymorphic microsatellite markers in a cephalopod: the veined squid *Loligo forbesi*. *Molecular Ecology*, 6(3): 297–298.

Shaw, P.W. & G.J. Adcock. 2002. Polymorphic microsatellite DNA markers for the Patagonian squid, *Loligo gahi* (Cephalopoda). *Molecular Ecology Notes*, 2(3): 331–333.

Shaw, P.W. & P.R. Boyle. 1997. Multiple paternity within the brood of single females of *Loligo forbesi* (Cephalopoda: Loliginidae), demonstrated with microsatellite DNA markers. *Marine Ecology Progress Series*, 160: 279–282.

***Shaw, P.W., G.J. Pierce & P.R. Boyle.** 1999. Subtle population structuring within a highly vagile marine invertebrate, the veined squid *Loligo forbesi*, demonstrated with microsatellite DNA markers. *Molecular Ecology*, 8: 407–417.

***Shaw, P.W., A.I. Arkhipkin, G.J. Adcock, W.J. Burnett, G.R. Carvalho, J.N. Scherbich & P.A. Villegas.** 2004. DNA markers indicate that distinct spawning cohorts and aggregations of Patagonian squid, *Loligo gahi*, do not represent genetically discrete subpopulations. *Marine Biology*, 144(5): 961–970.

Shchenikova, N.V. 1992. Effect of storage conditions and thermal treatment on phospholipids in the Pacific squid. *Voprosy pitaniia*, 2: 71–73.

Shchenikova, N.V., Eh.V. Pavlycheva, S.A. Davydova, S.V. Isag & L.I. Sokolova. 1987. Fatty acid composition of lipids from mantle and liver of some cephalopods. *Voprosy pitaniia*, 6: 61–64.

Shchetinnikov, A.S. 1989. Food spectrum of squid *Dosidicus gigas* (Oegopsida) and its variations in ontogenesis. *Zoologicheskij Zhurnal*, 68(7): 28–39.

Shchetinnikov, A.S. 1992. Feeding spectrum of squid, *Sthenoteuthis oualaniensis*, in the eastern Pacific. *Journal of the Marine Biological Association of the United Kingdom*, 72(4): 849–860.

Shea, E.K. 1995. The early life histories of three families of cephalopods (Order Teuthoidea) and an examination of the concept of a paralarva. *M.Sc. Thesis, College William and Mary, Williamsburg, VA*, 133 p.

***Shea, E.K. & M. Vecchione.** 2002. Quantification of ontogenetic discontinuities in three species of oegopsid squids using model II piecewise linear regression. *Marine Biology*, 140: 971–979.

***Shea, E.K. & M. Vecchione.** 2006. Deep-sea pelagic cephalopods of Bear Seamount. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 37.

Shen, J., S. Han, X. Cui, H. Huang, S. Zhou, W. Fan, Y. Dong & D. Gao. 2003. An explanation on the poorer harvest of flying squid in the North Pacific in 2001. *Journal of Fisheries of China*, 27(4): 350–357.

Shen, X., W. Fan & X. Cui. 2004. Study on the relationship of fishing ground distribution of *Ommastrephes bartramii* and water temperature in the Northwest Pacific Ocean. *Marine Fisheries Research [Haiyang Shuichan Yanjiu]*, 25(3): 10–14.

Sherborn, C.D. & F.J. Griffin. 1934. On dates of publication of the natural history portions of Alcide d'Orbigny's "Voyage dans l'Amérique méridonale." *Annals and Magazine of Natural History series 13,*10(13): 130–134.

Shevchenko, A.I. 2005. Basic results of the studies in the laboratory of industrial fishery for the last 10 years. *Transactions of the Pacific Research Fisheries Centre*, 141: 372–381.

*Shevtsov, G.A. & N.B. Bessmertnaya.** 1996. Preliminary data on ripening and spawning of squid *Gonatopsis octopedatus* (Gonatidae, Cephalopoda) in the Russian Zone of the Japan Sea. *In*: *11th International Symposium "Okhotsk Sea and Sea Ice"*, Mombetsu, Hokkaido, Japan, 356–359.

Shevtsov, G.A. & O.N. Katugin. 2006. Species composition and occurrence of cephalopods in the South China Sea in spring 1986. Cephalopod International Advisory Council Symposium 2006, Abstract: 101.

*Shevtsov, G.A. & N.M. Mokrin.** 1998. Fauna of cephalopod molluscs in the Russian zone of the Japan Sea in summer–autumn. *Izvestiya TINRO (Transactions of the Pacific Research Institute of Fisheries and Oceanography)*, 123: 191–206 (In Russian, English summary).

Shevtsov, G.A., O.N. Katugin & V.I. Radchenko. 2000. Record of an egg mass of the sepiolid squid, *Rossia pacifica* Berry, 1911 in the Okhotsk Sea. *Ruthenica*, 10(2): 153–158.

*Shevtsov, G.A., O.N. Katugin & M.A. Zuev.** 2004a. Distribution and biology of *Gonatus kamtschaticus* (Cephalopoda, Gonatidae) in the Sea of Okhotsk and Pacific waters off the Kuril Islands. *In*: *Molluscs of the Northeastern Asia and Northern Pacific: Biodiversity, Ecology, Biogeography and Faunal History.* Vladivostok, Russia: 143–145.

Shevtsov, G.A., O.N. Katugin & M.A. Zuev. 2005a. Distribution of the large-sized boreopacific gonatid squid (*Gonatopsis borealis*) in the northwestern Pacific Ocean and adjacent marine areas. *In*: *PICES XIV*, Annual Meeting, Vladivostok, Russia, Abstract, 171.

*Shevtsov, G.A., A.Yu. Shigalin & Y. Ueno.** 2004b. Distribution of Cephalopoda in the Subarctic Front zone in the northwestern Pacific Ocean in July, 2000. *Transactions of the Pacific Research Institute of Fisheries and Oceanography*, 136: 181–196.

Shevtsov, G.A., O.N. Katugin, M.A. Zuev & G.V. Khen. 2006. Distribution of cephalopods in the western Subarctic Boundary in the autumn of 2001. *In*: *PICES XV*, Annual Meeting, Yokohama, Japan, Abstract: 55.

Shevtsov, G.A., M.A. Zuev, O.N. Katugin & N.M. Mokrin. 2005b. Distribution and biology of the Japanese common squid (*Todarodes pacificus*) in the Pacific Ocean off the Kuril islands and eastern Kamchatka in summer. *Ruthenica*, 15(2): 99–108.

*Shevtsova, S.P., A.P. Brestkin, K.N. Nesis & E.V. Rozengardt.** 1979. The differences in the cholinesterases properties of optic ganglia of squids, *Ommastrephes bartramii*, as markers of population isolation in the different parts of the disrupted species range. *Okeanologia*, 19(3): 481–486 (In Russian with English abstract).

Shevyrev, A.A. 2006. The cephalopod macrosystem: a historical review, the present state of knowledge, and unsolved problems. 1. Major features and overall classification of cephalopod mollusks. *Paleontologicheskii Zhurnal*, 6: 33–42.

Shieh, H.H. & T.S. Chiu. 2005. Analysis on the stock structure of *Ommastrephes bartramii*. *Journal of Fisheries Society of Taiwan*, 32(1): 53.

Shigeno, S. & M. Yamamoto. 2005. Embryonic brain development of loliginids: axonal scaffold and neuropil formation related to early life styles. *Phuket Marine Biological Center Research Bulletin*, 66: 155–165, 8 figs.

Shigeno S., K. Tsuchiya & S. Segawa. 2001. Conserved topological patterns and heterochronies in loliginid cephalopods: comparative developmental morphology of the oval squid *Sepioteuthis lessoniana*. *Invertebrate reproduction and development*, 39(3): 161–174.

Shimek, R.L., D. Fyfe, L. Ramsey, A. Bergey, J. Elliot & S. Guy. 1984. A note on the spawning of the Pacific market squid, *Loligo opalescens* (Berry, 1911), in the Barkley Sound region, Vancouver Island, Canada. *Fishery Bulletin*, 82: 445–446.

Shimizu, T. & M. Hamabe. 1975. A note on biology of the common squid, *Todarodes pacificus*, in the Yellow Sea viewed from the rate of copulation and the condition of maturity. *Bulletin of Tokai Regional Fisheries Research Laboratory*, 82: 1–23.

*Shimko, B.P.** 1984. Ageing and biological peculiarities of *Todaroders sagittatus* (Lamarck). *ICES Council Meeting1984/K*:12 1–12.

*__Shimko, B.P.__ 1989. Biology and peculiarities of the squid *Todarodes sagittatus* (Lamarck) distribution at early life stages. *ICES Council Meeting1989/K*:17 1–12.

*__Shimura, S., S. Abe, J.R. Bower, T. Kubodera & Y. Sakurai.__ 2006. Molecular species identification and morphology of gonatid squid paralarvae from the north Pacific. Cephalopod International Advisory Council Symposium 2006, Abstract: p.101.

Shimura, T., J. Yamamoto, Y. Kamai & Y. Sakurai, Y. 2005. *In*: C. Chotiyaputta, E.M.C. Hatfield, C.C. Lu, eds. *Phuket Marine Biological Center Research Bulletin*, 66: 267–273.

Shin, H.C., D.H. Kang & Y.S. Yang. 2005. Fate of the common squid population in Korean waters; a natural oceanographic experiment over various time scales. *PICES 14th Annual Meeting Book of Abstracts*, p. 127.

Shin, P.K.S. 1982. The Hong Kong squid fishery. *FAO Fisheries Report*, 175: 112–114.

Shinn, G.L. & N. McLean. 1989. *Hochbergia moroteuthensis* gen.et sp. nov., a giant protistan parasite from the giant squid *Moroteuthis robusta* (Mollusca: Cephalopoda). *Diseases of Aquatic Organisms*, 6(3): 197–200.

Shiomi, K. & H. Ogi. 1992. Feeding ecology and body size dependence on diet of the sooty shearwater, *Puffinus griseus*, in the North Pacific. *Japan National Institute of Polar Research*, 5: 105–113.

Shirai, T. & N. Kikuchi. 1997. Taste components of boreo pacific gonate squid *Gonatopsis borealis*. *Fisheries Science*, 63(5): 772–778.

Shojima, Y. 1970. Cephalopod larvae and eggs taken at the surface in the northern South China Sea. *Bulletin of the Seikai National Fisheries Research Institute*, 38: 61–77.

Shojima, Y. 1972. The common squid, *Todarodes pacificus*, in the East China Sea. II. Eggs, larvae and spawning ground. *Bulletin of the Seikai National Fisheries Research Institute*, 42: 25–58.

Shojima, Y. & H. Hotta. 1972. On common squid distributed in the east China Sea. *Research Report of the Technical Council of Agriculture, Forestry and Fisheries*, 57: 31–43.

Shotton, R. 2005. Northwest Atlantic. Review of the state of world marine fishery resources. *FAO Fisheries Technical Paper*, 457: 15–22,

Shukhgalter, O.A. & C.M. Nigmatullin. 2001. Parasitic helminths of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in open waters of the central east Pacific. *Fisheries Research*, 54(1): 95–110.

Shulman, G.E., A.M. Shchepkina & M.V. Chesalin. 1992. Physiologo-biochemical analysis of the food supply of squid in dynamically active zones of the East Atlantic. *Transactions of the Russian Academy of Sciences*, 322(4): 813–816.

Shulman, G.E., M.V. Chesalin, G.I. Abolmasova, T.V. Yuneva & A. Kideys. 2002. Metabolic strategy in pelagic squid of genus *Sthenoteuthis* (Ommastrephidae) as the basis of high abundance and productivity: An overview of the Soviet investigations. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(2): 815–836.

Shuntov, V.P. & V.V. Sviridov. 2005. The Bering Sea ecosystems at the brink of 20 and 21 centuries. *Transactions of the Pacific Research Fisheries Centre*, 142: 3–29.

Shvetsova, V.D. 1974. Cephalopoda of the Indian Ocean. *Rybokhozyaistvennoe Ispol'zovanie Resursov Mirovogo Okeana*, series 1, 8: 4–18.

Siegstad, H., P.B. Neve, M.P. Heide-Joergensen & T. Haerkoenen. 1998. Diet of the ringed seal (*Phoca hispida*) in Greenland. *In* M.P. Heide-Joergensen & C. Lydersen, eds. Ringed seals in the North Atlantic. *North Atlantic Marine Mammal Commision*, 1: 229–241.

Sifner, S.K. & N. Vrgoc. 2004. Population structure, maturation and reproduction of the European squid, *Loligo vulgaris*, in the Central Adriatic Sea. *Fisheries Research*, 69: 239–249.

Sifner, S.K., E. Lefkaditou, N. Ungaro, L. Ceriola, K. Osmani, S. Kavadas & N. Vrgoc. 2005. Composition and distribution of the cephalopod fauna in the eastern Adriatic and eastern Ionian sea. *Israel Journal of Zoology*, 51(4): 315–330.

*__Silas, E.G.__ 1968. Cephalopoda of the west coast of India collected during the cruises of the research vessel 'Varuna', with a catalogue of the species known from the Indian Ocean. Proceedings of the Symposium on Mollusca, Part I. *Marine Biological Association of India*, pp. 277–359.

*__Silas, E.G. (ed).__ 1986. Cephalopod Bionomics, Fisheries and Resources of the Exclusive Economic Zone of India. *Bulletin of the Central Marine Fisheries Research Institute*, 37: 195 pp.

*** Silas, E.G., K.P. Nair & R. Sarvesan.** 1985. New record of a loliginid squid, *Doryteuthis sibogae*, Adam 1954, (Cephalopoda; Loliginidae), from Indian waters. *Indian Journal of Fisheries*, 32: 281–287.

*** Silas, E.G., K.S. Rao, R. Sarvesan, K.P. Nair & M.M. Meiyappan.** 1982. The exploited squid and cuttlefish resources of India: a review. *Marine Fisheries Information Service, T & E, Series*, 34: 16 pp.

*** Silas, E.G., K.S. Rao, R. Sarvesan, K.P. Nair, K. Vidyasagar, M.M. Meiyappan, Y.A. Sastri & B.N. Rao.** 1986a. Some aspects of the biology of squids. *In*: E.G. Silas, ed. Cephalopod Bionomics, Fisheries and Resources of the Exclusive Economic Zone of India. *Bulletin of the Central Marine Fisheries Research Institute*, 37: 38–48.

Silas, E.G., R. Sarvesan, M.M. Meiyappan, K.P. Nair, K.S. Rao, K.Vidyasagar, Y.A. Sastri, P.V. Srinivasan & B.N. Rao. 1986b. Cephalopod fisheries at selected centres in India. *In*: E.G. Silas, ed. Cephalopod Bionomics, Fisheries and Resources of the Exclusive Economic Zone of India. *Bulletin of the Central Marine Fisheries Research Institute*, 37: 116–128.

*** Silva-Mello, R. de L.** 1998. Cephalopoda in the stomach content of pelagic fish collected at the southwestern Atlantic. Taxonomy. Fisheries considerations. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco*, 26(1): 43–49.

Silver, S.C., J.A. Patterson & P.G. Mobbs. 1983. Biogenic amines in cephalopod retina. *Brain Research*, 273(2): 366–368.

Simon, F., F. Rocha & A. Guerra. 1995. The small-scale hand-jig squid fishery in the northwestern Iberian Peninsula analysed using a model based on short fishery statistics survey. *Copenhagen Denmark ICES*, 12 pp.

Simon, F., F. Rocha & A. Guerra. 1996. The small-scale squid hand-jig fishery off the northwestern Iberian Peninsula: Application of a model based on a short survey of fishery statistics. *Fisheries Research*, 25(3–4): 253–263.

Simon, J.E. & P.A. Comeau. 1994. Summer distribution and abundance trends of species caught on the Scotian Shelf from 1970–1992, by the research vessel groundfish survey. *Canadian Technical Report of Fisheries and Aquatic Science*, 1953, 155 pp.

Simon, M.J., T.K. Kristensen, O.S. Tendal, C.C. Kinze & S. Tougaard. 2003. *Gonatus fabricii* (Mollusca, Theuthida) as an important food source for sperm shales (*Physeter macrocephalus*) in the northeast Atlantic. *Sarsia*, 88(3): 244–246.

*** Simone, L.R.L.** 1997. Redescription of *Lolliguncula brevis* (Blainville) (Myopsida, Loliginidae) from southeastern Brazil. *IHERINGIA, Serie Zoolgica*, 82:141–150.

Sims, D.W., M.J. Genner, A.J. Southward & S.J. Hawkins. 2001. Timing of squid migration reflects North Atlantic climate variability. *Proceedings of the Royal Society of London*, 268: 2607–2611.

Sinclair, B., L. Briskey, W. Aspden& G. Pegg. 2007. Genetic diversity of isolated populations of *Nautilus pompilius* (Mollusca, Cephalopoda) in the Great Barrier Reef and Coral Sea. *Reviews in Fish Biology and Fisheries*, 17(2–3): 223–235.

Sinclair, E.H. 1991. Review of the biology and distribution of the neon flying squid (*Ommastrephes bartramii*) in the North Pacific Ocean. *NOAA NMFS Technical Report*, 105: 57–67.

Sinclair, E.H., A.A. Balanov, T. Kubodera, V.I. Radchenko & Y.A. Fedorets. 1999. Distribution and ecology of mesopelagic fishes and cephalopods. *In*: T.R. Loughlin & K. Ohtani, eds. Dynamics of the Bering Sea, Alaska Sea Grant College Program, pp. 485–508.

*** Siraimeetan, P.** 1990. Cephalopod resources of the Gulf of Kutch, in Guajarat Coast. *Journal of the Marine Biological Association of India*, 32: 227–235.

Siriraksophon, S. & Y. Nakamura. 2001. Ecological aspects of the purpleback flying squid, *Sthenoteuthis oualaniensis* (Lesson) in the West Coast of Philippines. *The Needs of Scientific Research Programmes for Oceanographic and Coastal Data*, pp. 187–194.

Siriraksophon, S., Y. Nakamura & S. Natinee. 2001a. Exploration of purpleback flying squid, *Sthenoteuthis oualaniensis*, resources in the South China Sea. *Research paper series, Southeast Asian Fisheries Development Center*, 48: 81 pp.

Siriraksophon, S., N. Sukramongkil & Y. Nakamura. 2001b. Exploration of oceanic squid, *Sthenoteuthis oualaniensis*, resources in the South China Sea, Vietnamese waters. *Southeast Asian Fisheries Development Center*, 44: 181–197.

*__Sissenwine, M.P. & A.M. Tibbetts.__ 1977. Simulating the effect of fishing on squid (*Loligo* and *Illex*) populations of the Northeastern United States. *ICNAF Selected Papers*, 2: 71–84.

Siwicki, A.K., T. Miyazaki & I. Komatsu. 1998. Effects of heat extract from firefly squid, *Watasenia scintillans*, on the nonspecific defence mechanisms and protection against furunculosis in rainbow trout (*Oncorhynchus mykiss*). *Archives of Poland Fisheries*, 6(1): 59–66.

Siwicki, A.K., T. Miyazaki, I. Komatsu & T. Matsusato. 1996. In vitro influence of heat extract from firefly squid *Watasenia scintillans* on the phagocyte and lymphocyte activities in rainbow trout *Oncorhynchus mykiss*. *Fisheries Pathology*, 31(1): 1–7.

Skinner, J.D. & N. Klages. 1994. On some aspects of the biology of the Ross seal *Ommatophoca rosii* from King Haaxon VII Sea, Antarctica. *Polar Biology*, 14: 467–472.

Skira, I.J. 1986. Food of the short-tailed shearwater, *Puffinus tenuirostris*, in Tasmania. Australian Wildlife Research, 13(3): 481–488.

Slip, D.J. 1995. The diet of southern elephant seals (*Mirounga leonina*) from Heard Island. *Canadian Journal of Zoology, Review of Canadian Zoology*, 73(8): 1519–1528.

Slip, D.J., G.J. Moore & K. Green. 1995. Stomach contents of a southern bottlenose whale, *Hiperodon planifrons*, stranded at Heard Island. *Marine Mammal Science*, 11: 575–584.

Slobodskoj, E.V. 1986. Methods for determination of concentration density of the pelagic squid. *In*: B.G. Ivanov, ed. Resources and Perspectives of the Commercial Squid in the Oceans. *Moscow: VNIRO Publication*, 85–93 (In Russian with English abstract).

Smale, M.J. 1996. Cephalopods as prey. 4. Fishes. *Philosophical Transactions of the Royal Society of London, Series B*, 351: 1067–1081.

Smale, M.J. & M.N. Bruton. 1985. Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in southeastern Cape waters of South Africa. *South African Journal of Zoology*, 20(3): 97–108.

*__Smale, M.J. & G. Cliff.__ 1998. Cephalopods in the diets of four shark species (*Galeocerdo cuvier*, *Sphyrna lewini*, *S. zygaena* and *S. mokarran*) from Kwazulu-Natal, South Africa. *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 241–253.

Smale, M.J., W.H.H. Sauer & R.T. Hanlon. 1995. Attempted ambush predation on spawning squids *Loligo vulgaris reynaudii* by benthic pyjama sharks, *Poroderma africanum*, off South Africa. *Journal of the Marine Biological Association of the United Kingdom*, 75(3): 739–742.

Smale, M.J., W.H.H. Sauer & M.J. Roberts. 2001. Behavioural interactions of predators and spawning chokka squid off South Africa: towards quantification. *Marine Biology*, 139(6): 1095–1105.

*__Smith, A.G.__ 1881. Account of the Zoological Collection made during the survey of H.M.S "Albert" in the Strait of Magellan and on the Coast of Patagonia, IV: Mollusca and Molluscoida. *Proceedings of the Zoological Society of London*, 1881(1): 22–44.

Smith H.K. 1983. The development potential of the southern calamary. South Australia Department of Fisheries, Adelaide.

Smith, H.K. 1983. Fishery and biology of *Nototodarus gouldi* (McCoy, 1888) in western Bass Strait. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Memoirs of the National Museum of Victoria, Australia*, 44: 285–290.

Smith, J.D. 1983. Radio-nuclides and heavy metals in *Nototodarus gouldi*. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. *Memoirs of the National Museum of Victoria, Australia*, 44: 201–203.

Smith, J.M. & G.J. Pierce. 2006. A case study of the socio-economics and catch and effort data on a small-scale, artisanal *Loligo* fishery in the northern Aegean Sea. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract, p.104.

Smith, J.M. & G.J. Pierce. 2006. The socio-economics and catch and effort data on a small-scale directed squid fishery in the Moray Firth, Scotland (UK). *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 103.

Smith, J.M., G.J. Pierce & A.F. Zuur. 2006. A comparison of seasonal patterns of investment in reproductive and somatic tissues in squid across several European stocks. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p.103.

Smith, J.W. 1984. Larval ascaridoid nematodes in myopsid and oegopsid cephalopods from around Scotland and in the northern North Sea. *Journal of the Marine Biological Association of United Kingdom*, 64(3): 563–572.

*__Smith, P.J., P.E. Roberts & R.J. Hurst.__ 1981. Evidence for two species of arrow squid in the New Zealand fishery. New Zealand *Journal of Marine and Freshwater Research*, 15: 247–253.

*__Smith, P.J., R.H. Mattlin, M.A. Roeleveld & T. Okutani.__ 1987. Arrow squids of the genus *Nototodarus* in New Zealand waters: Systematics, biology and fisheries. *New Zealand Journal of Marine and Freshwater Research*, 21(2): 315–326.

Smith, S.C. & H. Whitehead. 2000. The diet of Galapagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. *Marine Mammal Science*, 16(2): 315–325.

Snyder, R. 1998. Aspects of the biology of the giant form of *Sthenoteuthis oualaniensis* (Cephalopoda: Ommastrephidae) from the Arabian Sea. *Journal of Molluscan Studies*, 64: 21–34.

Sodikin, D. 1992. Review of squid fisheries in Indonesia. Proceedings of the Second World Cephalopod Conference, Squid '91, Madrid, Spain, 11–13 November 1991. *Agra-Europe, London*, pp. 129–144.

Soeda, J. 1956. Studies on the ecology and the breeding habits of the squid, *Ommastrephes sloani pacificus* (Steenstrup). *Bulletin of Hokkaido Regional Fisheries Experimental Research Laboratory*, 14: 1–24 (in Japanese with English summary).

Solem, A. & C.F.E. Roper. 1975. Structures of recent cephalopod radulae. *Veliger*, 18(2): 127–133.

Son, M.H. & S.Y. Hong. 1993. A short note on *Enoploteuthis* (*Paraenoploteuthis*) *chunii* (Cephalopoda: Enoploteuthidae) from the Korean waters. *Contributions of the Korea Institute of Ocean Science of National Fisheries, University of Pusan*, 25: 255–259.

Song, H., G.W. Baeck & S. Kim. 2005. Food and feeding of the commond squid *Todarodes pacificus* (Cephalopoda: Ommastrephidae) Off Busan, Korea. *PICES 14th Annual Meeting Book of Abstracts*, p. 128.

Song, H., T. Ding, K. Yu, J. Shen, X. Wang & B. Ruan. 1999. Species composition and quantitative distribution of cephalopod in the north of East China Sea. *Journal of the Zhejiang Ocean University of Natural Science*, 18: 99–106.

Soro, S. & M. Paolini. 1994. *Illex coindetii* (Verany, 1839): aspetti biologici ed evoluzione della popolazione in alto e medio Adriatico. *Biologia Marina Mediterranea*, 1: 213–218.

Soro, S. & G. Piccinetti Manfrin. 1989. Biologia e pesca di cefalopodi in Adriatico. *Nova Thalassia*, 10(Suppl. 1): 493–498.

Soselisa, J., S. Marjuki & W. Subani. 1986. Production and fishing season of squids (*Loligo* spp.) in Lombok (West Nusa Tenggara) and adjacent waters. *Journal of Marine Fisheries Research*, 34: 79–90.

*__Souleyet, F.L.__ 1841–1852. Mollusques (1852). *In*: Voyage autour du monde execute pendant les années 1836 et 1837 sur la corvette La Bonite. *Zoologie par MM. Eydoux et Souleyet*. 2 volumes and atlas of 101 plates [atlas published 1841, but without Latin species names]. Paris, 2: 664 pp.

Sousa Reis, C. 1989a. Distribution of early juvenile cephalopods at the west coast of Portugal. *Açoreana*, 7(1): 77–82.

Sousa Reis, C. 1989b. Premières observations sur la migration "trophique" des jeunes cephalopods ("larves") de la côte ouest du Portugal. *Açoreana*, 7(1): 83–85.

Spratt, J.D. 1978. Age and growth of the market squid, *Loligo opalescens* Berry, in Monterey Bay. *Fishery Bulletin*, 169: 35–44.

Squires, H.J. 1991. An hypothesis on occurrences of bait squid in Newfoundland waters. *Journal of Cephalopod Biology*, 2(1): 65–70.

Sreenivasan, P.V. & R. Sarvesan. 1990. On the cephalopods collected during the exploratory survey by FORV Sagar Sampada in the Andaman-Nicobar Sea. *In*: K.J. Mathew, ed. Proceedings of the first workshop on scientific results of FORV Sagar-Sampada, 5–7 June, 1989, Cochin. *Central Marine Fisheries Research Institute*, 409–413.

Stanley, D.W. & H.O. Hultin. 1981. Influence of processing variables on squid quality. *Institut International du Froid*, pp. 141–151.

Stanley, D.W. & H.O. Hultin. 1984a. Amine and formaldehyde production in North American squid and their relation to quality. *Canadian Institute of Food Technology*, 17(3): 157–162.

Stanley, D.W. & H.O. Hultin. 1984b. Proteolytic activity in North American squid and its relation to quality. *Canadian Institute of Food Technology*, 17(3): 163–167.

Stark, K.E. 2006a. Environmental influences on the spatio-temporal distribution and abundance of the southern Australian arrow squid, *Nototodarus gouldi*. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 49.

***Stark, K.E.** 2006b. Variability in the arrow squid (*Nototodarus gouldi*) jig fishery in southern Australia: do evironmental conditions influence annual abundance? Cephalopod International Advisory Council Symposium 2006, Abstract: 105.

Stark, K.E., G.D. Jackson & J.M. Lyle. 2005. Tracking arrow squid movements with an automated acoustic telemetry system. *Marine Ecology Progress Series*, 299: 167–177.

***Starovoytov, A.N., I.I. Glebov & V.V. Sviridov.** 2004. Contemporary status of epipelagic nekton communities in the western Bering Sea. *Voprosy Rybolovstva. Moscow*, 5(1): 6–27.

Starr, R.M. & R.E. Thorne. 1998. Acoustic assessment of squid stocks. *In*: P.G. Rodhouse, E.G. Dawe & R.K. O'Dor, eds. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 181–198.

Staudinger, M.D. 2006. Seasonal and size-based predation on two species of squid by four fish predators on the northwest Atlantic continental shelf. *Fishery Bulletin*, 104(4): 605–615.

Staudinger, M.D. & F. Juanes. 2006. Prey size-predator size relationships of squid and their predators in the northwest Atlantic. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 24.

***Steenstrup, J.** 1855. Kjaeber af en kolossal Blaeksprutte. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1855(5/6): 199–200.

***Steenstrup, J.** 1856. Hectoctyldannelsen hos Octopodslaegterne *Argonauta* og *Tremoctopus*, oplyst ved lagttagelse af lignende Dannelser hos Blacksprutterne i Almindelighed.Kongelige Danske Videnskabernes Selskabs Skrifter, 5 Raekke. *Naturvidenskabelig og Mathematisk*, 4: 185–216.

***Steenstrup, J.** 1857a. Prof. Steenstrup foreviste og beskrev nogle nye blaeksperutter, *Dosidicus Eschrichtii* Stp. og *Onychoteuthis* (?). *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobenhavn*, 1856–57: 120–121.

***Steenstrup, J.** 1857b. Oplysninger om Atlanterhavets colossale Blacksprutter. *Forhandlinger ved de Skandinaviske Naturforskeres Syvende Mode*, 7[1856]: 182–185.

***Steenstrup, J.** 1857c. Oplysning om en ny Art af Blaeksprutter, *Dosidicus Eschrichtii*. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1857(1/2): 11–14.

***Steenstrup, J.** 1861. Overblik over de i Kjobenhavns Museer opbevarede Blaeksprutter fra det aabne Hav (1860–61). *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1861: 69–86.

***Steenstrup, J.** 1875. Hemisepius, en ny Slaegt af Sepia-Blacksperutternes Familie, med Bemaerkninger om Sepia-Formerne i Almindelighed. *Danske Videnskabernes Selskabs Skrifter, 5 Raekke, Naturvidenskabelig og Mathematisk*, 10(7): 465–482, 2 pls.

***Steenstrup, J.** 1880. De Ommatostrephagtige Blaeksprutter indbyrdes Forhold. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1880: 73–110, 12 figs, 1 pl.

***Steenstrup, J.** 1881. *Sepiadarium* og *Idiosepius* to nye Slaegter af Sepiernes Familie. Med Bemaerkninger om de to beslaegtede Former Sepiolidea D'Orb. og Spirula Lmk. *Danske Videnskabernes Selskabs Skrifter, 6 Raekke, Naturvidenskabelig og Mathematisk*, 1(3): 211–242.

***Steenstrup, J.** 1882a. Notae teuthologicae, 3. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger*, 1882: 53–164.

***Steenstrup, J.** 1882b, Videnskabelige Meddelelser fra den Naturhistoriske Forening I Kjøbenhaven, series 4(3): 293–294.

Steer, M.A. 2004. Embryonic development and early life history of the southern calamary *Sepioteuthis australis* Quoy & Gaimard, 1832. Ph.D. Dissertation, school of Aquaculture, University of Tasmania, 125 pp.

Steer, M.A. & N.A. Moltschaniwskyj. 2007. The effects of egg position, egg mass size, substrate and biofouling on embryo mortality in the squid *Sepioteuthis australis*. *Reviews in Fish Biology and Fisheries*, 17(2–3): 173–182.

*__Steer, M.A., M.T. Lloyd & W.B. Jackson.__ 2006. Southern Calamary (*Sepioteuthis australis*) Fishery. Fishery Assessment Report to PIRSA. *South Australian Research and Development Institute (SARDI), Aquatic Sciences Publications, Adelaide*, RD 05/0006–2.

*__Steer, M.A., M.T. Lloyd & W.B. Jackson.__ 2007. Assessing the feasibility of using 'by-product' data as a pre-recruit index in South Australia's southern calamary (*Sepioteuthis australis*) fishery. *Fisheries Research (Amsterdam)*, 88(1–3): 42–50.

Steer, M.A., N.A. Moltschaniwskyj & F.C. Gowland. 2002. Temporal variability in embryonic development and mortality in the southern calamari, *Sepioteuthis australis*: a field assessment. *Marine Ecology Progress Series*, 243: 143–150.

Steer, M.A., N.A. Moltschaniwskyj & A.R. Jordan. 2003a. Embryonic development of southern calamari (*Sepioteuthis australis*) within the constraints of an aggregated egg mass. *Marine and Freshwater Research*, 54: 217–226.

Steer, M.A., G.T. Pecl & N.A. Moltschaniwskyj. 2003b. Are bigger calamary *Sepioteuthis australis* hatchlings more likely to survive? A study based on statolith dimensions. *Marine Ecology Progress Series*, 261: 175–182.

*__Steer, M.A., A.J. Fowler, W.B. Jackson & P.R. Jennings.__ 2005. Southern Calamary (*Sepioteuthis australis*) Fishery. Fishery Assessment Report to PIRSA. *South Australian Research and Development Institute SARDI), Aquatic Sciences Publications, Adelaide*, RD 05/0006.

Steimer, S. 1993. Zur Biologie der Cephalopodenfauna der südlichen Nordsee. Diploma thesis, University Kiel.

Stephen, A.C. 1937. Recent invasion of the squid *Todarodes sagittatus* (Lam.) on the st coast of Scotland. *Scott. Nat.*, 131: 2.

Stephen, A.C. 1944. The Cephalopoda of Scottish and adjacent waters. T*rans. Roy. Soc. Edinb.*, 61: 247–270.

*__Stephen, S.J.__ 1985a. Systematics of the pelagic squid genus *Octopoteuthis* Rüppell, 1844 (Cephalopoda: Teuthoidea) with emphasis on species in the North Atlantic. *Bulletin of Marine Science*, 49(1–2): pp. 668.

*__Stephen, S.J.__ 1985b. The distribution of larvae of the Genus *Octopoteuthis* Rüppell, 1844. *Vie et Milieu*, 35(3/4): 175–179.

Stephen, S.J. 1992. Family Thysanoteuthidae, Keferstein 1866. *In* M.J. Sweeney *et al.*, eds. Larval and Juvenile Cephalopods: A Manual for their Identification. *Smithsonian Contributions to Zoology*, 513: 121.

*__Stephen, S.J. & K. Jefferts.__ 1992. Octopoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 165–166.

Stolbov, A.Ya. 1988. Oxygen consumption by tissues in *Sthenoteuthis oualaniensis* Lesson from the Tropical Indian Ocean. *Ehkol. Mor.*, 29: 62–64.

Stowasser, G., G.J. Pierce, C. Moffat & M.A. Collins. 2002. Investigating the diet of two squid species *Loligo forbesi* and *Illex coindetii*: Application of fatty acid and stomach content analyses. *Bulletin of Marine Science*, 71(2): 1141.

Stowasser, G., P. Bustamante, C.D. MacLeod, J. Wang & G.J. Pierce. 2005. Spawning areas and selected metal concentrations in squid (*Loligo forbesi*) in UK waters, with notes on metal concentrations in other squid species. *Project Report Department of Trade and Industry, UK*.

Stowasser, G., G.J. Pierce, C.F. Moffat, M.A. Collins & J.W. Forsythe. 2006. Experimental study on the effect of diet on fatty acid and stable isotope profiles of the squid *Lolliguncula brevis*. *Journal of Experimental Marine Biology and Ecology*, 333(1): 97–114.

Strugnell, J.M. & A.R. Lindgren. 2007. A barcode of life database for the Cephalopoda? Considerations and concerns. *Reviews in Fish Biology and Fisheries*, 17(2–3): 337–344.

*__Su, W., R. Ma, L. Yu, M,-N. Liao, D. He & L. Hu.__ 2005. Antitumor effects of extract from the ink of *Loligo chinensis*. *Chinese journal of marine drugs*, (24(2): 47–50.

Suda, M. 2007. Two species population dynamics model for Japanese sardine and chub mackerel using object oriented modeling. *The Changing North Pacific: Previous Patterns, Future Projections and Ecosystem Impacts*, p. 36.

Sudjoko, B. 1987. Catch composition of squids (Cephalopods) by using bagan (lift net) in Probolinggo waters, East Java. *Journal of Marine Fisheries Research*, 41: 81–89.

Sugimoto, T. & H. Tameishi. 1992. Warm-core rings, streamers and their role on the fishing ground formation around Japan. *Deep-Sea Research*, 39: S183–S201.

Sugisaki, H., M. Moku, K. Uchikawa, K. Tsuchiya, Y. Okazaki & M. Okamoto. 2006. Vertical distribution and feeding habit of mesopelagic fishes and squids off northeastern Japan. *PICES XV. Book of Abstracts*, p. 60.

Sukhanov, V.V. & O.A. Ivanov. 2004. Species structure of nekton near Kurile Islands. *In*: A.I. Kafanov, ed. *Main Problems in Marine Biogeography: In memory of the academician O.G. Kussakin*. Vladivostok, Dalnauka: 200–229 (In Russian, English summary).

Suklim, K., J.G. Flick Jr, J.E. Marchy & W.N. Eigel. 2003. Effect of starch and egg white albumin on the textural and cooking properties of restructured squid patties (*Illex illecebrosus*). *Journal of Aquatic Food Product Technology*, 12(2): 47–60.

Sukramongkol, N., K. Tsuchiya & S. Segawa. 2007. Age and maturation of *Loligo duvauceli* and *L. chinensis* from the Andaman Sea of Thailand. *Reviews in Fish Biology and Fisheries*, 17(2–3): 237–246.

Summers, W.C. 1969. Winter population of *Loligo pealei* in the Mid Atlantic Bight. *Biological Bulletin*, 137: 202–216.

***Summers, W.C.** 1971. Age and growth of *Loligo pealei*, a population study of the common Atlantic coast squid. *Biological Bulletin*, 146: 279–290.

***Summers, W.C.** 1983. *Loligo pealei*. *In*: P.R. Boyle, ed. Cephalopod Life Cycles. Vol I . Species Accounts. *Academic Press*, London (UK), 115–142.

Summers, W.C. 1985. Comparative life history adaptations of some Myopsid and Sepiolid squids. *NAFO Scientific Council Studies*, 9: 139–142.

Sumner, F.G., R.C. Osburn & L.J. Cole. 1913. A biological survey of Woods Hole and vicinity. *Bulletin of the United States Bureau of Fisheries*, 31(1–2): 860 pp.

Sundet, J.H. (1985). A short review on the biology and fishery of the squid *Todarodes sagittatus*. *ICES Council Meeting 1984/K:44*, 10 pp.

Supongpan, M. 1984. The cephalopod fisheries and resources in the Gulf of Thailand. *Thai Fisheries Gazette*, 37: 340–346.

Supongpan, M. 1988. Assessment of Indian squid (*Loligo duvauceli*) and mitre squid (*L. chinensis*) in the Gulf of Thailand. *In*: S. C. Venema, J. M. Christensen & D. Pauly, eds., Contributions to Tropical Fisheries Biology, Papers prepared by the Participants at the FAO Danish Follow–up Training Course on Fish Stock Assessment in the Tropics, Hhirtshals, Denmark, 5–30 May 1986 and Manila, Philippines, 12 January–6 February 1987, pp. 25–41,

Supongpan, M. & M. Sinoda. 1998. Sexual maturity size of Indian squid *Loligo duvauceli* in the Gulf of Thailand. *Thai Marine Fisheries Research Bulletin*, 6: 1–9.

Suzuki, S., A. Kuwahara & K. Washio. 1983. Study on the fishing conditions and an ecological aspect of squids, *Loligo edulis budo* and *Sepioteuthis lessoniana* in the coastal waters off Kyoto Prefecture. *Bulletin of the Japanese Society of Fishery and Oceanography*, 42: 21–27.

Suzuki, T. 1990. Japanese common squid – *Todarodes pacificus* Steenstrup. *Marine Behaviour and Physiology*, 18: 73–109.

Suzuki, T. & H. Takahashi. 1988. Response of the retina of the flying squid, *Sthenoteuthis oualaniensis* (Lesson), to light changes. *Bulletin of the Faculty of Fisheries of Hokkaido University*, 39(1): 21–26.

Suzuki, T., S. Yamamoto, K. Ishii & W.M. Matsumoto. 1986. On the flying squid, *Sthenoteuthis oualaniensis* (Lesson), in Hawaiian waters. *Bulletin of the Faculty of Fisheries of Hokkaido University*, 37(2): 111–123.

Sweedler, J.V., L. Li, P. Floyd & W. Gilly. 2000. Mass spectrometric survey of peptides in cephalopods with an empasis on the FMRFamide-related peptides. *Journal of Experimental Biology*, 203(23): 3565–3573.

***Sweeney, M.J. & C.F.E. Roper.** 1998. Classification, type localities, and type repositories of recent Cephalopoda. *In*: N.A. Voss, M.V. Vecchione, R.B. Toll & M.J. Sweeney, eds. Systematics and Biogeography of Cephalopods, Vol. II. *Smithsonian Contributions to Zoology*, 586: 561–599.

Sweeney, M.J. & M. Vecchione. 1998. Generic and specific names introduced in the squid family Loliginidae (Cephalopoda: Myopsida). *In*: N.A. Voss, M. Vecchione, R.B. Toll and M.J. Sweeney, eds. Systematics and Biogeography of Cephalopods. *Smithsonian Contributions to Zoology*, 586(I–II): pp. 223–237.

***Sweeney, M.J. & R.E. Young.** 2003a. Taxa associated with the Family Ancistrocheiridae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003b. Taxa associated with the Family Architeuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003c.Taxa associated with the Family Bathyteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003d. Taxa associated with the Family Batoteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003e. Taxa associated with the Family Brachioteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003f. Taxa Associated with the Family Chiroteuthidae Gray, 1849. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003g. Taxa Associated with the Family Chtenopterygidae Grimpe 1922. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003h.Taxa Associated with the Family Cranchiidae Prosch, 1847. Tree of Life Project. http://tolweb.org

***Sweeney, M.J. & R.E. Young.** 2003i.Taxa Associated with the Family Cycloteuthidae Naef, 1923. Tree of Life Project. http://tolweb.org

***Sweeney, M.J. & R.E. Young.** 2003j.Taxa Associated with the Family Enoploteuthidae Pfeffer, 1900. Tree of Life Project. http://tolweb.org

***Sweeney, M.J. & R.E. Young.** 2003k. Taxa Associated with the Family Gonatidae Hoyle, 1886. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003l. Taxa Associated with the Family Histioteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003m. Taxa Associated with the Family Joubiniteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003n. Taxa Associated with the Family Lepidoteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003o. Taxa Associated with the Family Loliginidae Lesueur, 1821. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003p. Taxa Associated with the Family Lycoteuthidae Pfeffer, 1908. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003q. Taxa Associated with the Family Magnapinnidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003r. Taxa associated with the Family Mastigoteuthidae Verrill, 1881. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003s. Taxa Associated with the Family Neoteuthidae Naef, 1921. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003t. Taxa associated with the Family Octopoteuthidae Berry, 1912. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003u. Taxa associated with the Family Ommastrephidae Steenstrup, 1857. Tree of Life http://tolweb.org

***Sweeney, M.J. & R.E. Young.** 2003v. Taxa associated with the Family Onychoteuthidae Gray, 1849. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003w. Taxa Associated with the Family Pholidoteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003y. Taxa Associated with the Family Promachoteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003x. Taxa Associated with the Family Psychroteuthidae Thiele, 1920. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003z. Taxa Associated with the Family Pyroteuthidae. Tree of Life Project. http://tolweb.org.

***Sweeney, M.J. & R.E. Young.** 2003aa. Taxa Associated with the Family Thysanoteuthidae Keferstein, 1866

Sweeney, M.J., Roper, C.F.E., Mangold, K.M., Clarke, M.R. & Boletsky, S.v. (eds). 1992. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Institution Press,* Washington D.C.

Tafur, R. P. Villegas, M. Rabi & C. Yamashiro. 2001. Dynamics of maturation, seasonality of reproduction and spawning grounds of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in Peruvian waters. *Fisheries Research*, 54(1): 33–50.

Taipe, A., C. Yamashiro, L. Mariategui, P. Rojas & C. Roque. 2001. Distribution and concentrations of jumbo flying squid (*Dosidicus gigas*) off the Peruvian coast between 1991 and 1999. *Fisheries Research*, 54(1): 21–32.

Takagi, K., T. Kitahara, N. Suzuki, J. Mori & A. Yatsu. 2002. The age and growth of *Sthenoteuthis oualaniensis*. *Bulletin of Marine Science*, 71(2): 1105–1108.

Takahashi, N. & T. Yahata. 1973. Histological studies on the maturation of the ovary in the squid, *Todarodes pacificus*. *Bulletin of the Faculty of Fisheries, Hokkaido University*, 24: 63–68.

Takahashi, T. 1974. Utilization of squid as food. *In*: R. Kreuzer, ed. *FAO Technical Conference on Fishery Products*, Tokyo, Dec. 1973.

Takai, N., S. Onaka, Y. Ikeda, A. Yatsu, H. Kidokoro & W. Sakamoto. 2000. Geographical variations in carbon and nitrogen stable isotope ratios in squid. *Journal of the Marine Biological Association of the United Kingdom*, 80(4): 675–684.

Takami, T. & T. Suzu-uchi. 1993. Southward migration of the Japanese common squid (*Todarodes, pacificus*) from northern Japanese waters. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology Tokai Univeristy Press, Tokyo*, pp. 537–543.

Takami, T. & S. Takayanagi. 1991. Differences in recapture rate betweeen anchor tags for the Japanese flying squid. *Science Reports Hokkaido Fisheries Experimental Station*, 37: 1–4.

Takayanagi, S. 1993. Changes in growth and maturity of Japanese common squid (*Todarodes pacificus*) related to differences in stock size in the Tsugaru Strait, Northern Japan. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology, Tokai Univeristy Press, Tokyo*, pp. 545–553.

Takechi, H. & T. Kawasaki. 1981. Population structure of the squid, *Loligo japonica*, distributed in Sendai Bay. *Tohoku Journal of Agricultural Research*., 32(3): 122–137.

***Takeda, R. & M. Tanda.** 1998. Fishing and migration of *Thysanoteuthis rhombus* Troschel in the Japan Sea. *In*: T. Okutani, ed. Contributed Papers to International Symposium on Large Pelagic Squids. *Japan Marine Fishery Resources Research Center, Tokyo*, pp. 191–198.

Takeda, R., T. Iwasa & T. Ohtani. 1995. A survey on firefly squid *Watasenia scintillans* (Berry) stranded on the beaches of the Tajima region, the western Sea of Japan. *Bulletin of Hyogo Prefecture of Fisheries Experiment Station*, 32: 19–25.

***Taki, I.** 1964. On eleven new species of the Cephalopoda from Japan, including two new genera of the Octopodinae. *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*, 5(2):297–343, 68 figs, 7 pls.

Tamaki, T., T. Ohtani & T. Okutani. 1990. Capture of a large *Gonatopsis makko* from an unusually shallow depth of the Japan Sea on the coast of Tajima. *Bulletin of the Hyogo Prefecture at the Fisheries Experiment Station*, 27: 51–54.

Tanabe, K., Y. Hikida & Y. Iba. 2006. Two coleoid jaws from the Upper Cretaceous of Hokkaido, Japan. *Journal of Paleontology*, 80(1): 138–145.

Tanaka, Y. 1993. Japanese common squid (*Todarodes pacificus*) preys on benthic polychaete (*Nereis pelagica*). *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biolog, Tokai Univeristy Press, Tokyo*, pp. 555–558.

***Targioni-Tozzetti, A.** 1869. Estratto di una catalogo sistematico e critico dei molluschi Cefalopodi del Mediterrananeo, posseduti dal R. Museo di Firenze, con alcune specie nuove. *Atti della Società Italiana di Scienze Naturali, Milano*, 12: 587–599.

Tashiro, M. 1977. Biology and fishery of the loliginid squid *Loligo edulis* in the coastal waters of northeastern Kyushu. *Nihonkai Block Shiken Kenkyu Shuroku*, 1: 81–98.

Tateyama, M., J. Yamamoto, Y. Kamei & Y. Sakurai. 2005. Distribution of epipelagic fishes and squids in the northwestern Pacific during summer, 1982–2004. *PICES 14th Annual Meeting Book of Abstracts*, p. 183.

***Thiele, J.** 1920. Cephalopoden der deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition 1901–1903. Zoology*, 16(8): 433–465, 4 pls. [publication date Dec. 1920].

*__Thiele, J.__ 1934. Handbuch der systematischen Weichtierkunde, 3: 779–1022, Jena. G. Fischer, (Cephalopoda: 948–995)?

Thierry, J. 2006. The Cephalopoda mollusca in the Annales de Paleontologie. *Annales de Paleontologie*, 92(2): 137–149.`

Thomas, R. & N.A. Moltschaniwskyi. 1999. Ontogenetic changes in size and shape of statoliths: implications for age and growth of the short-lived tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae). *Fishery Bulletin*, 97(3): 636–645.

Thomas, S. & S.J. Kizhakudan. 2006. Cephalopod fishery and population dynamics of *Loligo duvauceli* (Orbigny) off Saurashtra region, Gujarat. *Indian Journal of Fisheries*, 53(4): 425–430.

Thompson, D., C.D. Duck, B.J. McConnell & J. Garrett. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. *Journal of Zoology*, 246(2): 135–146.

Thompson, J.T. & W.M. Kier. 2002. Ontogeny of squid mantle function: changes in the mechanics of escape-jet locomotion in the Oval squid, *Sepioteuthis lessoniana* Lesson, 1830. *Biological Bulletin, Marine Biological Laboratory, Woods Hole*, 203(1): 14–26.

Thompson, J.T. & W.M. Kier. 2006. Ontogeny of mantle musculature and implications for jet locomotion in oval squid, *Sepioteuthis lessoniana*. *Journal of Exerimental Biology*, 209: 433–443.

Thompson, K.R. 1992. Quantitative analysis of the use of discards from squid trawlers by black-browed albatrosses *Diomedea melanophris* in the vicinity of the Falkland Islands. *IBIS*, 134(1): 11–21.

Thompson, K.R. 1993. Variation in Magellanic penguin *Spheniscus magellanicus* diet in the Falkland Islands. *Marine Ornithology*, 21(1–2): 57–67.

Thore, S. 1949. Cephalopoda collected by the Skagerak expedition in the eastern Atlantic 1946. *Goteborgs Vetensk Saml. Handl.19486B*, 5(1): 1–12.

*__Thrower, S.J.__ 1978. Catching and handling squid. Methods used by Japanese vessel during trial off Tasmania. *Australian Fisheries*, 37(9): 20–25.

Tian, Y. 2006. Impact of the late 1980s regime shift on the abundance and distribution of loliginid squid *Loligo bleekeri* in the southwestern Japan Sea. *PICES XV, Book of Abstracts*, p. 86.

*__Tian, Y.__ 2007. Interannual-interdecadal variations in the abundance of spear squid *Loligo bleekeri* in the southwestern Japan/East Sea: Impacts of the late 1980s climatic regime shift and trawl fishing with recommendations for management. *The Changing North Pacific: Previous Patterns, Future Projections and Ecosystem Impacts*, p. 57.

Tibbetts, A.M. 1977. Squid fisheries (*Loligo pealei* and *Illex illecebrosus*) off the Northeastern Coast of the United States of America, 1963–1974. *Selected Papers ICNAF*, 2: 85–109.

Tikhomirov, Eh.H. 1974. Material on the food and feeding habits of Antarctic seals. *Studies on fish biology and fishery oceanography*, Issue 5, USSR TINRO, pp. 129–136.

Tinbergen, L. & J. Verwey. 1945. The biology of *Loligo vulgaris* Lam. *Translation Series, Fisheries Research Board of Canada*, 2733: 35 pp.

Tioda, M. 1915. A contribution to the investigationof the surume fishery. *Niigata Prefecture Fisheries Report*, pp. 53–66.

Tobita, A., N. Yamashita, S. Torisawa, M. Shimizu & K. Nashimoto. 2002. Scanning electron microscopic observation on the ciliated cells in the larval body surface of a Japanese spear squid, *Loligo bleekeri*. *Fisheries Science*, 68(suppl. 1): 455–456.

Tokai, T. & Y. Ueta. 1999. Estimation of size selectivity for oval squid *Sepioteuthis lessoniana* in the squid jigging fishery of Tokushima Prefecture. *Fishery Science*, 65: 448–454.

Tokai, T. & Y. Ueta. 2002. Size selectivity of squid jig for oval squid *Sepioteuthis lessoniana*, and its relationship to prey-size selectivity. *Bulletin of Marine Science*, 71(2): 1141–1142.

*__Toll, R.B.__ 1982. The comparative morphology of the gladius in the order Teuthoidea (Mollusca: Cephalopoda) in relation to systematics and phylogeny. *MS, Ph.D. Dissertation, The University of Miami*.

Toll, R.B. 1983. The Lycoteuthid genus *Oregoniateuthis* Voss, 1956, a synonym of *Lycoteuthis* Pfeffer, 1900 (Cephalopoda: Teuthoidea). *Proceedings of the Biological Society of Washington*, 96(3): 365–369.

*__Toll, R.B.__ 1985. The reinstatement of *Bathypolypus faeroenensis* (Russel, 1909) (Octopoda: Bathypolypodinae). *Proceedings of the Biological Society of Washington*, 98(3): 598–603.

Toll, R.B. 1988. Functional morphology and adaptive patterns of the teuthoid gladius. *In* E.R. Truman & M.R. Clarke, eds. *The Mollusca II: Form and Function*. New York: *Academic Press*, pp. 167–182.

Toll, R.B. 1990. The cross sectional morphology of the gladius in the family Ommastrephidae (Cephalopoda: Teuthoidea) and its Bearing on Intrafamilial Systematics. *Malacologia*, 31(2):319–332.

Toll, R.B. 1998. The gladius in teuthoid systematics. *Smithsonian Contributions to Zoology*, 586 (1): 55–67.

Toll, R.B. & S.C. Hess. 1981. Cephalopods in diet of swordfish *Xiphias gladius*, from the Florida Straits. *Fishery Bulletin*, 79(4): 765–774.

Tomas, A.R.G., M.A. Gasalla, B.G. Loyo & C.A. Marques. 2004. Cephalopods in the trawl fisheries in the southeastern Brazil (1979–2000). *ICES Council Meeting Documents Copenhagen*.

Tomita, K., S.I. Yokobori, T. Oshima, T. Ueda & K. Watanabe. 2002. The Cephalopod *Loligo bleekeri* Mitochondrial Genome: Multiplied Noncoding Regions and Transposition of tRNA Genes. *Journal of Molecular Evolution*, 54(4): 486–500.

Tomiyama, M. 2002 . Resource management of *Loligo bleekeri* Keferstein in eastern Ensh-Nada. Ikaru Shingen Kenkyu Kaigi Hokoku. *Heisei*, 13: 47–55.

Tomiyama, T. & T. Hibiya. 1978. Fisheries in Japan, squid and cuttlefish. *In*: Fisheries in Japan. Tokyo. J*apan Marine Products Photo Materials Association*.

*****Tomlin, J.R. le B.** 1931. Some preoccupied generic names – III. *Proceedings of the Malacological Society of London*, 19(4): 174–175.

Torchio, M. 1966. Euribatia di teutacei, spiaggiamenti ed apporto di acque di origine continentale. *Atti della Società Italiana di Scienze Naturali di Milano*, 4: 317–342.

Torchio, M. 1968. Elenco dei Cefalopodi del Mediterraneo con considerazioni biogeografiche ed ecologiche. *Annali del Museo Civico di Storia Naturale di Genova*, 77: 257–269.

Torres, D. & A. Aguayo. 1979. Feeding Habits of *Lissodelphis peronii* (Lacepede 1804) in Central Chile (Cetacea: Delphinidae). *Revista de biologia marina*, 16(3): 221–224.

Tremblay, Y., E. Guinard & Y. Cherel. 1997. Maximum diving depths of northern rockhopper penguins (*Eudyptes chrysocome moseleyi*) at Amsterdam Island. *Polar Biology*, 17(2): 119–122.

Triantafillos, L. 2001. Population biology of southern calamary *Sepioteuthis australis* in Gulf St. Vincent, South Australia. *Ph.D. Dissertation Northern Territory University.*

Triantafillos, L. 2004. Effects of genetic and environmental factors on growth of southern calamary, *Sepioteuthis australis*, from southern Australian and northern New Zealand. *Marine and Freshwater Research*, 55(4): 439–446.

*****Triantafillos, L. & M. Adams.** 2001. Allozyme analysis reveals a complex population structure in the southern calamary, *Sepioteuthis australis*, from Australia and New Zealand. *Marine Ecology Progress Series*, 212: 193–209.

*****Triantafillos, L. & M. Adams.** 2005. Genetic evidence that the northern calamary, *Sepioteuthis lessonian*a, is a species complex in Australian waters. *ICES Journal of Marine Science*, 62(8): 1665–1670.

Triantafillos, L. & A.J. Fowler. 2000. *Southern calamary. South Australian Fisheries Assessment Series No. 2000/14, South Australian Research and Development Institute (SARDI)*, Adelaide.

Triantafillos, L., G.D. Jackson, M. Adams & B.L. McGrath-Steer. 2004. An allozyme investigation of the stock structure of arrow squid *Nototodarus gouldi* (Cephalopoda: Ommastrephidae) from Australia. *ICES Journal of Marine Science*, 61(5): 829–835.

Tricas, T.C. 1979. Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. *Fishery Bulletin*, 77(1): 175–182.

Trilles, J.-P. & A. Öktener. 2004. *Livoneca sinuata* (Crustacea; Isopoda; Cymothoidae) on *Loligo vulgaris* from Turkey, and unusual cymothoid associations. *Diseases of Aquatic Organisms*, 61: 235–240.

*****Troschel, F.H.** 1857. Bermerkungen über die Cephalopoden von Messina. *Archiv fur Naturgeschichte*, 23(1):40–76, 2 pls.

Trotsenko, B.G. & M.A. Pinchukov. 1994. Peculiarities in mesoscale distribution of the purpleback squid, *Sthenoteuthis oualaniensis*, depending on the structure of the upper quasi-homogenous layer in the western Indian Ocean. *Okeanologia*, 34(3): 417–423 (In Russian with English abstract).

Tsangridis, A., E. Lefkaditou & A. Adamidou. 1998. Analysis of catch and effort data of *Loligo vulgaris* in the W. Thracian Sea (NE Mediterranean, Greece) using a depletion mode. *Rapp. Comm. Int. Mer Medit.*, 35: 494–495.

Tserpes, G., P. Peristeraki, G. Potamias & N. Tsimenides. 1999. Species distribution in the southern Aegean Sea based on bottom-trawl surveys. *Aquatic Living Resources*, 12(3): 167–175.

***Tsuchiya, K.** 1991. Abralia fasciolata, a new species of Enoploteuthid squid from the Western Indian Ocean (Cephalopoda: Oegopsida). *Bulletin of the National Science Museum, Series A Zoology*, 17(2): 69–79.

***Tsuchiya, K.** 1993. Distribution and zoogeography of the family Enoploteuthidae in the northwest Pacific. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 571–585.

***Tsuchiya, K.** 2007. *Watasenia* Ishikawa 1914. *Watasenia scintillans*. Version 16 June 2007 (under construction). http://tolweb.org/Watasenia_scintillans/19645/2007.06.16 in The Tree of Life Web Project, http://tolweb.org/

***Tsuchiya, K.** 2009. *Enoploteuthis* Orbigny in Rüppell 1844. Version 23 July 2009 (under construction). http://tolweb.org/Enoploteuthis/19641/2009.07.23 in The Tree of Life Web Project, http://tolweb.org/

Tsuchiya, K. & K. Mori. 1998. A note on an early juvenile specimen of *Architeuthis* sp. Collected from the south of Central Honshu, Japan (Cephalopoda: Architeuthidae). *Venus Japanese Journal of Malacology*, 57(3): 225–230.

***Tsuchiya, K. & T. Okutani.** 1988. Subgenera of *Enoploteuthis*, *Abralia* and *Abraliopsis* of the squid family Enoploteuthidae (Cephalopoda, Oegopsida). *Bulletin of National Science Museum, Tokyo Series A*, 14(3): 119–136.

***Tsuchiya, K. & T. Okutani.** 1990. *Abraliopsis pacificus*, a new species of the squid family Enoploteuthidae from the northwest Pacific. *Bulletin of the National Science Museum Series A Zoology*, 16(2): 47–60.

***Tsuchiya, K & T. Okutani.** 1992[1991]. Growth stages of *Moroteuthis robusta* (Verrill, 1881) with the re-evaluation of the genus. *Bulletin of Marine Science*, 49(1–2): 137–147.

Tsuchiya, K. & T. Okutani. 1993. Rare and interesting squids in Japan: 10 recent occurrences of big squids from Okinawa. *Venus Japanese Journal of Malacology, Kaizatsu*, 52(4): 299–311.

Tsuchiya, K. & R.E. Young. 2008. Enoploteuthidae Pfeffer 1900. Version 23 April 2008. http://tolweb.org/Enoploteuthidae/19634/2008.04.23 in The Tree of Life Web Project, http://tolweb.org/

Tsuchiya, K., H. Okamoto & Y. Uozomi. 1998. Cephalopods eaten by pelagic fishes in the tropical East Pacific, with special reference to the feeding habitat of pelagic fish. *La mer*, 36: 57–66.

***Tsuchiya, K., U. Piatkowski & T. Okutani.** 1991. Distribution and re-description of *Abraliopsis lineata* Goodrich, 1896 (Cephalopoda: Enoploteuthidae) from the Arabian Sea. *Journal of Natural History*, 25(5): 1121–1133.

Tsuchiya, K., H. Miyata, K. Mori, T. Kinoshita & S. Segawa. 2006. Distribution of two enoploteuthid species in the north Pacific transition zone. Cephalopod International Advisory Council Symposium 2006, Abstract: p. 107.

Tsuji, F.I. 1990. Biochemistry of bioluminescence in the deep-sea squid, *Watasenia scintillans*. *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 2: 53–58.

Tsuji, F.I. 2004. Bioluminescence reaction in the firefly squid, *Watasenia scintillans*. *Luminescence*, 19(3): 180.

Tu, Y., Y. Luo, L. Zhu & D. Deng. 1997. Study on the fatty acid of dried squid slices. *Marine Fisheries*, 19(3): 121–123.

***Tung, I.H.** 1978. A list of decapodous cephalopods in Taiwan. *Report of the Institute of Fishery Biology of Ministry of Economic Affairs and National Taiwan University.*, 3(3): 65–67 [in Chinese with English summary].

Turk, P.E., R.T. Hanlon, L.A. Bradford & W.T. Yang. 1986. Aspects of feeding, growth and survival of the European squid, *Loligo vulgaris* Lamarck, 1799, reared through the early growth stages. *Vie et Milieu*, 36(1): 9–13.

Tursi, A. & G. D'Onghia. 1992. Cephalopods of the Ionian Sea (Mediterranean Sea). *Oebalia*, 18: 25–43.

***Tursi, A., G. d'Onghia, A. Matarrese, P. Panetta & P. Maiorano.** 1994. Finding of uncommon cephalopods (*Ancistroteuthis lichtensteinii*, *Histioteuthis bonnellii*, *Histioteuthis reversa*) and first record of *Chiroteuthis veranyi* in the Ionian Sea. *Cahiers de Biologie Marine*, 35(3): 339–345.

Tutara, J. 2006. Optimizing a closed system for culturing New Zealand broad squid, *Sepioteuthis australis*. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 53.

Uchikawa, K., J.R. Bower, Y. Sato & Y. Sakurai. 2004. Diet of the minimal armhook squid (*Berryteuthis anonychus*) (Cephalopoda: Gonatidae) in the northeast Pacific during spring. *Fishery Bulletin*, 102(4): 733–739.

Uchino, K., A. Yamasaki, S. Fujita & T. Tojima. 1994. Food habits of the flatfish *Hippoglossoides dubius* (Schmidt), in the sea off Kyoto Prefecture. *Bulletin of Kyoto Institute of Ocean Fisheries Science*, 17: 41–45.

Uchiyama, I. 1999. Composition of stomach content of walleye pollack, *Theragra chalcogramma*, in Toyama Bay. *Bulletin of Toyama Prefecture Fisheries Experiment Station*, 11: 9–18.

Ueno, Y., I. Shimizu & A.P. Shershnev. 1990. Surface water type and distribution of juvenile fishes and cephalopods in Pacific coast waters of Hokkaido and the Kuril Islands in summer, 1989. *Bulletin of National Research Institute of Far Seas Fisheries*, 27: 57–70.

Ueta, Y. 2006. Comparison between the hatching date back-calculated on statolith growth ring analysis and the actual hatching period of the oval squid, *Sepioteuthis lessoniana. In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: 107.

Ueta, Y. & Y. Jo. 1989. Notes on ecology of the oval squid *Sepioteuthis lessoniana* in outer waters adjacent to the Kii Channel. *Bulletin of the Japanese Society of Scientific Fishery*, 55: 1699–1702 [In Japanese].

Ueta, Y. & S. Segawa. 1995. Reproductive ecology and recruitment of juvenile of oval squid, *Sepioteuthis lessoniana* in outer waters adjacent to the Kii Channel. *Bulletin of the Japanese Society of Fishery and Oceanography*, 4: 409–415 [In Japanese].

Ueta, Y., T. Tokai & S. Segawa. 1999. Relationship between year-class abundance of the oval squid *Sepioteuthis lessoniana* and environmental factors off Tokushima Prefecture, Japan. *Fishery Science*, 65(3): 424–431.

Ueta, Y., I. Kitakado, S. Segawa, M. Tenjin, Y. Jo, M. Fukunaga & Y. Kangawa. 1995. Selection of spawning ground and spawning bed in oval squid *Sepioteuthis lessoniana. Fisheries Engineering*, 31(3): 189–194.

***Unger, M.A., G.G. Vadas, E. Harvey & M. Vecchione.** 2006. Accumulation of persistent organic pollutants and tributyltin in nine species of Atlantic deep sea cephalopods. *Cephalopod International Advisory Council Symposium 2006*, Abstract: p. 108.

***Unsal, I., N. Unsal, M.H. Erk & H. Kabasakal.** 1999. Demersal cephalopods from the Sea of Marmara with remarks on some ecological characteristics. *Acta Adriatica*, 40: 105–110.

Uozumi, Y. 1998. Fishery biology of arrow squids, *Nototodarus gouldi* and N. sloanii, in New Zealand waters. *Bulletin of National Research Institute of Far Seas Fisheries*, 35: 1–111.

Uozumi, Y. & E. Förch. 1995. Distribution of juvenile arrow squids *Nototodarus gouldi* and *N. sloanii* (Cephalopoda: Oegopsida) in New Zealand waters. *Fishery Science*, 61(4): 566–573.

Uozumi, Y. & H. Ohara. 1993. Age and growth of *Nototodarus sloanii* (Cehpalopoda: Oegopsida) based on daily increment counts in statoliths. *Bulletin Japan Society Science and Fisheries*, 59(9): 1469–1477.

Uozumi, Y. E.C. Förch & T. Okazaki. 1991, Distribution and morphological characters of immature *Martialia hyadesi* (Cephalopoda: Oegopsida) in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research*, 25(3): 275–282.

Uozumi, Y., S. Koshida & S. Kotoda. 1995. Maturation of arrow squid *Nototodarus gouldi* and *N. sloanii* with age in New Zealand waters. *Fisheries Science*, 61(4): 559–565.

Uozumi, Y., A. Yatsu & D.A. Robertson. 1987. Japan-New Zealand trawl survey off southern New Zealand, April 1983. *New Zealand Fisheries Technical Report, Wellington*, 4: 52 pp.

Uozumi, Y., H. Hatanaka, A.I.L. Payne & C.J. Augustyn. 1985. Report on the Japan/South Africa joint trawl survey on of groundfish resources on the Agulhas Bank in June 1982. *Publs Far Seas Fisheries Research Lab., S Series*, 13: 1–78.

Uozumi, Y., H. Hatanaka, T. Sato, C.J. Augustyn, A.I.L. Payne & R.W. Leslie. 1983. Report on the Japan/South Africa joint trawling survey on the Agulhas Bank in November/December 19812. *Far Seas Fisheries Research Laboratory, S Series*, 11: 1–91.

Vagelli, C., M. Chelli, S. Vannucci, R. Silvestri & A. Voliani. 2006. Teuthoidea in the southern Ligurian Sea. *Biologia Marina Mediterranea*, 13(2): 290–291.

Valavanis, V.D., S. Georgakarakos, D. Koutsoubas, C. Arvanitidis & J. Haralabous. 2002. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(2): 867–882.

Valencia-Perez, A.Z., M.H. Garcia-Morales, J.S. Cardenas-Lopez, J.R. Herrera-Urbina, O. Rouzaud-Sandez & J.M. Esquerra-Brauer. 2008. Effect of thermal process on connective tissue from jumbo squid (*Dosidicus gigas*) mantle. *Food Chemistry*, 107(4): 1371–1378.

Van Camp, L.M., S.C. Donnellan, A.R. Dyer & P.G. Fairweather. 2004 Multiple paternity in field- and captive-laid egg strands of *Sepioteuthis australis* (Cephalopoda: Loliginidae). *Marine and Freshwater Research*, 55(8): 819–824.

Van Camp, L.M., P.G. Fairweather, M.A. Steer, S.C. Donnellan & J.N. Havenhand. 2005. Linking morphology to reproductive success in captive squid (*Sepioteuthis australis*) using microsattelite markers. *Marine and Freshwater Research*, 56(7): 933–941.

Van Camp, L.M., K.M. Saint, S. Donnellan, J.N. Havenhand & P.G. Fairweather. 2003. Polymorphic microsatellite markers for paternity assessment in southern calamari *Sepioteuthis australis* (Cephalopoda: Loliginidae). *Molecular Ecology Notes*, 3(4): 654–655.

Van den Hoff, J. 2003. A comparative study of the cephalopod prey of Patagonian toothfish (*Dissostichus eleginoides*) and southern elephant seals (*Mirounga leonina*) near Macquarie Island. *Polar Biology*, 27(10): 604–612.

Van den Hoff, J., H. Burton & R. Davies. 2003. Diet of male southern elephant seals (*Mirounga leonine* L.) hauled out at Vincennes Bay, East Antarctica. *Polar Biology*, 26(1): 27–31.

Van Heezik, Y. 1989. Diet of the Fiodland crested penguin during the post-guard phase of chick growth. *Notornis*, 36: 151–156.

Van Heezik, Y. 1990a. Seasonal, geographical and age related avriations in the diet of the yellow-eyed penguin *Magapdyptes antipodes*. *New Zealand Journal of Zoology*, 17: 201–212.

Van Heezik, Y. 1990b. Diets of yellow-eyed, Fierdland crested, and little blue penguins breeding sympatrically on Codfish Island, New Zealand. *New Zealand Journal of Zoology*, 17: 543–548.

Van Leeuwen, J.L. & W.M. Kier. 1997. Functional design of tentacles in squid: linking sarcomere ultrastructure to gross morphological dynamics. *Philosphical Transactions of the Royal Society of London*, B. 352: 551–571.

Vanyushin, G. & T. Barkanova. 2005. Effects of the Falkland Current on fishing for squid *Illex argentinus* according to satellite monitoring of Sea Surface Temperatures. *Geophysical Research Abstracts*, 7: 04442.

Vaske-Junior, T. 2005. Cefalopodes oceanicos da Zona Economica Exclusiva do nordeste do Brasil. *Boletim do Instituto de Pesca Sao Paulo*, 31(2): 137–146.

Vaske-Junior, T. & J.P. Castello. 1998. Stomach contents of yellowfin tuna, *Thunnus albacares*, during winter and spring in Southern Brazil. *Revista Brasileira de Biologia*, 58(4): 639–647.

Vaske-Junior, T. & G. Rincon-Filho. 1998. Stomach content of blue sharks (*Prionace glauca*) and anequim (*Isurus oxyrinchus*) from oceanic waters of southern Brazil. *Review of Brazil Biology*, 58(3): 445–452.

Vaske-Junior, T., C.M. Vooren & R.P. Lessa. 2004. Feeding habits of four species of Istiophoridae (Pisces: Perciformes) from northeastern Brazil. *Environmental Biology of Fishes*, 70(3): 293–304.

Vaughan, D.L. & C.W. Recksiek. 1979. Detection of market squid, *Loligo opalescens*, with echo sounders. *Reports of California Cooperative Oceanic Fisheries Investigations*, 20: 40–50.

Vecchione, M. 1981. Aspects of the early life history of *Loligo pealei* (Cephalopoda: Myopsida). *Journal of Shellfish Research*, 1(2): 171–180.

Vecchione, M. 1982. Morphology and development of planktonic *Lolliguncula brevis* (Cephalopoda: Myopsida). *Proceedings of the Biological Society of Washington*, 95(3): 602–609.

Vecchione, M. 1987. Juvenile ecology. *In*: P.R. Boyle, ed. *Cephalopod Life Cycles, Vol. II Comparative Reviews, Academic Press, London*, pp. 61–84.

Vecchione, M. 1988. In-situ observations on a large squid-spawning bed in the eastern Gulf of Mexico. *In*: R.T. Hanlon, ed. (1988). AMU International Symposium on Life History, Systematics and Zoogeography of Cephalopods. *Malacologia*, 29(1): 135–141.

Vecchione, M. 1991. Observations on the paralarval ecology of a euryhaline squid *Lolliguncula brevis* (Cephalopoda: Loliginidae). *Fishery Bulletin*, 89(3): 515–521.

***Vecchione, M.** 1992 [1991]a. A method for examining the structure and contents of the digestive tract in paralarval squids. *Bulletin of Marine Science*, 49(1–2): 300–308 [Date on title page is 1991; actually published in 1992].

Vecchione, M. 1992 [1991]b. Dissolved oxygen and the distribution of the euryhaline squid *Lolliguncula brevis*. *Bulletin of Marine Science*, 49(1–2): 668–669.

Vecchione, M. 1999. Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987. *Fishery Bulletin*, 97(4): 1025–1030.

Vecchione, M. 2001. Cephalopods of the Continental Slope East of the United States. *American Fisheries Society*, 25:153–160.

***Vecchione, M.** 2002. Cephalopods. *In* K.E. Carpenter, ed. The living marine resources of the western central Atlantic. Volume 1: introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes and chimaeras. *FAO*, Rome. 2002: i–xiv, 1–599. Chapter pagination: 149–244.

***Vecchione, M.** 2008a. *Afrololigo* Brakoniencki 1986. *Afrololigo mercatoris* (Adam, 1941). Version 04 March 2008 (under construction). in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008b. *Alloteuthis* Wulker, 1920. Version 04 March 2008 (under construction). http://tolweb.org/Alloteuthis/23876/2008.03.04 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008c. *Doryteuthis* Naef, 1912. Version 04 March 2008 (under construction). http://tolweb.org/Doryteuthis/23877/2008.03.04 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008d. *Heterololigo* Natsukari, 1984. *Heterololigo bleekeri* (Keferstein, 1866). Version 04 March 2008 (temporary). http://tolweb.org/Jeterp;p;ogp_bleekeri/23878/2008.03.04 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008e. *Loligo* Lamarck, 1798. Inshore squid. Version 04 March 2008 (under construction). http://tolweb.org/Loligo/19858/2008.03.04 In: The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008f. *Loliolus* Steenstrup, 1856. Version 04 March 2008 (under construction). http://tolweb.org/Loliolus/19859/2008.03.04 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008g. *Lolliguncula* Steenstrup, 1881. Brief squids. Version 04 March 2008 (under construction). http://tolweb.org/Lolliguncula/19860/2008.03.04 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008h. *Pickfordiateuthis* Voss, 1953. Grass squid. Version 04 March 2008 (under construction). http://tolweb.org/Pickfordiateuthis/19861/2008.03.04 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008i. *Selenoteuthis* Voss, 1958. *Selenoteuthis scintillans* Voss, 1958. Moon Squid. Version 03 June 2008. http://tolweb.org/Selenoteuthis_scintillans /19734/2008.06.03 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008j. *Sepioteuthis* Blainville, 1824. Reef squids. Version 04 March 2008 (under construction). http://tolweb.org/Sepioteuthis/19862/2008.03.04 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M.** 2008k. *Uroteuthis* Rehder, 1945. Version 04 March 2008 (under construction). http://tolweb.org/Uroteuthis/19863/2008.03.04 In: The Tree of Life Web Project, http://tolweb.org/

Vecchione, M. & J. Galbraith. 2001. Cephalopod species collected by deepwater exploratory fishing off New England. *Fisheries Research*, 51: 385–391.

Vecchione, M. & M.R. Lipinski. 1995. Descriptions of the paralarvae of two loliginid squids in southern African waters. *South African Journal of Marine Science*, 15: 1–7.

***Vecchione, M. & G. Pohle.** 2002. Midwater cephalopods in the western North Atlantic Ocean off Nova Scotia. *In*: P.R. Boyle, M.A. Collins & G.J. Pierce, eds. Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(2): 883–892.

***Vecchione, M. & C.F.E. Roper.** 1986. Occurrence of larval Illex illecebrosus and other young cephalopods in the Slope Water/Gulf Stream interface. *Proceedings of the Biological Society of Washington*, 99(4): 703–708.

***Vecchione, M. & C.F.E. Roper.** 1992 [1991]. Cephalopods observed from submersibles in the western North Atlantic. *Bulletin of Marine Science*, 49(1–2): 433–445 [Date on title page is 1991; actually published in 1992].

Vecchione, M. & C.F.E. Roper. 1992. T*aningia danae* Joubin, 1931 (Mollusca. Cephalopoda). Proposed precedence over *Taningia persica* (Naef, 1923). *Bulletin of Zoological Nomenclature., 49(4): 261–263.*

***Vecchione, M. & R.E. Young.** 1998. The Magnapinnidae, a newly discovered family of oceanic squid (Cephalopoda: Oegopsida). *In*: A.I. Payne, M.R. Lipiñski, M.R. Clarke & M.A.C. Roeleveld, eds. Cephalopod biodiversity, ecology and evolution. *South African Journal of Marine Science*, 20: 429–437.

*****Vecchione, M. & R.E. Young.** 1999a. Lycoteuthidae Pfeffer, 1908. Version 01 January 1999. http://tolweb.org/Lycoteuthidae/19636/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 1999b. *Lycoteuthis lorigera* (Steenstrup 1875). Version 01 January 1999. http://tolweb.org/Lycoteuthis_lorigera/19738/1999.01.01 In The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 1999c. *Nematolampas regalis* Berry, 1913. Version 01 January 1999. http://tolweb.org/Nematolampas_regalis/19733/1999.01.01 In The Tree of Life Web Project http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2003a. *Neoteuthis* Naef, 1921. *Neoteuthis thielei* Naef, 1921. Version 01 January 2003 (under construction). http://tolweb.org/Neoteuthis_thielei/19926/2003.01.01 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2003b. *Nototeuthis* Nesis & Nikitina, 1986. *Nototeuthis dimegacotyle* Nesis & Nikitina, 1986. Version 01 January 2003 (under construction). http://tolweb.org/Nototeuthis_dimegacotyle/19927/2003.01.01 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2006. The squid family Magnapinnidae (Mollusca: Cephalopoda) in the Atlantic Ocean, with a description of a new species. *Proceedings of the Biological Society of Washington*, 119(3): 365–372.

*****Vecchione, M. & R.E. Young.** 2007a. *Mastigoteuthis agassizii* Verrill, 1881. Version 19 November 2007. http://tolweb.org/Mastigoteuthis_agassizii/19508/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2007b. *Mastigoteuthis atlantica* Joubin, 1933. Version 19 November 2007. http://tolweb.org/Mastigoteuthis_atlantica19509 /2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2007c. *Mastigoteuthis danae* (Joubin, 1933). Version 19 November 2007 (under construction). http://tolweb.org /Mastigoteuthis_danae/19511/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2007d. *Mastigoteuthis hjorti* Chun, 1913. Version 19 November 2007. http://tolweb.org/Mastigoteuthis_hjorti/19517/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2007e. *Mastigoteuthis magna* Joubin, 1913. Version 19 November 2007 (under construction). http://tolweb.org/Mastigoteuthis_magna/19520/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2007f. Pholidoteuthidae Adam, 1950. *Pholidoteuthis* Adam, 1950. Version 18 December 2007 (under construction). http://tolweb.org/Pholidoteuthis/19835/2007.12.18 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2008a. Ancistrocheiridae Pfeffer 1912. *Ancistrocheirus lesueurii* (Orbigny 1842). Ancistrocheirus Gray 1849. Version 06 July 2008 (under construction). http://tolweb.org/Ancistrocheirus_lesueurii/19632/2008.07.06 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2008b. Myopsida Naef, 1916. Version 21 April 2008. http://tolweb.org/Myopsida/52670/2008.04.21 in The Tree of Life Web Project, http://tolweb.org/ CHECK THE INTRODUCTORY SECTION ON MYOPSID SQUID – THE LETTER WILL HAVE TO BE CHANGED

*****Vecchione, M. & R.E. Young.** 2008c. Neoteuthidae Naef, 1921. Version 08 September 2008 (under construction). http://tolweb.org/Neoteuthidae/19417/2008.09.08 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M. & R.E. Young.** 2008d. *Pholidoteuthis massyae* (Pfeffer, 1912). Version 06 July 2008 (under construction). http://tolweb.org/Pholidoteuthis_ massyae /19854/2008.07.06 in The Tree of Life Web Project, http://tolweb.org/

Vecchione, M., T. Kubodera & R.E. Young. 2008a. *Taningia Joubin* 1931. *Taningia danae* Joubin 1931. Version 04 April 2008. http://tolweb.org/Taningia_danae/19840/2008.04.04 in The Tree of Life Web Project, http://tolweb.org/

*****Vecchione, M., B.H. Robison & C.F.E. Roper.** 1992. A tale of two species: tail morphology in paralarval *Chiroteuthis* (Cephalopoda: Chiroteuthidae). Proceeding of the Biological Society of Washington, 105(4): 683–692.

*****Vecchione, M., C.F.E. Roper & K. Jackson.** 1994. Distribution and biology of non-commercial cephalopod species from the northeastern continental shelf of the United States. ICES Theme Session on non-Target Species, paper C.M. 1994/0:4. 5 pp.

*****Vecchione, M., C.F.E. Roper & M.J. Sweeney.** 1989. Marine flora and fauna of the eastern United States Mollusca: Cephalopoda. *NOAA Technical Report of NMFS*, 73: 1–22.

***Vecchione, M., C.F.E. Roper & M. Sweeney.** 1998a. In situ observations on ommastrephid squids in the western North Atlantic. *ICES Denmark*, 2 pp.

Vecchione, M., R.E. Young & D.B. Carlini. 2000. Reconstruction of ancestral character states in neocoleoid cephalopods based on parsimony. *American Malacolocial Bulletin*, 15(2): 179–193.

***Vecchione, M., R.E. Young & A. Lindgren.** 2007a. Mastigoteuthidae Verrill, 1881. *Mastigoteuthis* Verrill, 1881. Whip-lash squid. In: The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young & K. Tsuchiya.** 2003a. *Onychoteuthis compacta* (Berry, 1913). Version 23 June 2003 (under construction). http://tolweb.org/Onychoteuthis_compacta/19964/2003.06.23 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young & K. Tsuchiya.** 2003b. *Onykia carriboea* Lesueur, 1821. Version 23 June 2003 (under construction). http://tolweb.org/Onykia_carriboea/19971/2003.06.23 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young & K. Tsuchiya.** 2003c. *Onykia ingens* (Smith 1881). Version 23 June 2003 (under construction). http://tolweb.org/Onykia_ingens/19972/2003.06.23 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young & K. Tsuchiya.** 2003d. *Onykia robsoni* (Adam, 1962). Version 23 June 2003 (under construction). http://tolweb.org//Onykia_robsoni/19975/2003.06.23 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young & K. Tsuchiya.** 2003e. *Onykia robusta* (Verrill, 1876). Version 23 June 2003 (under construction). http://tolweb.org/Onykia_robusta/19976/2003.06.23 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young & K. Tsuchiya.** 2007b. *Onychoteuthis banksii* (Leach, 1817). Version 09 July 2007 (under construction). http://tolweb.org//Onychoteuthis_banksii/19962/2007.07.09 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young & K. Tsuchiya.** 2008b. *Ancistroteuthis* Gray 1849. *Ancistroteuthis lichtensteinii* (Ferussac 1835). Version 28 April 2008 (under construction). http://tolweb.org/Ancistroteuthis_lichtensteinii/19952/2008.04.28 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., T.F. Brakoniecki, Y. Natsukari & R.T. Hanlon.** 1998b. A provisional generic classification of the family Loliginidae. *In* Voss, Nancy A., Michael Vecchione, Ronald B. Toll and Michael J. Sweeney, eds. Systematics and Biogeography of Cephalopods. *Smithsonian Contribution to Zoology*, 586: 215–222.

***Vecchione, M., C.F.E. Roper, M.J. Sweeney & C.C. Lu.** 2001. Distribution, relative abundance, and developmental morphology of paralarval cephalopods in the western North Atlantic Ocean. *NOAA Technical Report of NMFS*, 152: 54 pp.

***Vecchione, M., C.F.E. Roper, E.A. Widder & T.M. Frank.** 2002. In situ observations on three species of large-finned deep-sea squids. In: Boyle, P.R., M.A. Collins & G.J. Pierce, eds Cephalopod Biomass and Production. *Bulletin of Marine Science*, 71(2): 893–901.

Vecchione, M., R.E. Young, D.T. Donovan & P.G. Rodhouse. 1999. Reevaluation of coleoid cephalopod relationships based on modified arms in the Jurassic coleoid Mastigophora. *Lethaia*, 32(2): 113–118.

***Vecchione, M., R.E. Young, K. Tsuchiya & K.S. Bolstad.** 2007c. Onychoteuthidae Gray, 1849. Hooksquids. Version 09 July 2007. http://tolweb.org/Onychoteuthidae/19419/2007.07.09 in The Tree of Life Web Project, http://tolweb.org/

Vecchione, M., R.E. Young, K. Tsuchiya & K.S. Bolstad. 2008c. *Onychoteuthis* Lichtenstein, 1818. Version 28 April 2008 (under construction). http://tolweb.org/Onychoteuthis/19955/2008.04.28 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., R.E. Young, K. Tsuchiya & K.S. Bolstad.** 2008d. *Onychoteuthis meridiopacifica* Rancurel & Okutani, 1990. Version 30 May 2008 (under construction). http://tolweb.org/Onychoteuthis_meridiopacifica/19965/2008.05.30 in The Tree of Life Web Project, http://tolweb.org/

***Vecchione, M., E. Shea, S. Bussarawit, F. Anderson, D. Alexeyev, C.C. Lu, T. Okutani, M. Roeleveld, C. Chotiyaputta, C.F.E. Roper, E. Jorgensen & N. Sukramongkol.** 2005. Systematics of Indo-West Pacific Loliginids. *Phuket Marine Biological Center Research Bulletin*, 66: 23–26.

*__Vega, M.A., F.J. Rocha, A. Guerra & C. Osorio.__ 2002. Morphological differences between the Patagonian squid *Loligo gahi* populations from the Pacific and Atlantic oceans. *Bulletin of Marine Science*, 71(2): 903–913.

*__Velain, C.__ 1877. Passage de Venus sur le Soleil (9 December 1874). Expedition Francaise aux Iles Saint-Paul et Amsterdam. Zoologie. Observations gÈnÈrales sur la fauna des deux Iles Suivies d'une description des Mollusques. *Archives de Zoologie Experimentale et Generale*, 6:1–143, 9 figs, 5 pls.

Velasco, F. I. Olaso & F. Sanchez. 2001. The role of cephalopods as forage for the demersal fish community in the southern Bay of Biscay. *Fisheries Research Amsterdam*, 52(1–2): 65–77.

Venter, J.D., S. Van Wyngaardt, J.A. Verschoor, M.R. Lipinski & H.M. Verheye. 1999. Detection of zooplankton prey in squid paralarvae with immunoassay. *Journal of Immunoassay*, 20(3): 127–149.

*__Verany, J.B.__ 1839. Memoire sur six nouvelles espèces de Céphalopodes trouves dans la Mediterranee a Nice. *Memorie della Reale Accademia delle Scienze di Torino*, (series 2)1: 91–98, 6 pls.

*__Verany, J.B.__ 1846. Catalogo degli animali invertebrati marini del Golfo di Genova e Nizza. 30 pp., 3 pls. Genoa.

*__Verany, J.B.__ 1847. [On six new species from the Mediterranean.] Atti della Ottava Riunione degli Scienziati Italiani tenuta in Genova dal XIV al XXXIX Settembre MDCCXLVI, pp. 512–514. [Plates in Verany, 1846 Catalogo degli animali ...]

*__Verany, J.B.__ 1851. Céphalopodes de la Méditerranée. *In* Mollusques Méditerranéens observé décrits figurés et chromolithographiés d'après le vivant ouvrage dedie à SM le Roi Charles Albert, 1: 1–132.

*__Verrill, A.E.__ 1873. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *In*: S. Baird, ed. U.S. Commission of Fish and Fisheries. *Report on the Condition of the Sea Fisheries of the South Coast of New England in 1871 and 1872*, Part I: 295–778.

*__Verrill, A.E.__ 1874. The giant cuttle-fishes of Newfoundland and the common squids of the New England Coast. *American Naturalist*, 8: 167–174.

*__Verrill, A.E.__ 1876. Note on gigantic cephalopods – a correction. *American Journal of Science and Arts*, (series 3)12:236–237.

*__Verrill, A.E.__ 1878. Notice of recent additions to the marine fauna of the eastern coast of North America. *American Journal of Science and Arts*, (series 3)16(20): 207–215.

*__Verrill, A.E.__ 1879. Notice of recent additions to the marine fauna of the eastern coast of North America, No. 3. *American Journal of Science and Arts*, (series 3)17(29): 239–243.

*__Verrill, A.E.__ 1879–1880. The cephalopods of the north-eastern coast of America. Part 1. – The gigantic squids (*Architeuthis*) and their allies; with observations on similar large species from foreign localities. *Transactions of the Connecticut Academy of Sciences*, 5(5): 177–257, 14 pls.

*__Verrill, A.E.__ 1880a. Synopsis of the Cephalopoda of the north-eastern coast of North America. *American Journal of Science*, 19: 284–295.

*__Verrill, A.E.__ 1880b. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. *American Journal of Science*, 20(41):3 90–403.

*__Verrill, A.E.__ 1880–1881. The cephalopods of the north-eastern coast of America. Part II. The smaller cephalopods, including the "squids" and the octopi, with other allied forms. *Transactions of the Connecticut Academy of Sciences*, 5(6): 259–446, 33 pls.

*__Verrill, A.E.__ 1881a. The Cephalopods of the northeastern Coast of America. Part II. The smaller Cephalopods, including the "Squids" and the Octopi, with Other Allied Forms. *Transactions of the Connecticut Academy of Science*, 5(6): 308–343.

*__Verrill, A.E.__ 1881b. Report on the cephalopods, and some additional species dredged by the U.S. Fish Commission Steamer "Fish Hawk," during the season of 1880. *Bulletin of the Museum of Comparative Zoology*, 8(5): 99–116, 8 pls.

*__Verrill, A.E.__ 1881c. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, No. 2. *American Journal of Science*, (series 3), 22(41): 292–303[298].

*__Verrill, A.E.__ 1882a. Reports on the cephalopods of the northeastern Coast of America. *Annals and Reports of the Commissioner of Fish and Fisheries for 1879*, 211–455.

*__Verrill, A.E.__ 1882b. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, No.7. *American Journal of Science*, (series 3), 24(40): 360–371.

*__Verrill, A.E.__ 1884. Second catalogue of the Mollusca, recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Sciences*, 6(1): 139–294, 6 pls.

*__Verrill, A.E.__ 1885. Third catalogue of Mollusca, recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transaction of the Connecticut Academy of Sciences*, 6(2): 395–452, 3 pls.

*__Vidal, E.A.G.__ 2006a. The influence of the pycnocline and primary production on the distribution of the paralarval and juvenile cephalopods off southern Brazil. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 109.

*__Vidal, E.A.G.__ 2006b. Relationship between RNA/DNA ratio and growth in reared squid paralarvae during starvation and refeeding. *In*: Cephalopod Life Cycles, Cephalopod International Advisory Council 2006, Hobart, Tasmania. Abstract: p. 51.

Vidal, E.A.G., P. Di Marco & P. Lee. 2006. Effects of starvation and recovery on the survival, growth and RNA/DNA ratio in loliginid squid paralarvae. *Aquaculture*, 260(1–4): 94–105.

Vidal, E.A.G., F.P. Di Marco & J.H. Wormuth. 2002a. Optimizing rearing conditions of hatchling loliginid squid. *Marine Biology*, 140: 117–127.

Vidal, E.A.G., F.P. Di Marco, J.H. Wormuth & P.G. Lee. 2002b. Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. *Bulletin of Marine Science*, 71(2): 915–931.

Vidyasagar K. & V.D. Deshmukh. 1992. Stock assessment of *Loligo duvaucelii* (D'Orbigny) in Bombay waters. *Journal of the Marine Biological Association of India*, 34(1–2): 14–17.

Vigliano, P.H. 1985. Contribucion al conocimiento de la biologia de *Loligo brasiliensis* Blainville,1823 (Mollusca, Cephalopoda) en aguas argentinas. Tesis Doctoral, Facultad de Ciencias Naturales. Universidad Nacional de La Plata, 183 pp.

Villa, H., J. Quintela, M.L. Coelho, J.D. Icely & J.P. Andrade. 1997. Phytoplankton biomass and zooplankton abundance on the south coast of Portugal (Sagres), with special reference to spawning of *Loligo vulgaris*. *Scientia Marina*, 61(2): 123–129.

Villanueva, R. 1992a. Deep-sea cephalopods of the north-western Mediterranean: indications of up-slope ontogenetic migration in two bathybenthic species. *J. Zool, London*, 227: 267–276.

Villanueva, R. 1992b. Interannual growth differences in the oceanic squid *Todarodes angolensis* Adam in the northern Benguela upwelling system, based on statolith growth increment. *Journal of Experimental Marine Biology and Ecology*, 159: 157–177.

Villanueva, R. 1994. Decapod crab zoeae as food for rearing cephalopod paralarvae. *Aquaculture*, 128: 143–152.

Villanueva, R. 2000a. Effect of temperature on statolith growth of the European squid *Loligo vulgaris* during early life. *Marine Biology*, 136: 449–460.

Villanueva, R. 2000b. Differential increment-deposition in embryonic statoliths of loliginid squid *Loligo vulgaris*. *Marine Biology*, 137: 161–168.

Villanueva, R. & P. Bustamante. 2006. Composition in essential and non-essential elements of early stages of cephalopods and dietary effects on the elemental profiles of *Octopus vulgaris* paralarvae. *Aquaculture*, 261(1): 225–240.

*__Villanueva, R. & P. Sanchez.__ 1989. Some data on the biology of the squid *Todarodes angolensis* (Cephalopoda: Ommastrephidae) in Namibian waters. *Selected Paper, International Commission for the South East Atlantic Fisheries*, 1: 17–22.

*__Villanueva, R. & P. Sanchez.__ 1993. Cephalopods of the Benguela Current off Namibia: new additions and considerations on the genus *Lycoteuthis*. *Journal of Natural History*, 27(1): 15–46.

Villanueva, R., N.A. Moltschaniwskyj & A. Bozzano. 2007. Abiotic influences on embryo growth: statoliths as experimental tools in the squid early life history. *Reviews in Fish Biology and Fisheries*, 17(2–3): 101–110.

Villanueva, R., M. Segonzac & A. Guerra. 1997. Locomotion modes of deep-sea cirrate octopods (Cephalopoda) based on observation from video recordings on the Mid-Atlantic Ridge. *Marine Biology*, 129: 113–122.

Villanueva, R., A. Arkhipkin, P. Jereb, E. Lefkaditou, M.R. Lipinski, C. Perales-Raya, J. Riba & F. Rocha. 2003. Embryonic life of the loliginid squid *Loligo vulgaris*: Comparison between statoliths of Atlantic and Mediterranean populations. *Marine Ecology Progress Series*, 253: 197–208.

***Villegas, P.** 2001. Growth, life cycle and fishery biology of *Loligo gahi* (d'Orbigny, 1835) off the Peruvian coast. *Fisheries Research*, 54: 123–131.

Vinogradov, V.I. & A.S. Noskov. 1979. Feeding of short-finned squid, *Illex illecebrosus*, and long-finned squid, *Loligo pealei*, off Nova Scotia and New England, 1974–75. *ICNAF Selected Papers*, 5: 31–36.

Vitturi, R., D. Colombera, E. Catalano & J.M. Arnold. 1990. Spermatocyte chromosome study of eight species of the class Cephalopoda (Mollusca). *Journal of Cephalopod Biology*, 1(2): 101–112.

***Vivanti, A.** 1912. *Charibditeuthis maculata* n.g. n.sp., nuovo cefalopodo abissale dello Stretto di Messina. Nota preliminare. *Rivista Mensile di Pesca e Idrobiologia*, 14(4–6):89–96, 5 figs.

***Voglar, J.F. & G.G. Robaina.** 1987. Sexual maturation of squid males *Sepioteuthis sepioidea* Blainville, 1823; on the coasts of Northeast Venezuela. *Contribución Cientificas, Nucleo de Nueva Esparta, Universidad de Oriente, Porlamar*, 11 40 pp [In Spanish].

Voight, J.R. 1996. The hectocotylus and other reproductive structures of *Berryteuthis magister* (Teuthoidea: Gonatidae). *Veliger*, 39(2): 117–124.

***Vojkovich, M.** 1998. The California fishery for market squid (*Loligo opalescens*). *Reports of California Cooperative Oceanic Fisheries Investigations*, 39: 55–60.

Volsoe, A., J. Knudsen & W. Rees. 1962. The cephalopod papers of *Japetus* Steenstrup, a translation into English. *Danish Science Press, Copenhagen*, 330 pp.

***Voss, G.L.** 1953. A new family, genus and species of myopsid squid from the Florida keys. *Bulletin of Marine Science of the Gulf and Caribbean*, 2: 602–609.

***Voss, G.L.** 1955. The Cephalopoda obtained by the Harvard-Havana Expedition off the coast of Cuba in 1938–39. *Bulletin of Marine Science of the Gulf and Caribbean*, 5(2):81–115, 5 figs.

***Voss, G.L.** 1956. A review of the cephalopods of the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean*, 6(2): 85–178.

Voss, G.L. 1957. Observations on *Ornithoteuthis antillarum* Adam, 1957 on Ommastrephid squid from the West Indies, *Bulletin of Marine Science Gulf and Caribbean*, 7(4): 370–378.

***Voss, G.L.** 1959. The cephalopods collected by the R/V Atlantis during the West Indian Cruise of 1954. *Bulletin of Marine Science of the Gulf and Caribbean*, 8(4)(1958): 369–389, 3 figs [Actual publication date, February 1959].

***Voss, G.L.** 1960. Bermudan cephalopods. *Fieldiana, Zoology*, 39(40): 419–446 [424].

***Voss, G.L.** 1962a. Six new species and two new subspecies of cephalopods from the Philippine Islands. *Proceedings of the Biological Society of Washington*, 75: 169–176.

***Voss, G.L.** 1962b. *Ascocranchia joubini* a new genus and species of cranchiid squid from the North Atlantic. *Bulletin of the Institute of Océanography, Monaco*, 1242: 1–6.

***Voss, G.L.** 1962c. A monograph of the cephalopoda of the North Atlantic I: the family Lycoteuthidae. *Bulletin of Marine Science*, 12(2): 264–305.

***Voss, G.L.** 1963a. Cephalopods of the Philippines Islands. *Bulletin of the United States National Museum*, 234: 180 pp.

***Voss, G.L.** 1963b. A new species of cranchiid squid, *Phasmatopsis lucifer* from the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean*, 13(1): 77–83, 2 figs.

***Voss, G.L.** 1967a. Some bathypelagic cephalopods from South African waters. *Annals of the South African Museum*, 50(5): 61–88.

Voss, G.L. 1967b. The biology and bathymetric distribution of deep-sea cephalopods. *Studies of Tropical Oceanography Institute of Marine Science, University of Miami*, 5: 511–535.

***Voss, G.L.** 1973. Cephalopod Resources of the World. *FAO Fisheries Circular*, 149: 75 pp.

*****Voss, G.L.** 1974. *Loligo surinamensis*, a new species of loliginid squid (Cephalopoda, Myopsida) from Northeastern South America. *Zoologische Mededelingen*, 48(6): 43–53.

Voss, G.L. 1983. A review of cephalopod fisheries biology. *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. Proceedings of the workshop on the biology and resource potential of cephalopods. *Memoirs of the National Museum Victoria*, 44: 229–242.

Voss, G.L. & T.F. Brakoniecki. 1985. Squid resources of the Gulf of Mexico and Southeast Atlantic coasts of the United States. *NAFO Scientific Council Studies*, 9: 27–37.

*****Voss, G.L. & G. Williamson.** 1971. Cephalopods of Hong Kong. *Hong Kong Government Press*, 138 pp, 35 pls.

*****Voss, N.A.** 1969. A monograph of the cephalopoda of the North Atlantic: the family Histioteuthidae. *Bulletin of Marine Science*, 19(4): 713–867.

*****Voss, N.A.** 1974. Biological results of the University of Miami Deep Sea Expeditions 109. Studies on the cephalopod family Cranchiidae. A redescription of Egea inermis Joubin, 1933. *Bulletin of Marine Science*, 24(4): 939–956.

*****Voss, N.A.** 1980. A generic revision of the Cranchiidae (Cephalopoda; Oegopsida). *Bulletin of Marine Science*, 30(2): 365–412.

*****Voss, N.A.** 1985. Systematics, biology, and biogeography of the cranchiid cephalopod genus *Teuthowenia* (Oegopsida). *Bulletin of Marine Science*, 36(1): 1–85.

*****Voss, N.A.** 1988. Evolution of the cephalopod family Cranchiidae (Oegopsida). *The Mollusca*, Vol. 12: 293–314.

*****Voss, N.A.** 1992. Promachoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 183–185.

*****Voss, N.A. & S.J. Stephen.** 1992. Lycoteuthidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 67–71.

*****Voss, N.A. & G.L. Voss.** 1962. Two new species of squids of the genus *Calliteuthis* from the western Atlantic with a redescription of *Calliteuthis reversa* Verrill. *Bulletin of Marine Science of the Gulf and Caribbean*, 12(2): 169–200, 6 figs.

*****Voss, N.A. & R.S. Voss.** 1983. Phylogenetic relationships in cephalopod family Cranchiidae (Oegopsida). *Malacologia*, 23(2): 397–426.

*****Voss, N.A., K.N. Nesis & P.G. Rodhouse.** 1998a. The cephalopod family Histioteuthidae (Oegopsida): systematics, biology, and biogeography. *In*: N.A. Voss, M.V. Vecchione, R.B. Toll & M.J. Sweeney, eds. Systematics and Biogeography of Cephalopods, Vol. II. *Smithsonian Contributions to Zoology*, 586: 293–372.

*****Voss, N.A., S.J. Stephen & Zh. Dong.** 1992a. Histioteuthidae. In: Sweeney, M.J., C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky: Editors, “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 73–91.

*****Voss, N.A., S.J. Stephen & Zh. Dong.** 1992b. Cranchiidae. *In*: M.J. Sweeney, C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky, eds. “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 187–210.

Voss, N.A., M.V. Vecchione, R.B. Toll & M.J. Sweeney (eds). 1998b. Systematics and Biogeography of Cephalopods, Vols. I and II. *Smithsonian Contributions to Zoology*, 586: 599 pp.

Vovk, A.N. 1972. Method of determining maturing stages in gonads of the squid *Loligo pealei*. *Zoologicheskij Zhurnal*, 51(1): 127–132.

Vovk, A.N. 1974. Fecundity of the North American squid *Loligo pealei* (Lesueur, 1821). [Translated from Russian (1972 *AtlantNIRO*, 42: 133–140) by Translation Series, Canada. Fisheries Marine Service, 3302].

Vovk, A.N. 1985. Feeding spectrum of longfin squid (*Loligo pealei*) in the Northwest Atlantic and its position in the ecosystem. *NAFO Scientific Council Studies*, 8: 33–38.

Wada, K. 1971. Food and feeding habit of northern fur seals along the coast of Sanriku. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 64: 1–37.

Wada, T. & S. Honda. 1992. Changes in stomach contents of pomfret, *Brama japonica*, with fluctuation in population size of Japanese sardine. *Bulletin of Hokkaido National Fisheries Research Institute*, 56: 71–74.

Wada, Y. 1993. On the multiple copulations of the oval squid, *Sepioteuthis lessoniana*. *Bulletin of the Kyoto Institute of Oceanic and Fishery Science*, 16: 58–60.

Wada, Y. & T. Kobayashi. 1995. On an iteroparity of oval squid *Sepioteuthis lessoniana*. *Nippon Suisan Gakkaishi*, 61: 151–158.

Wada, Y., J. Nishioka & M. Tanaka. 1995. On the spawning of the oval squid *Sepioteuthis lessoniana* in the coastal waters off Kyoto Prefecture. *Nippon Suisan Gakkaishi*, 61(6): 838–842.

Wade, M., B. Stait & W.B. Saunders. 1998. Subclass Nautiloidia. *In*: P.L. Beesley, G.J.B. Ross, & A. Wells, eds. Mollusca: The Southern Synthesis. Fauna of Australia. Vol. 5. *CSIRO Publishing: Melbourne*, Part A xvi: 485–498.

Wadley, V.A. 1993. Cephalopods from demersal trawling on Australia's northwest slope. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 607–617.

Wadley, V.A. & C.C. Lu. 1983. Distribution of mesopelagic cephalopods around a warm-core ring in the East Australian Current (Abstract). *In*: C.F.E. Roper, C.C. Lu & F.G. Hochberg, eds. Proceedings of the workshop on the biology and resource potential of cephalopods. *Memoirs of the National Museum Victoria*, 44: 197–198.

Wadley, V.A. & M.C. Dunning. 1998. Cephalopods of commercial importance in Australian fisheries. *Australian Fisheries Management Authority, Canberra.*

Wakabayashi, T., K. Saito, K. Tsuchiya & S. Segawa. 2002. Descriptions of *Eucleoteuthis luminosa* (Sasaki, 1915) and *Ornithoteuthis volatilis* Sasaki, 1915) paralarvae in the northwestern Pacific. *Venus*, 60 (4): 237–260.

*****Wakabayashi, T., T. Kubodera, M. Sakai, T. Ichii & S. Chow.** 2007. Molecular evidence for synonymy of the genera *Moroteuthis* and *Onykia* and identification of their paralarvae from northern Hawaiian waters. *Journal of the Marine Biological Association of the United Kingdom*, 87(4): 959–965.

*****Wakabayashi, T., N. Suzuki, M. Sakai, T. Ichii & S. Chow.** 2006. Identification of ommastrephid squid paralarvae collected in northern Hawaiian waters and phylogenetic implications for the family Ommastrephidae using mtDNA analysis. *Fisheries Science*, 72(3): 494–502.

*****Wakiya & C. Ishikawa.** 1921. Review of myopsid cephalopods in Japan [In Japanese]. *Zoological Magazine, Tokyo*, 33: 279–292, 12 figs.

Walker, W.A. 1996. Summer feeding habits of Dall's porpoise, *Phocoenoides dalli*, in the southern Sea of Okhotsk. *Marine Mammal Science*, 12(2): 167–181.

Waller, R. & R. Wicklund. 1968. Observations from a research submersible – mating and spawning of the squid *Doryteuthis plei*. *Biological Science*, 18: 110–111.

Walsh, L.S., P.E. Turk & P.G. Lee. 2002. Mariculture of the loliginid squid *Sepioteuthis lessoniana* through seven successive generations. *Aquaculture*, 212(1–4): 245–262.

Waluda, C.M. & G.J. Pierce. 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. *South African Journal of Marine Science*, 20: 323– 336.

Waluda, C.M. & P.G. Rodhouse. 2005. *Dosidicus gigas* fishing grounds in the eastern Pacific as revealed by satellite imagery of the light-fishing fleet. *Phuket Marine Biological Center Research Bulletin*, 66: 321–328.

Waluda, C.M. P.G. Rodhouse. 2006. Remotely sensed mesoscale oceanography of the Central Eastern Pacific and recruitment variability in *Dosidicus gigas*. *Marine Ecology Progress Series*, 310: 25–32.

Waluda, C.M., P.N. Trathan & P.G. Rodhouse. 1999. Influence of oceanographic variability on recruitment in the genus *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. *Marine Ecology Progress Series*, 183: 159–167.

*****Waluda, C.M., P.N. Trathan & P.G. Rodhouse.** 2004a. Synchronicity in southern hemisphere squid stocks and the influence of the Southern Oscillation and Trans Polar Index. *Fisheries Oceanography*, 13(4): 255–266.

*****Waluda, C.M., C. Yamashiro & P.G. Rodhouse.** 2006. Influence of the ENSO cycle on the light-fishery for *Dosidicus gigas* in the Peru Current: An analysis of remotely sensed data. *Fisheries Research*, 79(1–2): 56–63.

Waluda, C.M., P.G. Rodhouse, P.N. Trathan & G.J. Pierce. 2001a. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. *Fisheries Oceanography*, 10: 207–216.

Waluda, C.M., P.G. Rodhouse, G.P. Podesta, P.N. Trathan & G.P. Pierce. 2001b. Oceanography of *Illex argentinus* (Cephalopoda: Ommastrephidae) hatching grounds and influences on recruitment variability. *Marine Biology*, 139: 671–679.

***Waluda, C.M., C. Yamashiro, C.D. Elvidge, V.R. Hobson & P.G. Rodhouse.** 2004b. Using lights to track squid fishing fleets from space. *Remote Sensing of Environment*, 91(2): 129–133.

Wang, C.H., A.J. Geffen & R.D.M. Nash. 2002. Three-dimensional imaging of statoliths in the veined squid *Loligo forbesi*. *Bulletin of Marine Science*, 71(2): 1143–1144.

Wang, C.H., C.S. Chen, W.N. Tzeng, C.F. You & T.S. Chiu. 2006. Microchemisty analysis of statoliths from neon flying squid. Cephalopod International Advisory Council Symposium 2006, Abstract.

Wang, M.C., W.A. Walker, K.T. Shao & L.S. Chou. 2002.Comparative analysis of the diets of pygmy sperm whales and dwarf sperm whales in Taiwanese waters. *Acta Zoology. Taiwan*, 13(2): 53–62.

Wang, M.C., W.A. Walker, K.T. Shao & L.S. Chou. 2003. Feeding habits of the pantropical spotted dolphin, *Stenella attenuata*, off the eastern coast of Taiwan. *Zoological Studies*, 42(2): 368–378.

Wang, Y. 2002. Fishery biological characteristics of swordtip squid *Loligo edulis* in the southern part of the East China Sea. *Marine Fisheries/Haiyang Yuye*, 24(4): 169–172.

Waring, G.T., P. Gerrior, P.M. Payne, B.L. Parry & J.R. Nicolas. 1990. Incidental take of marine mammals in foreign fishery activities off the northeast United States, 1977–1988. *Fishery Bulletin*, 88(2): 347–360.

Warneke-Cremer, C. 1986. Contributions to the systematics of ommastrephid squid (Mollusca, Cephalopoda, Teuthoidea) and their distribution in the Atlantic, based on the catches of FFS Walther Herwig made during 1966 and 1968. *Mitteilungen aus dem Institut Seefischerei Bundesforschungsanstellung Fischerei, Hamburg*, 40: 1–116.

Warneke-Cremer, C. & M. Dzwillo. 1993. The dentition of the arm suckers as taxonomical feature in the family of Ommastrephidae (Mollusca, Cephalopoda, Teuthoidea). *Mitteilungen aus dem Naturhistorischen Museum Hamburg*, 90: 99–122.

Washio, K., K. Ueda & Y. Sakano. 1982. Some characteristics on the fluctuation of catch of squid, *Loligo bleekeri* Keferstein, migrating to the coast of Kyoto Prefecture. *Bulletin of Kyoto Institute of Oceanography and Fisheries Science*, 6: 7–12.

Watanabe, H., T. Kubodera & S. Kawahara. 2003. Feeding habits of Pacific Pomfret *Brama japonica* in the transition zone of the Central North Pacific. *Fisheries Science*, 69(2): 269–276.

Watanabe, H., T. Kubodera & S. Kawahara. 2006a. Summer feeding habits of the Pacific pomfret *Brama japonica* in the transitional and subarctic waters of the central North Pacific. *Journal of Fish Biology*, 68(5): 1436–1450.

Watanabe, H., T. Kubodera, T. Ichii & S. Kawahara. 2004a. Feeding habits of neon flying squid *Ommastrephes bartramii* in the transitional region of the central North Pacific. *Marine Ecology Progress Series*, 266: 173–184.

***Watanabe, H., T. Kubodera, S. Masuda & S. Kawahara.** 2004b. Feeding habits of albacore *Thunnus alalunga* in the transition region of the central North Pacific. *Fisheries Science*, 70(4): 573–579.

***Watanabe, H., T. Kubodera, M. Moku & K. Kawaguchi.** 2006b. Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. *Marine Ecology Progress Series*, 315: 187–197.

Watanabe, K., K. Ando, K. Tsuchiya & S. Segawa. 1998. Late embryos and paralarvae of diamondback squid *Thysanoteuthis rhombus* Troschel, 1857. *Venus: Japanese Journal of Malacology*, 57(4): 291–301.

Watanabe, K., Y. Sakurai, S. Segawa & T. Okutani. 1996. Development of an ommastrephid squid *Todarodes pacificus* from fertilized egg to the rhynchoteuthion paralarva. *American Malacological Bulletin*, 13: 73–88.

Watanabe, T. 1965. Ecological distribution of rhynchoteuthion larva of common squid, *Todarodes pacificus* (Steenstrup, in the southeastern waters off Japan during the winters, 1959–1962. *Bulletin Tokai Regional Fisheries Research Laboratory*, 43: 1–12 (in Japanese with English abstract).

Watanabe, T. & H. Inada. 1998. Effective use of fishing lights for jigging of large-sized *Ommastrephes bartramii*. *In* T. Okutani, ed. Contributed papers of the International Symposium of Large Pelagic Squids. Tokyo: JAMARC Publication: 77–87.

***Watase, S.** 1906. On luminous cephalopods. *Dobutsu-Gaku, Zasshi [Zoological Magizine, Tokyo]*, 18:195–196.

Waugh, S.M., H. Weimerskirch, Y. Cherel, U. Shankar, P.A. Prince & P.M. Sagar. 1999. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Marine Ecological Progress Series*, 177: 243–254.

Webb, D.J., P.D. Kilworth, A.C. Coward & S.R. Thompson. 1991. The FRAM Atlas of the Southern Ocean. *Swindon: Natural Environment Research Council*, 67 p.

Weimerskirch, H., A. Gault & Y. Cherel. 2005. Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology Washington D.C.*, 86(10): 2611–2622.

***Weindl, T.** 1912. Vorlaufige mitteilung über die von S.M. Schiff `Pola' im Roten Meere gefundenen Cephalopoden. *Anzeiger der Kaiserlichen Akademic der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse Wien*, 49(17): 270–275.

Wells, M.J. & A. Clarke. 1996. Energetics, the costs of living and reproducing for an individual cephalopod. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 351: 1083–1104.

***Wells, M.J. & P.J.S. Smith.** 1987. The performance of the octopus circulatory system: a triumph of engeneering over design. *Experientia*, 43: 487–499.

Wentworth, S.L. & W.R.A. Muntz. 1989. Asymmetries in the sense organs and central nervous system of the squid *Histioteuthis*. *Journal of Zoology*, 219(4): 607–619.

Wharton, D.Z., M.L. Hassall & O. Aalders. 1999. *Anisakis* (*Nematoda*) in some New Zealand inshore fish. New Zealand *Journal of Marine and Freshwater Research*, 33(4): 643–648.

***Whitaker, J.D.** 1978. A contribution to the biology of *Loligo pealei* and *Loligo plei* (Cephalopoda, Myopsida) off the southeastern coast of the United States. *M. Sc. Thesis, College of Charleston*, 164 pp.

Whitehead, H., C.D. MacLeod & P. Rodhouse. 2003. Differences in niche breadth among some teuthivorous mesopelagic marine mammals. *Marine Mammal Science*, 19(2): 400–406.

Wiborg, K.F. 1972a. *Todarodes sagittatus* (Lamarck). Investigation in Norwegian and North Atlantic waters in 1970–1972). *Fisken Havet*, 3: 5–14.

Wiborg, K.F. 1972b.The squid *Todarodes sagittatus* (Lamarck). Norwegian investigations in the Norwegian Sea and North Atlantic waters 1970–1972. *ICES Council Meeting* 1972/K:25.

Wiborg, K.F. 1978. Squid, *Todarodes sagittatus* (Lamarck) in Norwegian coastal waters during the autumn 1977 and spring 1978. *ICES Council Meeting* 1978/K:16.

Wiborg, K.F. 1979a *Todarodes sagittatus* (Lamarck). Investigation in Norwegian coastal waters, in the northern North Sea and south of the Faroes during October 1978–1979. *Fisken og Havet*, 3:9–19.

***Wiborg, K.F.** 1979b. *Gonatus fabricii* (Lichtenstein). A possible fishery resource in the Norwegian Sea. *Fisken Havet*, 1: 33–46.

Wiborg, K.F. 1980a. *Gonatus fabricii* (Lichtenstein). Investigation in Norwegian Sea and the western Barents Sea, June–September 1979. *Fisken og Havet*, 1: 1–7.

Wiborg, K.F. 1980b. The squid *Todarodes sagittatus* Lamarck: immigration and occurrence at the Norwegian coast and adjacent ocean areas from the autumn 1979 to the spring 1980. *Fisken Havet*, (3): 13–27 (In Norwegian, English summary).

Wiborg, K.F. 1981. Akkar *Todarodes sagittatus* (Lamarck). A Norwegian investigations April–December 1980. *Fisken og Havet,* 2: 31–45.

Wiborg, K.F. 1986. The Norwegian squid fishery in 1985. *Fiskets Grang*, 36: 593–596.

Wiborg, K.F. 1987. Investigation on the squid, *Todarodes sagittatus* (Lamarck), in Norwegian coastal and bank waters in September–December 1984, April and August–September 1985, at Shetland in July 1984, and at the Faroes in August 1985. *Fisken og Havet*, 2: 1–85.

***Wiborg, K.F. & I.M. Beck.** 1984. The squid *Todarodes sagittatus* (Lamarck). Investigations in Norvegian coastal and bank waters, July 1983–January 1984, and west of the British Isles, March–April 1984. *International Council for the Exploration of the Sea (CM Papers and Reports)*, CM1984/K: 20, 14 pp.

***Wiborg, K.F. & J. Gjøsæter.** 1981. The squid *Todarodes sagittatus* (Lamarck). Distribution and biology in northern waters, April 1980– April 1981. *ICES Council Meeting* 1981/K: 14.

Wiborg, K.F., I.M. Beck & J. Gjøsaeter. 1984. The squid *Gonatus fabricii*, investigations in the Norwegian Sea and western Barents Sea, 1982–1983. *ICES Council Meeting* 1984/K: 19.

Wiborg, K.F., J. Gjøsæter, I.M. Beck & P. Fossum. 1982. Squid *Todarodes sagittatus* (Lamarck) distribution and biology in northern waters, April 1981–April 1982. *ICES Council Meeting* 1982/K: 30.

Wiborg, K.F., J. Gjøsæter, I.M. Beck & P. Fossum. 1983. Squid *Todarodes sagittatus* (Lamarck) distribution and biology in northern waters, April 1982–June 1983. *ICES Council Meeting* 1983/K: 7.

Wienecke, B. & G. Robertson. 2006. Comparison of foraging strategies of incubating king penguins *Aptenodytes patagonicus* from Macquarie and Heard islands. *Polar Biology*, 29(5): 424–438.

Williams, L. 1909. The anatomy of the common squid, *Loligo pealii* Lesueur. *Leiden*, 92 pp.

Williamson, R. 1989a. Electrical coupling between secondary hair cells in the statocyst of the squid *Alloteuthis subulata*. *Brain Research*, 486(1): 67–72.

Williamson, R. 1989b. Secondary hair cells and afferent neurones of the squid statocyst receive both inhibitory and excitatory efferent inputs. *Journal of Comparative Physiology*, 165(6): 847–860.

Wimmer, T. & H. Whitehead. 2004. Movements and distribution of northern bottlenose whales, *Hyperoodon ampullatur*, on the Scotian Slope and in adjacent waters. *Canadian Journal of Zoology*, 82(11): 1782–1794.

Wing, B.L. & R.W. Mercer. 1990. Temporary northern range extension of the squid *Loligo opalescens* in southeast Alaska. *Veliger*, 33(3): 238–240.

Wingham, E.A. 1985. Food and feeding range of the Australasian gannet *Morus serrator* (Gray). *Emu*, 85: 231– 239.

Winstanley, R.H., M.A. Potter & A.E. Caton. 1983. Australian cephalopod resources. *In*: C.F.E. Roper, Lu, C.C. & F.G. Hochberg, eds. *Proceedings of the workshop on the biology and resource potential of cephalopods. Memoirs of the National Museum Victoria*, 44: 243–254.

Wood, J.B. & R.K. O'Dor. 2002. How slow can they grow? Not all coleoid cephalopods live fast and die young. *Bulletin of Marine Science*, 71(2): 1145.

Worms, J. 1979. L'utilisation des prises commerciales en biologie des pêches. Application à l'étude d'une population de *Loligo vulgaris* (Cephalopoda, Teuthoïdea) du golfe du Lion. Thèse 3ème cycle, USTL Montpellier, France, 197pp.

***Worms, J.** 1983a. *Loligo vulgaris*. *In*: P.R. Boyle, ed. Cephalopods Life Cycle. Vol. I. Species Account. *Academic Press*, London. pp: 143–157.

***Worms, J.** 1983b. Migratory pattern of a population of *Loligo vulgaris* Lam. (Cephalopoda, Teuthoidea) from the Gulf of Lion (France). *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, 28: 277–279.

***Wormuth, J.H.** 1976. The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. *Bulletin of the Scripps Institute of Ocean*, 23: 1–90.

***Wormuth, J.H.** 1998. Workshop Deliberations on the Ommastrephidae: *In*: N.A. Voss, M. Vecchione, R.B. Toll & M.J. Sweeney, eds. A Brief History of their Systematics and a Review of the Systematics, Distribution, and Biology of the genera Martialia Rochebrune and Mabille, 1889, Todaropsis Girard, 1890, Dosidicus Steenstrup, 1857, Hyaloteuthis Gray, 1849, and Eucleoteuthis Berry, 1916. *Smithsonian Contributions to Zoology*, 586: 373–383.

Wormuth, J.H., R.K. O'Dor, N. Balch, M.C. Dunning, E.C. Forch, R.F. Harman & T.W. Rowell. 1992. "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 105–119.

Wray, T. 1996. City feeds the world's appetite for squid. *Seafood International*, 11(4): 41.

Wu, S., C. Wu & H. Chen. 2003. Cuticle structure of squid *Illex argentinus*. *Fisheries Science*, 69(4): 849–855.

***Wülker, G.** 1913. Cephalopoden der Aru- und Kei-inseln. Anhang: Revision der Gattung *Sepioteuthis*. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 34: 451–488, 7 figs, 1 pl.

***Wülker, G.** 1920. Über Cephalopoden der Roten Meeres. *Senkenbergiana*, 2(1): 48–58.

Würtz, M. & E. Giuffra. 1989. Growth and reproduction of *Loligo vulgaris* in the Ligurian Sea. *Oebalia*, 15(2): 831–834

Würtz, M. & D. Marrale. 1991. On the contents of striped dolphins (*Stenella coeruleoalba*, Meyen 1933) from the Ligurian coast, central Mediterranean sea. European Research on Cetaceans. In P.G.H. Evans, ed. *Proceeding of 5th Conference of European Cetacean Society, Sandefjord*, 5: 62–63.

Würtz, M., R. Poggi & M.R. Clarke. 1992. Cephalopods from the stomachs of a Risso's Dolphin (*Grampus griseus*) from the Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, 72: 861–867.

Xavier, J.C., J..P. Croxall & K.A. Cresswell. 2005. Boluses: an effective method for assessing the proportions of cephalopods in the diet of albatrosses. *The Auk., 122(4): 1182–1190.*

Xavier, J.C., P.G. Rodhouse & J.P. Croxall. 2002a. New estimates of the *Martialia hyadesi* stock based on predator diet – implications for South Atlantic squid fisheries, *ICES Annual Report Zoology Oslo*, p. 22.

Xavier, J.C., P.G. Rodhouse & J.P. Croxall. 2002b. Unusual occurrence of *Illex argentinus* (Cephalopoda: Ommastrephidae) in the diet of albatrosses breeding at Bird Island, South Georgia. *Bulletin of Marine Science*, 71(2): 1109–1112.

Xavier, J.C., G.A. Tarling & J.P. Croxall. 2006. Determining prey distribution patterns from stomach-contents of satellite-tracked high predators of the Southern Ocean. *Ecography*, 29(2):260–272.

Xavier, J.C., J.P. Croxall, P.N. Trathan & P.G. Rodhouse. 2003a. Inter-annual variation in the cephalopod component of the diet of the wandering albatross, *Diomedea exulans*, breeding at Bird Island, South Georgia. *Marine Biology*, 142(3): 611–622.

Xavier, J.C., J.P. Croxall, P.N. Trathan & A.G. Wood. 2003b. Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Marine Biology*, 143(2): 221–232.

Xavier, J.C., P.G. Rodhouse, P.N. Trathan & A.G. Wood. 1999. A geographical information system Atlas of cephalopod distribution in the Southern Ocean. *Antarctic Science*, 11(1): 61–62.

Xavier, J.C., A.G. Wood, P.G. Rodhouse & J.P. Croxall. 2007. Interannual variations in cephalopod consumption by albatrosses at South Georgia implications for future commercial exploitation of cephalopods. *Marine and Freshwater Research*, 58(12): 1136–1143.

***Xavier J.C., P.G. Rodhouse, M.G. Purves, T.M. Daw, J. Arata & G.M. Pilling.** 2002c. Distribution of cephalopods recorded in the diet of the Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia. *Polar Biology*, 25(5): 323–330.

Xu, Z., X. Cui & H. Huang. 2004. Distribution of zooplankton in *Ommastrephes bartramii* fishing ground of the North Pacific Ocean and its relationship with the fishing ground. *Journal of Fisheries of China*, 28(5): 515–521.

Xu, Z., X. Gu & F. Zhang. 2007. Species composition, diversity and density of pelagic Ostracoda in the East China Sea. *Acta Oceanologica Sinica Haiyang Xuebao*, 26(5): 96–106.

Yamada, H., K. Takayanagi, M. Tateishi, H. Tagata & K. Ikeda. 1997. Organotin compounds and polychlorinated biphenyls of livers in squid collected from coastal waters and open oceans. *Environmental Pollution*, 96(2): 217–226.

Yamaguchi, H. & T. Okutani. 1990. Notes on young squids dip-netted and incidentally jigged during the exploratory fishing on *Dosidicus gigas* in the eastern Pacific, December 1987–March 1988. *Journal of Tokyo University Fisheries Tokyo Suisandai-Kempo*, 77(1): 1–8.

Yamamoto, H. 1997. Estimated hatch dates from counts of daily rings in statoliths of the Japanese common squid *Toarodes pacificus*. *Bulletin Iwate Prefectural Fisheries Technological Center*, 1: 21–26.

Yamamoto, J., T. Shimura, R. Uji, S. Masuda, S. Watanabe & Y. Sakurai. 2004. Vertical distribution of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) paralarvae near the Oki Islands, southwestern Sea of Japan. *PICES 13th Annual Meeting Book of Abstracts*, p. 213.

***Yamamoto, K. & T. Okutani.** 1975. Studies on early life history of decapodan Mollusca. 5. Systematics and distribution of epipelagic larvae of decapod cephalopods in the southwestern waters of Japan during the summer in 1970. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, 83: 45–96.

Yamamura, O. & T. Inada. 2001. Importance of micronekton as food of demersal fish assemblages. *Bulletin of Marine Science*, 68(1): 13–25.

Yamamura, O., T. Inada & K. Shimazaki. 1993. Predation on firefly squid *Watasenia scintillans* by demersal fishes off Sendai Bay, North Japan. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent advances in cephalopod fisheries biology. Tokai University Press*, 633–639.

Yamamura, O., S. Honda, O. Shida & T. Hamatsu. 2002. Diets of walleye pollock *Theragra chalcogramma* in the Doto area, northern Japan: Ontogenetic and seasonal variations. *Marine Ecology Progress Series*, 238: 187–198.

Yamanaka, H., M. Matsumoto, K. Hatae & H. Nakaya. 1995. Studies on components of off-flavor in the muscle of American jumbo squid. *Nippon Suisan Gakkaishi*, 61(4): 612–618.

Yamashiro, C., L. Mariategui, J. Rubio, J. Arguelles, R. Tafur, A. Taipe & M. Rabi. 1998. Jumbo flying squid fishery in Peru. *In*: T. Okutani, ed. Large Pelagic Squids. *Japan Marine Fishery Resources Center, Tokyo*, 119–125.

Yang, D. 1991. The fishing ground environment of the East China Sea and the distribution for Todarodes pacificus. *J. Fish. China Shuichan-Xuebao*, 15(1): 77–81.

*****Yang, J. & X. Tan.** 2000. Food analysis of three cephalopod species in the Bohai Sea. *Marine sciences, Qingdao*, 24(4): 53–55.

Yang, M.S. & P.A. Livingston. 1988. Food habits and daily ration of Greenland halibut, *Reinhardtius hippoglossoides*, in the eastern Bering Sea. *Fishery Bulletin*, 86(4): 675–690.

Yang, T.C.S. & A.P.P. Yang. 1986. Squid tentacle protein: Extraction and its effects on the quality of Atlantic pollock surimi gels. *Canadian Institute of Food Science Technology*, 19(4): 158–162.

Yang, W.T., R.T. Hanlon, R.F. Hixon & W.H. Hulet. 1980. First success in rearing hatchlings of the squid *Loligo pealei* Lesueur 1821. *Malacological Review*, 13(1–2): 79–80.

Yang, W.T., R.T. Hanlon, M.E. Krejci, R.F. Hixon & W.H. Hulet. 1980. Culture of California market squid from hatching – first rearing of Loligo to subadult stage. *Aquabiology*, 2(6): 312–318.

*****Yang, W.T., R.F. Hixon, P.E. Turk, M.E. Krejci, W.H. Hulet & R.T. Hanlon.** 1986. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens* cultured through the life cycle. *Fishery Bulletin*, 84(4): 771–798.

Yasui, T. & Y. Ishito. 1955. A study on the growth rate and the spawning season of *Ommastrephies sloani pacificus* (Steenstrup). *Bulletin of Tohoku Regional Fisheries Research Laboratory*, 4: 173–179.

Yatsu, A. 1995a. The role of slender tuna, *Allothunnus fallai*, in the pelagic ecosystems of the South Pacific Ocean. *Japanese Journal of Ichthyology, 41(4): 367–377.*

Yatsu, A. 1995b. Zoogeography of the epipelagic fishes in the South Pacific Ocean and the Pacific sector of the Subantarctic, with special reference to the ecological role of slender tuna, *Allothunnus fallai*. *Bulletin of the National Research Institute of Far Seas Fisheries*, 32: 1–145 (In Japanese with expanded English abstract, legends of tables, figs).

*****Yatsu A. & J. Mori.** 2000. Early growth of the autumn cohort of neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. *Fisheries Research*, 45: 189–194.

Yatsu A. & T. Watanabe. 1996. Interannual variability in neon flying squid abundance and oceanographic conditions in the Central North Pacific, 1982–1992. *Bulletin of the National Research Institute of Far Seas Fisheries*, 33: 123–138.

Yatsu A., K. Hiramatsu & Sh. Hayase. 1993. A review of the Japanese squid drifting fishery with notes on the cetacean bycatch. *Report of International Whaling Commnission, Special issue*, 15: 365–379.

Yatsu, A., H. Kazuhiko & S. Hayase. 1994. A review of the Japanese squid driftnet fishery with notes on the cetacean by-catch. *Cambridge, International Whaling Commission. Special Issue*, 15: 365–379.

Yatsu, A., K. Nagasawa & T. Wada. 2003. Decadal changes in abundance of dominant pelagic fishes and squids in the northwestern Pacific Ocean since the 1970s and implications on fisheries management. *American Fisheries Society Symposium*, 38: 675–684.

Yatsu, A., H. Tanaka & J. Mori. 1998. Population structure of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. *In*: T. Okutani, ed. Contributed Papers of the International Symposium of Large Pelagic Squids. *Tokyo: JAMARC Publication*, 31–48.

Yatsu, A., R. Tafur & C. Maravi. 1999a. Embryos and rhynchoteuthion paralarvae of the jumbo flying squid *Dosidicus gigas* (Cephalopoda) obtained through artificial fertilization from Peruvian waters. *Fisheries Science*, 65(6): 904–908.

Yatsu, A., K. Yamanaka & C. Yamashiro. 1999b. Tracking experiments of the jumbo flying squid, *Dosidicus gigas*, with an ultrasonic telemetry system in the eastern Pacific Ocean. *Bulletin of National Research Institute of Far Seas Fisheries*, 36: 55–60.

Yatsu, A., S. Midorikawa, T. Shimada & Y. Uozumi. 1997. Age and growth of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. *Fisheries Research*, 29: 257–270.

Yatsu, A., K. Katto, F. Kakizoe, K. Yamanaka & K. Muzuno. 1998. Distribution and biology of *Sthenoteuthis oualaniensis* in the Indian Ocean. Preliminary results from the research cruise of the R/V Shoyo-Maru in 1995. *In*: T. Okutani, ed. Contributed Papers of the International Symposium on Large Pelagic Squids. *Tokyo: JAMARC Publication*, pp. 131–143.

Yau, C. 1994. The ecology and ontogeny of cephalopod juveniles in Scottish waters. Ph.D. thesis, University Aberdeen.

Yau, C. & J. Mauchline. 1992. Distribution of pelagic cephalopod in the Rockall Trough. *Bulletin of Marine Science*, 49(1–2): 670.

Ye, X. 2002. Conclusion and analysis on the experimental fishing of *Dosidicus gigas* in the offlying sea of Peru and Costa Rica in 2001. *Marine Fisheries*, 24(4): 165–168.

***Yeatman, J.M.** 1993. Genetic and morphological aspects of Australian *Photololigo* spp. (Loliginidae: Cephalopoda). Ph.D. Thesis, James Cook University, North Queensland, Australia.

***Yeatman, J.M. & J.A.H. Benzie.** 1993. Cryptic speciation in *Loligo* from northern Australia. *In*: T. Okutani, R.K. O'Dor & T. Kubodera, eds. *Recent Advances in Cephalopod Fisheries Biology, Tokyo*, pp. 641–652.

***Yeatman, J.M. &. J.A.H. Benzie.** 1994. Genetic structure and distribution of *Photololigo* spp. in Australia. *Marine Biology*, 118: 79–87.

Yeh, S.Y. & I.H. Tung. 1993. Review of Taiwanese pelagic squid fisheries in the North Pacific. *In*: J. Ito, W. Shaw & R.L. Burgner, eds. *Biology Distribution and Stock Assessment of Species caught in the High Seas Driftnet Fisheries in the North Pacific Ocean*, 53: 71–76.

***Yokawa, K.** 1994. Allozyme differentiation of sixteen species of ommastrephid squid (Mollusca, Cephalopoda). *Antarctic Science*, 6(2): 201–204 (Abstract).

Yokobori, S.I., N. Fukuda, M. Nakamura, T. Aoyama & T. Oshima. 2004. Long-term conservation of six duplicated structural genes in cephalopod mitochondrial genomes. *Molecular Biology and Evolution*, 21(11): 2034–2046.

Yokogawa, K. & Y. Ueta. 2000. Genetic analysis of oval squid (*Sepioteuthis lessoniana*) around Japan. *Venus, Japanese Journal of Malacology*, 59(1): 45–55.

Yokota, M., S. Kitada, K. Udono & S. Watanabe. 1998. Prediction of the firefly squid catch by analysis of environmental factors in Toyama Bay. *Nippon Suisan Gakkaishi*, 64(6): 975–978.

Yokoyama, Y. 1984. Biology of Yari-ika, Heterololigo bleekeri, in Shiribeshi waters, Hokkaido, their egg-laying inn aquaria and embryonic development. *Journal of Hokkaido Fisheries Experimental Station*, 41: 1–23 [in Japanese].

Yonezaki, S., M. Kiyota, H. Okamura & N. Baba. 2006. Possibility of diet selection of northern fur seals in the northwestern Pacific. *PICES XV. Book of Abstracts*, p. 269.

Yoshioka, T., Y. Kinoshita, H. Yoshino, S. Park, K. Konno & N. Seki. 2003. Change in translucency of squid mantle muscle upon storage. *Fisheries Science*, 69(2): 408–413.

Young, I.A.G., G.J. Pierce, H.I. Daly, M.B. Santos, L.N. Key, N. Bailey, J.-P. Robin, A.J. Bishop, G. Stowasser, M. Nyegaard, S.K. Cho, M. Rasero & J.M.F. Pereira. 2004. Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). *Fisheries Research*, 69: 211–227.

Young, I.A.G., G.J. Pierce, G. Stowasser, M.B. Santos, J. Wang, P.R. Boyle, P.W. Shaw, N. Bailey, I. Tuck & M.A. Collins. 2006. The Moray Firth directed squid fishery. *Fisheries Research*, 78(1): 39–43.

Young, J., M. Lansdell, S. Riddoch & A. Revill. 2006. Feeding ecology of broadbill swordfish, *Xiphias gladius*, off eastern Australia in relation to physical and environmental variables. *Bulletin of Marine Science*, 79(3): 793–809.

***Young, J.Z.** 1970. The stalked eyes of *Bathothauma* (Mollusca, Cephalopoda). *Pacific Science*, 29(3): 243–255.

***Young, J.Z.** 1989. The angular acceleration receptor system of diverse cephalopods. *Philosophical Transactions of the Royal Society of London*, B 325(1227): 189–237.

Young, R.E. 1964. A note on three specimens of the squid, *Lampadioteuthis megaleia* Berry, 1916 (Cephalopoda:Oegopsida) from the Atlantic Ocean, with a description of the male. *Bulletin of Marine Science of the Gulf and Caribbean*, 14(3):444–452.

***Young, R.E.** 1972a. The systematics and areal distribution of pelagic cephalopods from the seas off Southern California. *Smithsonian Contributions to Zoology*, 97: 159 pp.

*__Young, R.E.__ 1972b. Function of extra-ocular photoreceptors in bathypelagic cephalopods. *Deep Sea Research Oceanography Abstract*, 19(9): 651–660.

*__Young, R.E.__ 1973a. Evidence for spawning by *Gonatus* sp. (Cephalopoda: Teuthoidea) in the high Arctic ocean. *Nature*, 87 (2): 53–58.

*__Young, R.E.__ 1973b. Information feedback from photophores and ventral countershading in mid-water squid. *Pacific Science*, 27(1): 1–7.

Young, R.E. 1975a. Function of the dimorphic eyes in the midwater squid *Histioteuthis dofleini*. *Pacific Science*, 29(2): 211–218.

*__Young, R.E.__ 1975b. Transitory eye shapes and the vertical distribution of two midwater squids. *Pacific Science*, 29(3): 243–255.

*__Young, R.E.__ 1978. Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. *Fishery Bulletin*, 76(3): 583–615.

*__Young, R.E.__ 1992 [1991]. Chiroteuthid and related paralarvae from Hawaiian waters. *Bulletin of Marine Science*, 49(1–2): 162–185 [Date on title page is 1991; actually published in 1992].

*__Young, R.E.__ 1995. Aspects of the natural history of pelagic cephalopods of the Hawaiian mesopelagic-boundary region. *Pacific Science*, 49(2): 143–155.

*__Young, R.E.__ 1999a. Cycloteuthidae Naef, 1923. Version 01 January 1999 (under construction). http://tolweb.org/Cycloteuthidae/19412/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E.__ 1999b. *Discoteuthis* Young and Roper, 1969. Version 01 January 1999 (under construction). http://tolweb.org/Discoteuthis/19621/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E.__ 1999c. *Octopoteuthis deletron* Young 1972. Version 01 January 1999. http://tolweb.org/Octopoteuthis_deletron/19843/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E.__ 2008a. Joubiniteuthidae Naef, 1922. *Joubiniteuthis portieri* Joubin, 1916. Version 16 October 2008. http://tolweb.org/Joubiniteuthis_portieri/19450/2008. 10.16 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E.__ 2008b. *Mastigoteuthis famelica* (Berry, 1909). Version 08 September 2008 (under construction). http://tolweb.org/Mastigoteuthis_famelica/19513/2008.09.08 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. & J.M. Arnold. 1982. The functional morphology of a ventral photophore from the mesopelagic squid, *Abralia trigonura*. *Malacologia*, 23(1): 135–164.

*__Young, R.E. & R.F. Harman.__ 1987. Description of the larvae of three species of the *Onychoteuthis banksii* complex from Hawaiian waters. *Veliger*, 29(3): 313–321.

*__Young, R.E. & R.F. Harman.__ 1998. Phylogeny of the "Enoploteuthid" families. In: Voss, N.A., M.V. Vecchione, R.B. Toll, & M.J. Sweeney: Editors, Systematics and Biogeography of Cephalopods, Vol. I. *Smithsonian Contributions to Zoology*, 586: 257–270.

*__Young, R.E. & J. Hirota.__ 1990. Description of *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) paralarvae with evidence for spawning in Hawaiian waters. *Pacific Science*, 44(1): 71–80.

Young, R.E. & J. Hirota. 1998. Review of the ecology of *Sthenoteuthis oualaniensis* near the Hawaiian Archipelago. *In* T. Okutani, ed. Contributed Papers of the International Symposium on Large Pelagic Squids. *Tokyo: JAMARC Publication*, pp. 131–143.

*__Young, R.E. & K.M. Mangold.__ 1996a *Megalocranchia* Pfeffer, 1884. Version 15 July 2008 (under construction). http://tolweb.org/Megalocranchia/19562/2008.07.15 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 1996b. *Pterygioteuthis* Fischer 1896. Version 01 January 1996 (under construction). http://tolweb.org/Pterygioteuthis_giardi/19751/ 1996.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 1996c. *Sandalops* Chun, 1906. *Sandalops melancholicus* Chun, 1906. The sandal-eye squid. Version 01 January 1996 (under construction). http://tolweb.org/Sandalops melancholicus/19551/1996.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 1999a. *Egea* Joubin, 1933. *Egea inermis* Joubin, 1933. Version 01 January 1999 (under construction). http://tolweb.org/Egea_inermis/19563/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 1999b. *Galiteuthis pacifica* Robson 1948. Version 01 January 1999 (under construction). http://tolweb.org/Galiteuthis_pacifica/19573/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 1999c. *Liguriella. in* The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 2007a. *Leachia* Lesueur 1821. Version 30 June 2007 (under construction). http://tolweb.org/Leachia/19544/2007.06.30 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 2007b. *Teuthowenia* Chun, 1910. Version 16 July 2006. http://tolweb.org/Teuthowenia/19560/2006.07.16 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 2008a. Cranchiidae Prosch, 1847. Bathyscaphoid squids. Version 22 April 2008. http://tolweb.org /Cranchiidae/19411/2008.04.22 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 2008b. *Helicocranchia* Massy, 1907. Piglet squid. Version 27 October 2008 (under construction). http://tolweb.org/Helicocranchia/19550/2008.10.27 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 2008c. *Helicocranchia pfefferi* Massy 1907. Banded piglet squid. Version 16 October 2008 (under construction). http://tolweb.org/Helicocranchia_pfefferi/19580/2008.10.16 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 2008d. *Megalocranchia* Pfeffer, 1884. Version 15 July 2008 (under construction). http://tolweb.org/Megalocranchia/19562/2008.07.15 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & K.M. Mangold.__ 2008e. *Taonius* Steenstrup, 1861. Version 15 July 2008 (under construction). http://tolweb.org/Megalocranchia/19562/2008.07.15 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 1968. The Batoteuthidae, a new family of squid (Cephalopoda; Oegopsida) from Antarctic waters. *Antarctic Research Series*, 2: 185–202, 6 pls.

*__Young, R.E. & C.F.E. Roper.__ 1969a. A monograph of the cephalopoda of the North Atlantic: the family Cycloteuthidae. *Smithsonian Contributions to Zoology*, 5: 24 pp.

*__Young, R.E. & C.F.E. Roper.__ 1969b. A monograph of the cephalopoda of the North Atlantic: the family Joubiniteuthidae. *Smithsonian Contributions to Zoology*, 15: 10 pp.

Young, R.E. & C.F.E. Roper. 1976. Bioluminescent countershading in midwater animals: evidence from living squid. *Science*, 191: 1046–1048

Young, R.E. & C.F.E. Roper. 1977. Intensity regulation of bioluminescence during countershading in living midwater animals. *Fishery Bulletin*, 75(2): 239–252.

*__Young, R.E. & C.F.E. Roper.__ 1998. Chiroteuthidae Gray, 1849. Version 01 January 1998 (under construction). http://tolweb.org/Chiroteuthidae/19451/1998.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 1999a. The chiroteuthid *Doratopsis* Stage. The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 1999b. *Planctoteuthis exopthalmica* (Chun 1910). Version 01 January 1999 (under construction). http://tolweb.org/Planctoteuthis_exopthalmica/19493/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 1999c. *Planctoteuthis oligobessa* Young 1972. Version 01 January 1999 (under construction). http://tolweb.org/Planctoteuthis_oligobessa19496/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 2007. *Asperoteuthis acanthoderma* (Lu, 1977) e. Version 08 March 2007 (under construction). http://tolweb.org /Asperoteuthis_acanthoderma/ 19466/2007.03.08 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 2008a. *Grimalditeuthis* Joubin, 1898. *Grimalditeuthis bonplandi* (Verany, 1839). Version 05 September 2008 (under construction). http://tolweb.org/Grimalditeuthis_bonplandi/19463/2008.09.05 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 2008b. *Planctoteuthis danae* (Joubin 1931). Version 05 September 2008 (under construction). http://tolweb.org/Planctoteuthis_danae/19492/2008.09.05 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E. & C.F.E. Roper.__ 2008c. *Planctoteuthis lippula* (Chun 1908). Version 15 September 2008 (under construction). http://tolweb.org/Planctoteuthis_lippula/19495/2008.09.15 in The Tree of Life Web Project, http://tolweb.org/

*Young, R.E. & C.F.E. Roper.** 2008d. Batoteuthidae Young and Roper, 1968. *Batoteuthis skolops* Young and Roper, 1968. The Bush-club Squid. Version 21 April 2008 (under construction). http://tolweb.org/Batoteuthis_skolops/19452/2008.04.21 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & K. Tsuchiya.** 2009a. *Abralia* Gray 1849. Version 26 July 2009 (under construction). http://tolweb.org/Abralia/19642/2009.07.26 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & K. Tsuchiya.** 2009b. *Abraliopsis* Joubin 1896. Version 01 August 2009 (under construction). http://tolweb.org/Abraliopsis/19644/2009.08.01 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. & M. Vecchione. 1996a. Analysis of morphology to determine primary sister-taxon relationships within coleoid cephalopods. *American Malacological Bulletin*, 12(1–2): 91–112.

***Young, R.E. & M. Vecchione.** 1996b. Octopoteuthidae Berry 1912. http://tolweb.org/Octopoteuthidae/19834/1996.01.01 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. & M. Vecchione. 1996c. Thysanoteuthidae Keferstein, 1866. *Thysanoteuthis rhombus* Troschel, 1857. The diamondback squid. Version 01 January 1996 (under construction). http://tolweb.org//Thysanoteuthis_rhombus/19420/1996.01.01 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. & M. Vecchione. 1999. Morphological observations on a hatchling and a paralarva of the vampire squid, *Vampyroteuthis infernalis* Chun (Mollusca: Cephalopoda). *Proceedings of the Biological Society of Washington*, 112(4): 661–666.

***Young, R.E. & M. Vecchione.** 2000. *Stigmatoteuthis dofleini* Pfeffer, 1912. Tree of Life Project, http://tolweb.org/.

***Young, R.E. & M. Vecchione.** 2001. *Chtenopteryx sepioloides* Rancurel 1970. Chubby combfin squid. Version 31 October 2001 (under construction). http://newsystem.tolweb.org/Chtenopteryx_sepioloides/19440/2001.10.31 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2003a. Promachoteuthidae Naef, 1912. *Promachoteuthis* Hoyle, 1885. Version 01 January 2003 (under construction). http://tolweb.org/Promachoteuthis/19454/2003.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2003b. *Promachoteuthis megaptera* Hoyle 1885. Version 01 January 2003. http://tolweb.org//Promachoteuthis_megaptera/19528/2003.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2003c. *Promachoteuthis* sp. B. Version 01 January 2003. http://tolweb.org/Promachoteuthis_sp._B/19530/2003.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2003d. *Promachoteuthis* sp. D. Version 01 January 2003 (under construction). http://tolweb.org/Promachoteuthis_sp. D/19532/2003.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2004. *Oegopsida* Orbigny, 1845. Version 18 August 2004 (under construction). http://tolweb.org/Oegopsida/19407/2004.08.18 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2005a. *Narrowteuthis nesisi*, a new genus and new species of the squid family Neoteuthidae (Mollusca: Cephalopoda). Proceedings of the Biological Society of Washington, 118(3): 566–569.

***Young, R.E. & M. Vecchione.** 2005b. *Narrowteuthis nesisi* Young and Vecchione, 2005. Tree of Life Project. http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2005c. *Discoteuthis* sp. B. Version 07 December 2005 (temporary). http://tolweb.org/Discoteuthis_sp._B/57150/2005.12.07 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2006a. *Chtenopteryx sicula* (Verany 1851). Version 08 July 2006 (under construction). http://tolweb.org/Chtenopteryx_sicula/19441/2006.07.08 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2006b. *Octopoteuthis deletron* Young 1972. Version 01 January 1999. http://tolweb.org/Octopoteuthis_deletron/19843/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2006c. *Promachoteuthis sloani* Young, Vecchione & Piatkowski 2006. Version 22 July 2006. http://tolweb.org/Promachoteuthis_sloani/ 19529/2006.07.22 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. & M. Vecchione. 2007a. *Asperoteuthis lui* Salcedo-Vargas 1999. Version 15 November 2007. http://tolweb.org/Asperoteuthis_lui/112030/2007.11.15 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2007b. Histioteuthidae Verrill, 1881. Version 21 May 2007 (under construction). http://tolweb.org/Histioteuthidae/19782/2007.05.21 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2007c. *Mastigoteuthis agassizii* group. Version 19 November 2007 (under construction). http://tolweb.org/Mastigoteuthis_agassizii_group/65306/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2007d. *Mastigoteuthis glaukopis* Chun, 1908. Version 19 November 2007 (under construction). http://tolweb.org/Mastigoteuthis_glaukopis/52637/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2007e. *Mastigoteuthis psychrophila* Nesis, 1977. Version 19 November 2007. http://tolweb.org/Mastigoteuthis_psychrophila/19522/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2007f. *Mastigoteuthis pyrodes* Young, 1972. Version 19 November 2007. http://tolweb.org/Mastigoteuthis_pyrodes/19523/2007.11.19 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2008a. Chtenopterygidae Grimpe 1922. *Chtenopteryx* Appellof 1890. Combfin squid. Version 11 August 2008 (under construction). http://tolweb.org/Chtenopteryx/19430/2008.08.11 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2008b. Lampadioteuthis Berry 1916. *Lampadioteuthis megaleia* Berry, 1916. Version 15 January 2008. http://tolweb.org/Lampadioteuthis_megaleia/19730/2008.01.15 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2008c. Lepidoteuthidae Pfeffer 1912. *Lepidoteuthis grimaldii* Joubin, 1895. The scaled squid. Version 02 June 2008 (under construction). http://tolweb.org/Lepidoteuthis_grimaldii/19833/2008.06.02 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & Vecchione M.** 2008d. *Mastigoteuthis cordiformis* Chun, 1908. Version 15 September 2008. http://tolweb.org/Mastigoteuthis_cordiformis/19510/2008.09.15 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2008e. *Mastigoteuthis microlucens*, a new species of the squid family Mastigoteuthidae (Mollusca: Cephalopoda). *Proceedings of the Biological Society of Washington, 121(2): 276–282.*

***Young, R.E. & M. Vecchione.** 2008f. *Octopoteuthis* Ruppell 1844. Version 06 July 2008. http://tolweb.org/Octopoteuthis/19839/2008.07.06 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2008g. Ommastrephinae Posselt 1891. Version 25 April 2008 (under construction). http://tolweb.org/Ommastrephinae/19941/2008.04.25 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2008h. *Stigmatoteuthis arcturi* Robson, 1948. Version 29 May 2008 (under construction). http://tolweb. org/Stigmatoteuthis _arcturi/19793/2008.05.29 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E. & M. Vecchione.** 2008i. *Stigmatoteuthis dofleini* Pfeffer, 1912. Version 29 May 2008 (under construction). http://tolweb.org /Stigmatoteuthis_dofleini/ 19794/2008.05.29 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. & M. Vecchione. 2008j. *Stigmatoteuthis hoylei* (Goodrich 1896). Version 29 May 2008 (under construction). http://tolweb.org/Stigmatoteuthis_hoylei/19795/2008.05.29 in The Tree of Life Web Project, http://tolweb.org/

Young, R.E. & M. Vecchione. 2008k. Todarodinae Adam 1960. Version 25 April 2008 (under construction). http://tolweb.org/Todarodinae/19934/2008.04.25 in The Tree of Life Web Project, http://tolweb.org/

***Young, R.E., R.F. Harman & K.M. Mangold.** 1985. The eggs and larvae of *Brachioteuthis* sp. (Cephalopoda: Teuthoidea) from Hawaiian waters. *In*: K.M. Mangold & S.v. Boletzky, eds. Biology and distribution of early juvenile cephalopods, *Cephalopod International Advisory Council, Plymouth, UK*, 35(3–4): 203–209.

***Young, R.E., A. Lindgren & M. Vecchione.** 2008a. *Mastigoteuthis microlucens*, a new species of the squid family Mastigoteuthidae (Mollusca: Cephalopoda). *Proceedings of the Biological Society of Washington, 121(2): 276–282.*

***Young, R.E., K.M. Mangold & M. Vecchione.** 1992. The Enoploteuthid group of families. In: Sweeney, M.J., C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.v. Boletzky: Editors, “Larval” and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, 513: 55–57.

Young, R.E., C.F.E. Roper & J.F. Walters. 1979a. Eyes and extraocular photoreceptors in midwater cephalopods and fishes: their roles in detecting downwelling light for counterillumination. *Marine Biology*, 51: 371–380.

***Young, R.E., M. Vecchione & M.A. Compagno Roeleveld.** 2009. Ommastrephidae Steenstrup 1857. Version 09 May 2009. http://tolweb.org/Ommastrephidae/19418/2009.05.09 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E., M. Vecchione & D.T. Donovan.__ 1998a. The evolution of coleoid cephalopods and their present biodiversity and ecology. *South African Journal of Marine Science*, 20: 393–420.

*__Young, R.E., M. Vecchione & A. Lindgren.__ 2008b. *Mastigoteuthis microlucens* Young, Lindgren & Vecchione 2008. Version 06 August 2008 (under construction). http://tolweb.org/Mastigoteuthis_microlucens/65304/2008.08.06 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E., M. Vecchione & U. Piatkowski.__ 1999a. *Alluroteuthis* Odhner, 1923. *Alluroteuthis antarcticus* Odhner, 1923. Version 01 January 1999 (under construction). http://tolweb.org/Alluroteuthis_antarcticus/19925/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E., M. Vecchione & U. Piatkowski.__ 2006a. *Promachoteuthis sloani*, a new species of the squid family Promachoteuthidae (Mollusca: Cephalopoda). *Proceedings of the Biological Society of Washington*, 119(2): 287–292, figs. 1–3.

*__Young, R.E., M. Vecchione & K. Tsuchiya.__ 2003. *Walvisteuthis* Nesis and Nikitina 1986. *Walvisteuthis rancureli* (Okutani 1981). Stubby hooksquid. Version 23 June 2003 (under construction). http://tolweb.org/Walvisteuthisrancureli/19957/2003.06.23 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E., M. Vecchione & C.F.E. Roper.__ 2007. A new genus and three new species of decapodiform cephalopods (Mollusca: Cephalopoda). *Review in Fish Biology and Fisheries*, 17: 353–365.

*__Young, R.E., M. Vecchione & C.F.E. Roper.__ 2008c. *Asperoteuthis mangoldae* Young, Vecchione and Roper, 2007. Version 08 September 2008 (under construction). http://tolweb.org/Asperoteuthis mangoldae/19467/2008.09.08 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E., M. Vecchione & C.F.E. Roper.__ 2008d. *Planctoteuthis* Pfeffer, 1912. Version 21 April 2008 (under construction). http://tolweb.org/Planctoteuthis/19464/2008.04.21 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E., M. Vecchione, U. Piatkowski & C.F.E. Roper.__ 1999b. *Planctoteuthis levimana* (Lonnberg 1896). Version 01 January 1999 (under construction). http://tolweb.org/Planctoteuthis_levimana/19494/1999.01.01 in The Tree of Life Web Project, http://tolweb.org/

*__Young, R.E., M. Vecchione, U. Piatkowski & C.F.E. Roper.__ 2006b. Redescription of *Planctoteuthis levimana* (Lönnberg, 1896) (Mollusca: Cephalopoda), with a brief review of the genus. *Proceedings of the Biological Society of Washington*,119(1): 150–159.

*__Young, R.E., L.A. Burgess, C.F.E. Roper, M.J. Sweeney & S.J. Stephen.__ 1998b. Classification of the Enoploteuthidae, Pyroteuthidae, and Ancistrocheiridae. *In*: N.A. Voss, M.V. Vecchione, R.B. Toll & M.J. Sweeney. eds. Systematics and Biogeography of Cephalopods. *Smithsonian Contributions to Zoology*, 586(I): 239–255.

Young, R.E., E.M. Kampa, S.D. Maynard, F.M. Mencher & C.F.E. Roper. 1980. Counterillumination and the upper depth limits of midwater animals. *Deep Sea Research*, 27A: 671–691.

*__Young, R.E., C.F.E. Roper, K. Mangold, G. Leisman & F.G. Hochberg.__ 1979b. Luminescence from non-bioluminescent tissues in oceanic cephalopods. *Marine Biology*, 53: 69–77.

Yuen, H.S. 1979. A night handline fishery for tunas in Hawaii. *Marine Fisheries Review*, 8: 7–14.

Yuneva, T.V., A.M. Shchepkina & G.E. Shulman. 1994. Peculiarities of lipids composition in squid tissues from tropical Atlantic. *Hydrobiology Journal*, 30(2): 78–86.

Yuuki, Y. 1985. Spawning and growth of Watasenia scintillans in the southwestern Japan Sea. *Bulletin of Japanese Society of Fisheries Oceanography*, 49: 1–6.

Yuuki, Y. & H. Kitazawa. 1986. *Berryteuthis magister* in the southwestern Japan Sea. *Nippon Suisan Gak-kaishi*, 52: 665–672 (In Japanese).

Zaidi-bin-Zakaria, M. 2000. Age and growth studies of oceanic squid, *Sthenoteuthis oualaniensis* using statoliths in the South China Sea, Area 3, Western Philippines. *Proceedings of the third Technical Seminar on Marine Fishery Resources Survey in the South China Sea*, 41: 118–134.

*__Zaleski, T.__ 2005. Posição sistemática e dinâmica populacional da lula *Lolliguncula brevis* (Mollusca: Cephalopoda) MS Thesis, UFPR, Curitiba, 176 pp.

*__Zaleski, T. & J.A. Perez.__ 2006. Morphology and morphometry of the squid *Lolliguncula brevis* of Brazilian coast: evidences for their taxonomic separation from North Atlantic *Lolliguncula*. TASMANIA CIAC, p.115

*__Zalygalin, V.P., Ch.M. Nigmatullin & R.M. Sabirov.__ 1983. Morphology and functioning of the male reproductive system of the squid *Ommastrephes bartramii* Lesueur. *In*: Ya.I. Starobogatov & K.N. Nesis, eds. Taxonomy and Ecology of Cephalopods. *Leningrad: Zoological Institute of the Academy of Sciences, USSR Publication*, 62–64 (In Russian).

Zamorov, V.V., M.V. Chesalin & T.V. Dotsenko. 1993. Squid value in the feeding of yellowfin tuna (*Thunnus albacares* Bonnaterre, 1788) in the western Indian Ocean. *Southern Scientific Research Institute of Marine Fisheries and Oceanography (YugNIRO), Kerch, Crimea, Ukraine*, 104–105.

Zecchini, F., M. Vecchione & C.F.E. Roper. 1996. A quantitative comparison of hectocotylus morphology between Mediterranean and Western Atlantic populations of the squid *Illex coindetii* (Mollusca: Cephalopoda: Ommastrephidae). *Proceedings of Biological Society of Washington*, 109(3): 591–599.

Zeidberg, L.D. 2004. Allometry measurements from in situ video recordings can determine the size and swimming speeds of juvenile and adult squid *Loligo opalescens* (Cephalopoda: Myopsida). *Journal of Experimental Biology*, 207: 4195–4203.

*__Zeidberg, L.D. & W.M. Hamner.__ 2002. Distribution of squid paralarvae, *Loligo opalescens* (Cephalopoda: Myopsida), in the Southern California Bight in the three years following the 1997–1998 El Nino. *Marine Biology*, 141: 111–122.

Zeidberg, L.D. & B.H. Robison. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences*, 104(31): 12948–12950.

*__Zeidberg, L.D., W.M. Hamner, K. Moorehead & E. Kristof.__ 2004. Egg masses of *Loligo opalescens* (Cephalopoda: Myopsida) in Monterey Bay, California, following the El Nino event of 1997–1998. *Bulletin of Marine Science*, 74: 129–141.

*__Zeidberg, L.D., W.M. Hamner, N.P. Nezlin & A. Henry.__ 2006. The fishery for California market squid (*Loligo opalescens*) (Cephalopoda: Myopsida), from 1981 through 2003. *Fishery Bulletin*, 104: 46–59.

Zeidler, W. 1981. A giant deep-sea squid, *Taningia* sp., from South Australian waters. *Transactions of the Royal Society of South Australia*, 105: 218.

Zeidler, W. & K.L. Gowlett-Holmes. 1996. A specimen of giant squid, *Architeuthis* sp., from South Australian waters. *Records of the South Australian Museum*, 29: 85–91.

Zeppelin, T.K. & R.R. Ream. 2006. Foraging habitats based on the diet of female northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands, Alaska. *Journal of Zoology, London*, 270(4): 565–576.

Zhang, B., D. Sun & Y. Wu. (1997). A brief survey of nektonic invertebrate resources in Jiaozhou Bay and adjacent waters. Studia marina sinica/Haiyang Kexue Jikan. *Qingdao*, 38: 169–174.

Zheng, X., J. Yang, X. Lin & R. Wang. 2004. Phylogenetic relationships among the decabrachia cephalopods inferred from mitochondrial DNA sequences. *Journal of Shellfish Research*, 23(3): 881–886.

Zheng, Y. 1994. Present status and rational utilization on the exploitation of the resources of cephalopods in the East China Sea region. *Marine Fishery, Haiyang Yuye*, 16: 199–203.

Zheng, Y., J. Ling, L. Yan, J. Zhou & J. Shen. 1999. Cephalopod resources and rational utilization in East China Sea. *Journal of Fishery Science, China*, 6: 52–56.

Zhou, F., Z. Ma, J. Huang & S. Jiang. 2005. Evaluation of protein nutritive value in 4 diets used for *Penaeus monodon* Broodstock. *Journal of Zhanjiang Ocean University*, 25(4): 9–13.

Zielinski, S. & H.O. Pörtner. 2000. Oxidative stress and antioxidative defense in cephalopods: a function of metabolic rate or age? *Comparative Biochemistry and Physiology*, B, 125(2): 147–160.

Zielinski, S., P.G. Lee & H.O. Pörtner. 2000. Metabolic performance of the squid *Lolliguncula brevis* (Cephalopoda) during hypoxia: an analysis of the critical P sub(O[sub]2). *Journal of Experimental Marine Biology and Ecology*, 243(2): 241–259.

Zimmer, I., U. Piatkowski & T. Brey. 2007. The trophic link between squid and the emperor penguin *Aptenodytes forsteri* at Pointe Geologie, Antarctica. *Marine Biology*, 152:1187–1195.

Zuev, G.V. 1966. Functional basis of the external structure in cephalopods. *Kiev: Naukova Dumka Publication*, 140 pp. (In Russian).

Zuev, G.V. 1971. Cephalopods of the Northwestern Indian Ocean. *Naukova Dumka, Kiev*, 223 pp. [In Russian].

*__Zuev, G.V.__ 2006. Squids of the family Enoploteuthidae in the epipelagic layer of the Kuroshio Current. *PICES XV. Book of Abstracts*, p. 65.

Zuev, G.V. & M.V. Chesalin. 2004. Biology and prospects for fishing of purple-back flying squid in the Arabian Sea. *Rybnoe Khozyaistvo*, 6: 38–40, 68.

Zuev, G.V. & D.K. Gutsal. 1989. Fishery-ecological characteristics of the *Sthenoteuthis oualaniensis* squid. *Rybnoe Khozjajstvo*, 2: 38–40 (In Russian).

*__Zuev, G.V., & K.N. Nesis.__ 1971. Role of squids in the food chains of the ocean. Chapter IV, pp. 78–83. *In*: Squid (Biology and Fishing), 1971, Pishchevaya Promyshlennost, Moscow, 360 pages. [In Russian]. English translation, 2003, *Smithsonian Institution Libraries*, 291 pp.

Zuev, G.V. & K.N. Nesis. 1973a. Prospects for the Soviet squid fishery. *Journal Squid Biology and Fishery*, 1973 (2593): 45–49. (translation).

Zuev, G.V. & K.N. Nesis. 1973b. The squid fishery abroad. *Journal of Fisheries Research Board of Canada*, 1973 (2598): 27–44. (translation).

Zuev, G.V. & Ch.M. Nigmatullin. 1975a. Elements of spatial areal structure in the oceanic squid *Ommastrephes pteropus* (Steenstrup) in the eastern Atlantic. *In* Biological Investigations in the Tropical Zone of the Oceans. *Kiev: Naukova Dumka Publication*, 56–67 (In Russian).

Zuev, G.V. & Ch.M. Nigmatullin. 1975b. On the distribution of the North Atlantic squid *Ommastrephes bartramii* (Lesueur, 1821). *Trudy AtlantNIRO*, 58: 187–192. Kaliningrad: AtlantNIRO Publication. (In Russian with English abstract).

Zuev, G.V. & V.N. Nikolsky. 1993. Ecological mechanisms related to the intraspecific structure of the nektonic squid *Sthenoteuthis pteropus* (Steenstrup). *In* T. Oktani, R.K. O'Dor & T. Kubodera, eds. Recent Advances in Cephalopod Fisheries Biology. *Tokyo: Tokai University Press*, pp. 653–664

*__Zuev, G.V., K.N. Nesis & Ch.M. Nigmatullin.__ 1975. Systematics and evolution of the squid genera *Ommastrephes* and *Symplectoteuthis* (Cephalopoda: Ommastrephidae). *Zoologicheskij Zhurnal*, 54(10): 1468–1479 (In Russian with English abstract).

Zuev, G.V., K.N. Nesis & Ch.M. Nigmatullin. 1976. Distribution of the genera *Ommastrephes* d'Orbigny, 1835, *Sthenoteuthis* Verrill, 1880, and *Todarodes* Steenstrup, 1880 (Cephalopoda: Oegopsida) in the Atlantic Ocean. *Bulletin of the Moscow Society of Natural Biology*, 81(4): 53–63. (In Russian with English abstract).

Zuev, G.V., Ch.M. Nigmatullin & V.N. Nikolsky. 1985. Nektonic oceanic squids (genus *Sthenoteuthis*). Moscow: Agropromizdat Publication: 224 p. (In Russian with English contents)

*__Zuev, G.V., V. Nicolsky & A.G. Trofimov.__ 1992 [1991]. Intraspecific differentiation of the squid, *Sthenoteuthis pteropus* (Steenstrup, 1855) in the Atlantic Ocean. *Bulletin of Marine Science*, 49(1–2): p. 670.

*__Zuev, G.V., Ch. Nigmatullin, M. Chesalin & K. Nesis.__ 2002. Main results of long-term worldwide studies on the tropical nektonic oceanic squid genus *Sthenoteuthis*: An overview of the Soviet investigations. *Bulletin of Marine Science*, 71(2): 1019–1060.

Zuev, M.A. 2004. Distribution and biomass of boreopacific gonate squid (*Gonatopsis borealis* Sasaki, 1929) in the Okhotsk Sea and Pacific waters off the Kuril Islands during winter period. In: *PICES Scientific Report*, 26: 162–164.

Zumholz, K. 2001. Fischereibiologische Untersuchungen zur Cephalopoden-Fauna der Nordsee. Diploma Thesis, University Kiel.

Zumholz, K. & R.P. Frandsen. 2006. New information on the life history of cephalopods off West Greenland. *Polar Biology*, 29(3): 169–178.

Zumholz, K. & U. Piatkowski. 2002. Beak length analysis of *Loligo forbesi*, *Todarodes sagittatus* and *Todaropsis eblanae* from the northern North Sea. *Bulletin of Marine Science*, 71(2): 1146.

Zumholz, K. & U. Piatkowski. 2004. New data on the biology of the Lesser Flying Squid, *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in the North Sea. Theme Session on Cephalopod Stocks: Review, Analyses, Assessment, and Sustainable Management (CC). *ICES Council Meeting documents*. Copenhagen.

Zumholz, K. & U. Piatkowski. 2005. Research cruise data on the biology of the lesser flying squid, *Todaropsis eblanae*, in the North Sea. *Aquatic Living Resources*, 18(4):373–376.

Zumholz, K., T.H. Hansteen, A. Kluegel & U. Piatkowski. 2006. Food effects on statolith composition of the common cuttlefish (Sepia officinalis). *Marine Biology Berlin*, 150(2): 237–244.

Zumholz, K., T.H. Hansteen, U. Piatkowski & P.L. Croot. 2007. Influence of temperature and salinity on the trace element incorporation into statoliths of the common cuttlefish (*Sepia officinalis*). *Marine Biology*, 151: 1321–1330.

Zumholz, K., A. Klugel, T. Hansteen & U. Piatkowski. 2007. Statolith microchemistry traces the environmental history of the boreoatlantic armhook squid *Gonatus fabricii*. *Marine Ecology Progress Series*, 333: 195–204.

Zumholz, K., T. Hansteen, F. Hillion, F. Horreard & U. Piatkowski. 2007. Elemental distribution in cephalopod statoliths: NanoSIMS provides new insights into nano-scale structure. *Reviews in Fish Biology and Fisheries*, 17(2–3): 487–491.

Zuur, A. & G.J. Pierce. 2004. Common trends in northeast Atlantic squid time series. *Journal of Sea Research*, 52: 57–72.

MAIN REFERENCES PUBLICATIONS ON CEPHALOPODS PUBLISHED SINCE 1984:

Abbott, J., Williamson, R. & Maddock, L. (eds). 1995. Cephalopod Neurobiology. Oxford University Press, New York. 542 pp.

Beesley, P.L., Ross, G.J.B. & Wells, A. (eds). 1998. Mollusca: The Southern Synthesis. *Fauna of Australia*, Vol. 5. CSIRO Publishing: Melbourne, Part A: 563 pp., Part B: 565-1234 pp. Cephalopods presented in Chapters 11, 12, 13, pp. 451–563.

Boletzky, S. v. (ed). 1995. Mediterranean Sepiolidae. *Bulletin de l'Institut océanographique, Monac*, Special Number 16:105 pp.

Boletzky, S.v., Fioroni P. & Guerra, A. (eds). 1997. Proceedings of the Second international symposium on functional morphology of cephalopods. *Vie Milieu*, 47: 87–187.

Boucaud-Camou, E. (ed.). 1991. La Sieche. The Cuttlefish. Centre de Publications de l"Universite de Caen, France, 358 pp.

Boyle, P.R. (ed.). 1987. Cephalopod Life Cycle. Vol. II. Comparative Reviews. Academic Press, London (UK), 441 pp.

Boyle, P.R. (ed.). 1991. The UFAW handbook on the care and management of cephalopods in the laboratory. Universities Federaton for Animal Welfare, Potters Bar, UK, 63 pp.

Boyle, P.R. & Pierce, G.J. (eds). 1994. Fishery biology of Northeast Atlantic squid. *Fisheries Research*, Special Issue, 21(1–2): 314 pp.

Boyle, P. & Rodhouse, P. 2005. Cephalopods. *Ecology and Fisheries*. Blackwell Publishing, 452 pp.

Budelmann, B.U., Schipp, R. & Boletzky, S.v. 1997. Cephalopoda *In* F.W. Harrison & A. Kohn, eds. Microscopic Anatomy of Invertebrates, Volume 6A, Mollusca II, New York, Wiley-Liss, pp 119–414.

Chotiyaputta, C., Hatfield, E.M.C. & Lu, C.C. (eds). 2005. Cephalopod biology, recruitment and culture. *Phuket Marine Biological Center Research Bulletin*, 66: 365 pp.

Clarke, M.R. (ed.). 1986. A Handbook for the Identification of Cephalopod Beaks. Clarendon Press, Oxford, UK, 273 pp.

Clarke, M.R. (ed.). 1996. The role of cephalopods in world Oceans. Philosophical Transactions of the Royal Society of London, Series B, 351: 977–1112.

Clarke, M.R. & Trueman, E.R. (eds). 1988. The Mollusca, Vol. 12. Paleontology and Neontology of Cephalopods. Academic Press, New York, 340 pp.

Guerra, A. 1992. Mollusca, Cephalopoda. *In* M.A. Ramos, *et al.,* eds. Fauna Iberica, vol.1. Museo Nacional de Ciencias Naturales. CSIC, Madrid, 327 pp.

Gilbert, D.L., Adelman, W.J. & Arnold, J.M. (ed.). 1990. Squid as experimental animals. Plenum Press, NY, 516 pp.

Hanlon, R.T. (ed.). 1988. International Symposium on Life History, Systematics and Zoogeography of Cephalopods in Honor of S. Stillman Berry. *Malacologia*, 29(1): 307 pp.

Hanlon, R.T. & Messenger, J.B. 1996. Cephalopod behaviour. Cambridge University Press, 232 pp.

Jereb, P. & Roper, C.F.R. (eds). 2005. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 1. Chambered nautiluses and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). *FAO Species Catalogue for Fishery Purposes*, 4(1): 262 p., 9 colour pls.

Jereb, P., Ragonese S. & von Boletzky, S. (eds). 1991. Squid age determination using statoliths. Note tecniche e reprints dell'Istituto di Tecnologia della Pesca e del Pescato (Mazara del Vallo, Italy), Special Publication, 1:127 pp.

Kinne, O. (ed.). 1990. Diseases of Marine Animals. Vol. III. Cephalopoda through Urocordata. Biologische Anstalt Helgoland, Hamburg, pp. 21–227.

Landman, N.H., Tanabe K. & Davis, R.A. (eds). 1996. Ammoniod Paleobiology. Plenum Press, NY, 857 pp.

Mangold, K. (ed.). 1989. Traité de Zoologie, Volume V: Céphalopodes. Masson, Paris, 804 pp.

Nesis, K.N. 1987. Cephalopods of the World. TFH Publications, 351 pp. (English version of the Russian original, published in 1982).

Nielsen, J. (ed.). 2007. Cephalopod life-cycles, biology, management. *Reviews in Fish Biology and Fisheries*, 17(2–3): 499 pp.

Nixon, M. & Young, J.Z. 2003. The brain and lives of Cephalopods. Oxford University Press, UK, 448 pp.

Norman, M.D. 2000. Cephalopods: A world guide. Conch Books, Hackenheim, 320 pp.

Northwest Atlantic Fisheries Organization. 1985. Special Session on Squids. NAFO Scientific Council Studie, 9: 175 pp.

Okutani, T. 1995. Cuttlefish and squids of the world in color. National Cooperative Association of Squid Processors, Japan, 185 pp.

Okutani, T., Tagawa, M. & Horikawa, H. 1987. Cephalopods from the continental shelf and slope around Japan. Japan Fisheries Resource Conservation Association, Tokyo, 194 pp.

Okutani, T., O'Dor, R.K. &Kubodera, T. (eds). 1993. Recent advances in cephalopod fisheries biology. Contributed papers to 1991 CIAC International Symposium and Proceedings of the Workshop on Age, Growth and Population Structure. Tokai University Press, Tokyo, 752 pp.

Payne, A.I.L., Lipinski, M.R. & Roeleveld M.A.C. (eds). 1998. Cephalopod biodiversity, ecology and evolution. South African Journal of marine Science, 20: 469 pp.

Piatkowski, U., Pierce, G.J. & Morais de Cunha, M. (eds). 2001. Impact of cephalopods in the food chain and their interaction with the environment. *Fisheries Research*, Special Issue, 52(1–2): 142 pp.

Pierce, G.J., Allcock, L., Bruno, I., Bustamante, P., González, A., Guerra, Á. Jereb, P., Lefkaditou, E., Malham, S., Moreno, A., Pereira, J., Piatkowski, U., Rasero, M., Sánchez, P., Begoña Santos, M., Santurtún, M., Seixas, S., Sobrino, I. & Villanueva, R. 2010. *Cephalopod biology and fisheries in Europe*. ICES Cooperative Research Report No. 303. 175 pp.

Pörtner, H.O. & O' Dor, R.K. (eds). 1994. Lifestyle and performance in cephalopods. Physiological Adaptations. *Mar. Freshw. Behav. Physiol.*, 25(1–3):207 pp.

Rodhouse, P.G., Dawe, E.G. & O'Dor, R.K. (eds). 1998. Squid recruitment dynamics. The genus *Illex* as a model, the commercial *Illex* species and influences on variability. *FAO Fisheries Technical Paper*, 376: 273 pp.

Rodhouse, P.G., Piatkowski, U. & Lu, C.C. (eds). 1994. Southern Ocean cephalopods: life cycle and populations. *Antarctic Science*, 6(2): 291 pp.

Rodhouse, P.G., Yamashiro, C. & Goss, C. (eds). 2001. Squid fishery biology in the Eastern Pacific coastal upwelling system. *Fisheries Research*, Special Issue, 54(1): 143 pp.

Roper, C.F.E, Sweeney, M.J. & Vecchione, M. (eds). 1991. Gilbert L. Voss Memorial Issue. *Bulletin of Marine Science*, 49(1 & 2): 670 pp.

Saunders, W. B. & Landman, N.H. (eds). 1987. Nautilus. The biology and paleobiology of a living fossil. Plenum Press, New York, 632 pp.

Sweeney, M.J., Roper, C.F.E., Mangold, K.M., Clarke, M.R. & Boletzky, S.v. (eds). 1992. "Larval" and Juvenile Cephalopods: a Manual for their Identification. *Smithsonian Contributions to Zoology*, 513: 282 pp.

Tomiyama, T. & Hibiya T. 1978. Fisheries in Japan, Squid and Cuttlefish. Japan Marine Products Photo Material Association, Tokyo, 161 pp.

Voss, N.A., Vecchione, M., Toll, R.B. & Sweeney, M.J. (eds). 1998. Systematics and Biogeography of Cephalopods. *Smithsonian Contribution to Zoology*, 586, Vol.I: 276 pp. and Vol. II: 599 pp.

Ward, P.D. 1987. Natural History of Nautilus. Allen and Unwin, London, 268 pp.

Wiedmann, J. & Kullmann J. (eds). 1988. Cephalopods past and present. E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart, Germany, 765 pp.

Young, R.E., Vecchione, M. & Mangold, K. (in constant progress). Cephalopoda. Tree of Life web project.

LINKS AT AVAILABLE DATA ON LINE:

Cephalopod International Advisory Council (CIAC): http://www.abdn.ac.uk/CIAC/

Coleoid Cephalopods through Time, International Symposium:
http://www.userpage.fu-berlin.de/%7epalaeont/palbio3/palbio3.htm

FAO catalogue Cephalopods of the World: ftp://ftp.fao.org/docrep/fao/009/ac479e/ac479e00.pdf

FAO Statistical Database: http://faostat.fao.org/faostat/default.jsp?version=int&hasbulk=1

GlobeFish (Cephalopods): http://www.globefish.org/cephalopods-market-reports.html

Integrated Taxonomic Information System: http://www.itis.gov/

National Museum of Natural History (NMFS): http://www.mnh.si.edu/cephs/

National Resource Center for Cephalopods: http://www.gulfbase.org/organization/view.php?oid=nrcc

Review of the state of world marine fishery resources, World squid resources:
ftp://ftp.fao.org/docrep/fao/007/y5852e/Y5852E19.pdf

Sea Around Us Project: http://www.seaaroundus.org/project.htm

SeaMounts Online: http://seamounts.sdsc.edu/

Smithsonian Institution research Information System (SIRIS): http://siris-bibliographies.si.edu/#focus

Species 2000: http://www.sp2000.org/

Squid Atlas, Geographical Information System (GIS): http://www.nerc-bas.ac.uk/public/mlsd/squid-atlas/

SquidFish: http://www.squidfish.net/

The Cephalopod Page: http://www.thecephalopodpage.org/

The Octopus News Magazine Online (TONMO): http://www.tonmo.com/

Tree of Life (Cephalopods): http://tolweb.org/tree?group=Cephalopoda&contgroup=Mollusca

6. INDEX OF SCIENTIFIC AND VERNACULAR NAMES

Explanation of the System

Italics : Valid scientific names (double entry by genera and species).

Italics : Synonyms, misidentifications, subgenera, subspecies and other combinations (double entry by genera and species).

ROMAN : Family names.

ROMAN : Scientific names of divisions, classes, subclasses, orders, suborders and subfamilies.

Roman : FAO names.

Roman : Local names.

7. LIST OF COLOUR PLATES

PLATE I

1. Squid jigging machines at night – Japan (W.F. Rathjen)
2. Trawl catch of squid – New England (W.F. Rathjen)
3. Off shore fishing boat (C.F.E. Roper)
4. Upright mesh screens (W.F. Rathjen)
5. Jigging machine (W.F. Rathjen)
6. Soft body and hard body (black) squid jigging hooks on reel – Japan (C.F.E. Roper)

PLATE II

7. Closing up purse seine with squid – Japan (C.F.E. Roper)
8. Squid catch on deck – Western North Atlantic (W.F. Rathjen)
9. Squid drying in the sun – Japan (C.F.E. Roper)
10. Squid drying in the sun – Japan (C.F.E. Roper)
11. Squid drying in the sun – Japan (C.F.E. Roper)

PLATE III

12. ***Loligo*** eggs (C.F.E. Roper)
13. ***Loligo*** embryos (C.F.E. Roper)
14. ***Loligo forbesii*** (P. Wirtz)
15. ***Loligo reynaudii*** (R. Smale)
16. ***Loligo reynaudii*** (M. Hanlon)
17. ***Alloteuthis subulata*** (P. Wirtz)

PLATE IV

18. ***Doryteuthis (Amerigo) opalescens*** (H. Hall)
19. ***Doryteuthis (Amerigo) opalescens*** (H. Hall)
20. ***Doryteuthis (Amerigo) pealeii*** (R. Hanlon)
21. ***Doryteuthis (Amerigo) pealeii*** (R. Hanlon)
22. ***Doryteuthis (Amerigo) pealeii*** (R. Hanlon)
23. ***Doryteuthis (Doryteuthis) plei*** (C.F.E. Roper)

PLATE V

24. ***Doryteuthis (Doryteuthis) plei*** (R. Hixon)
25. ***Doryteuthis (Doryteuthis) plei*** (R. Hixon)
26. ***Pickfordiateuthis pulchella*** (C.F.E. Roper)
27. ***Sepioteuthis australis*** (M. Norman)
28. ***Sepioteuthis lessoniana*** (M. Norman)
29. ***Sepioteuthis lessoniana*** (M. Norman)

PLATE VI

30. ***Sepioteuthis sepioidea*** (R. Hanlon)
31. ***Sepioteuthis sepioidea*** (R. Hanlon)
32. ***Architeuthis*** sp. (T. Kubodera)
33. ***Uroteuthis (Photololigo) edulis*** (I. Soyama)
34. ***Chiroteuthis*** sp. (C.F.E. Roper)
35. ***Chiroteuthis spoeli*** (M. Vecchione)

PLATE VII

36. ***Cranchia scabra*** (R. Young)
37. Cranchiid squid (C.F.E. Roper)
38. ***Sandalops melancholicus*** (C.F.E. Roper)
39. ***Teuthowenia megalops*** (M. Vecchione)
40. ***Abraliopsis*** sp. (C.F.E. Roper)
41. ***Histioteuthis corona cerasina*** (C.F.E. Roper & R. Young)
42. ***Joubiniteuthis portieri*** (R. Young)
43. ***Histioteuthis hoylei*** (C.F.E. Roper & R. Young)

PLATE VIII

44. ***Lycoteuthis*** sp. (C.F.E. Roper)
45. ***Mastigoteuthis*** sp.(C.F.E. Roper)
46. ***Mastigoteuthis hjorti*** (M. Vecchione)
47. ***Taningia danae*** (C.F.E. Roper)
48. ***Taningia danae*** (C.F.E. Roper)
49. Ommastrephid *Rhynchoteuthion* (C.F.E. Roper)
50. ***Illex coindetii*** (M. Vecchione)
51. ***Illex coindetii*** (M. Vecchione)

PLATE IX

52. ***Illex*** sp. (M. Vecchione)
53. ***Illex illecebrosus*** (M. Vecchione)
54. ***Dosidicus gigas*** (H. Hall)
55. ***Ornithoteuthis antillarum*** (M. Vecchione)
56. ***Ornithoteuthis antillarum*** (M. Vecchione)
57. ***Ornithoteuthis antillarum*** (M. Vecchione)

PLATE X

58. ***Sthenoteuthis oualaniensis*** (R. Young)
59. ***Nototodarus hawaiiensis*** (R. Young)
60. ***Onychoteuthis*** sp. (R.Young)
61. ***Onykia*** sp. (R. Young)
62. ***Pyroteuthis addolux*** (R. Young)
63. ***Pterygioteuthis*** sp. (C.F.E. Roper)

ADDITIONAL INFORMATION

Plate III

Fig. 14: ***Loligo forbesii*** – Notice the characteristic, flamelike stripes on the ventrolateral sides of the mantle.
Fig. 15: ***Loligo reynaudii*** – The animal has just caught a fish and holds it with its mouth and arms.

Plate IV

Fig. 18: ***Doryteuthis (Amerigo) opalescens*** – The diver looks small on the impressive bed of squid eggs.
Fig. 19: ***Doryteuthis (Amerigo) opalescens*** – Squids busy in the spawning event.
Fig. 20: ***Doryteuthis (Amerigo) pealeii*** – Animal resting on the bottom.
Fig. 21: ***Doryteuthis (Amerigo) pealeii*** – Example of disruptive camouflage.
Fig. 22: ***Doryteuthis (Amerigo) pealeii*** – Hatchling, the young squid newly hatched from the egg.
Fig. 23: ***Doryteuthis (Doryteuthis) plei*** – a) Embryos; b) hatchling.

Plate V

Fig. 26: ***Pickfordiateuth pulchella*** – Animal in aquarium.
Fig. 29: ***Sepioteuthis lessoniana*** – Small school of squids.

Plate VI

Fig. 30: ***Sepioteuthis sepioidea*** – Example of disruptive camouflage.
Fig. 31: ***Sepioteuthis sepioidea*** – Animal on coral reef (on a grass bed).
Fig. 33: ***Architeuthis*** sp. – a) Animal attacking the bait; b) hooked tentacle; c) club of the broken tentacle on board.
Fig. 35: ***Chiroteuthis spoeli*** – Animal in aquarium.

Plate VII

Fig. 43: ***Histioteuthis hoylei*** – Detail of the crown of photophores around the eye.

Plate VIII

Fig. 47: ***Taningia danae*** – Ventral view of the animal in aquarium.
Fig. 48: ***Taningia*** – Oral view of the animan in aquarium.
Fig. 49: Ommastrephid *Rhynchoteuthion*, the characteristic paralarval stage with the two tentacles fused into a trunk-like proboscis.
Fig. 50: ***Illex coindetii*** – Photo by submersible.
Fig. 51: ***Illex coindetii*** – Photo by submersible.

Plate IX

Fig. 52: ***Illex*** sp. – Photo by submersible.
Fig. 53: ***Illex illecebrosus*** – Animal in aquarium.
Fig. 55: ***Ornithoteuthis antillarum*** – Photo by submersible.
Fig. 56: ***Ornithoteuthis antillarum*** – Photo by submersible.
Fig. 57: ***Ornithoteuthis antillarum*** – Photo by submersible.

Plate IX

Fig. 58: ***Stenoteuthis oualaniensis*** – Animal in a ship-board aquarium.
Fig. 59: ***Nototodarus hawaiiensis*** – Animal in a ship-board aquarium.
Fig. 61: ***Onkia*** sp. – Juvenile in aquarium.
Fig. 62: ***Pterygioteuthis*** sp. – Detail of the photophores around the eye.

ADDITIONAL INFORMATION

Plate III

Fig. 14: ***Loligo forbesii*** – Notice the characteristic, flamelike stripes on the ventrolateral sides of the mantle.
Fig. 15: ***Loligo reynaudii*** – The animal has just caught a fish and holds it with its mouth and arms.

Plate IV

Fig. 18: ***Doryteuthis (Amerigo) opalescens*** – The diver looks small on the impressive bed of squid eggs.
Fig. 19: ***Doryteuthis (Amerigo) opalescens*** – Squids busy in the spawning event.
Fig. 20: ***Doryteuthis (Amerigo) pealeii*** – Animal resting on the bottom.
Fig. 21: ***Doryteuthis (Amerigo) pealeii*** – Example of disruptive camouflage.
Fig. 22: ***Doryteuthis (Amerigo) pealeii*** – Hatchling, the young squid newly hatched from the egg.
Fig. 23: ***Doryteuthis (Doryteuthis) plei*** – a) Embryos; b) hatchling.

Plate V

Fig. 26: ***Pickfordiateuth pulchella*** – Animal in aquarium.
Fig. 29: ***Sepioteuthis lessoniana*** – Small school of squids.

Plate VI

Fig. 30: ***Sepioteuthis sepioidea*** – Example of disruptive camouflage.
Fig. 31: ***Sepioteuthis sepioidea*** – Animal on coral reef (on a grass bed).
Fig. 33: ***Architeuthis*** sp. – a) Animal attacking the bait; b) hooked tentacle; c) club of the broken tentacle on board.
Fig. 35: ***Chiroteuthis spoeli*** – Animal in aquarium.

Plate VII

Fig. 43: ***Histioteuthis hoylei*** – Detail of the crown of photophores around the eye.

Plate VIII

Fig. 47: ***Taningia danae*** – Ventral view of the animal in aquarium.
Fig. 48: ***Taningia*** – Oral view of the animan in aquarium.
Fig. 49: Ommastrephid *Rhynchoteuthion*, the characteristic paralarval stage with the two tentacles fused into a trunk-like proboscis.
Fig. 50: ***Illex coindetii*** – Photo by submersible.
Fig. 51: ***Illex coindetii*** – Photo by submersible.

Plate IX

Fig. 52: ***Illex*** sp. – Photo by submersible.
Fig. 53: ***Illex illecebrosus*** – Animal in aquarium.
Fig. 55: ***Ornithoteuthis antillarum*** – Photo by submersible.
Fig. 56: ***Ornithoteuthis antillarum*** – Photo by submersible.
Fig. 57: ***Ornithoteuthis antillarum*** – Photo by submersible.

Plate IX

Fig. 58: ***Stenoteuthis oualaniensis*** – Animal in a ship-board aquarium.
Fig. 59: ***Nototodarus hawaiianensis*** – Animal in a ship-board aquarium.
Fig. 61: ***Onkia*** sp. – Juvenile in aquarium.
Fig. 62: ***Pterygioteuthis*** sp. – Detail of the photophores around the eye.

COLOUR PLATES

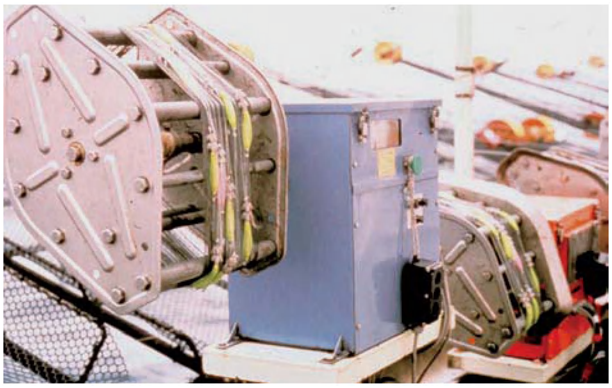
PLATE I

1. Squid jigging machines at night – Japan
(W.F. Rathjen)

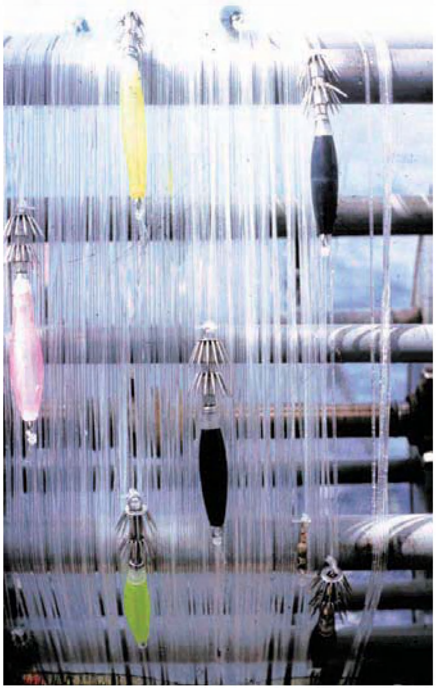
2. Trawl catch of squid – New England
(W.F. Rathjen)

3. Off shore fishing boat
(C.F.E. Roper)

4. Upright mesh screens
(W.F. Rathjen)



5. Jigging machine
(W.F. Rathjen)



6. Soft body and hard body (black)
squid jigging hooks on reel – Japan
(C.F.E. Roper)

PLATE II

7. Closing up purse seine with squid – Japan
(C.F.E. Roper)

8. Squid catch on deck – Western North Atlantic
(W.F. Rathjen)

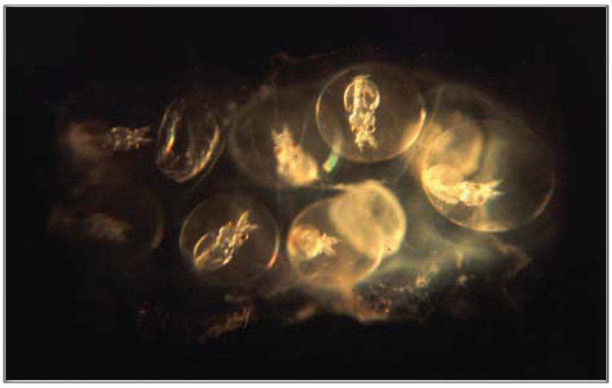
9. Squid drying in the sun – Japan
(C.F.E. Roper)

10. Squid drying in the sun – Japan
(C.F.E. Roper)

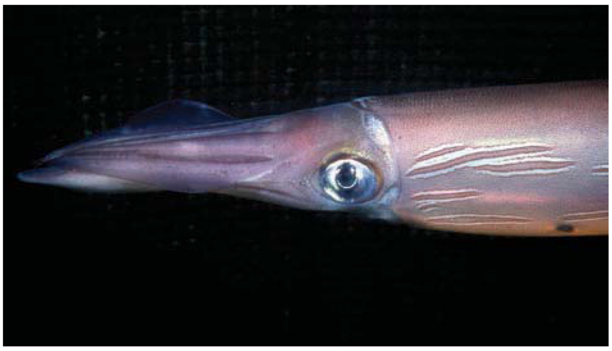
11. Squid drying in the sun – Japan
(C.F.E. Roper)

PLATE III

12. *Loligo* eggs
(C.F.E. Roper)



13. *Loligo* embryos
(C.F.E. Roper)



14. *Loligo forbesii*
(P. Wirtz)

15. *Loligo reynaudii*
(M. Smale)

16. *Loligo reynaudii*
(R. Hanlon)

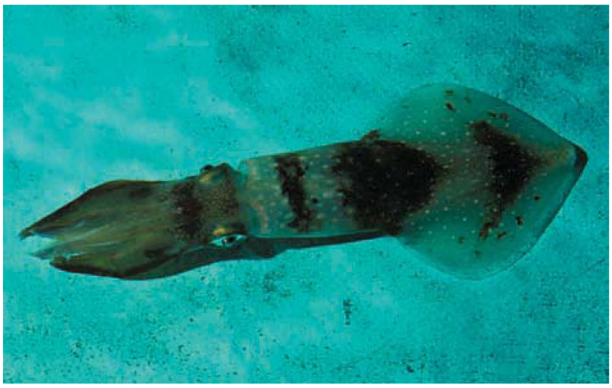
17. *Alloteuthis subulata*
(P. Wirtz)

PLATE IV

18. *Doryteuthis (Amerigo) opalescens*
(H. Hall)

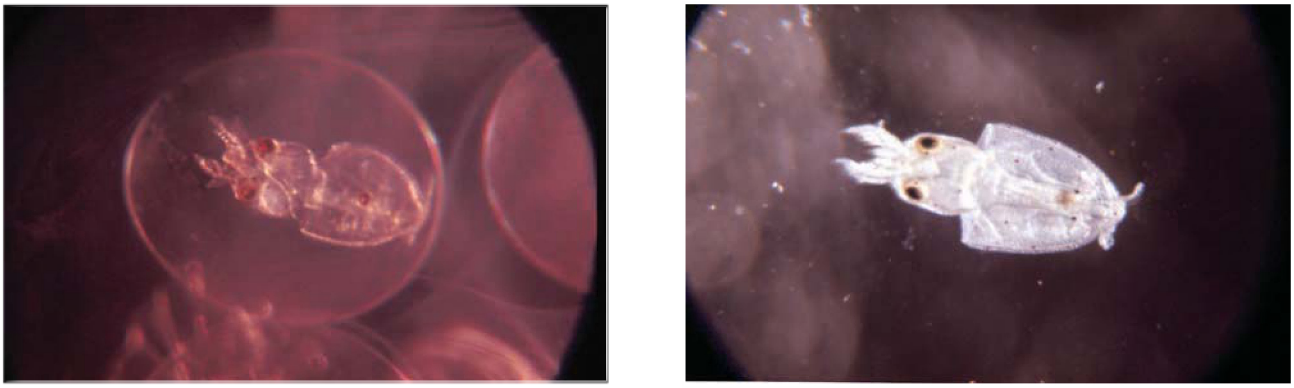
19. *Doryteuthis (Amerigo) opalescens*
(H. Hall)

20. *Doryteuthis (Amerigo) pealeii*
(R. Hanlon)



21. *Doryteuthis (Americo) pealeii*
(R. Hanlon)

22. *Doryteuthis (Amerigo) pealeii*
(R. Hanlon)



a) **b)**

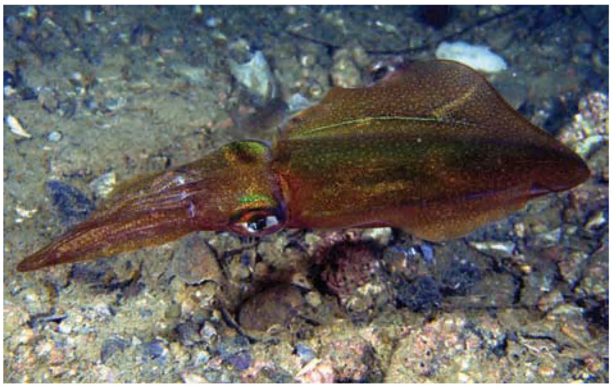
23. *Doryteuthis (Doryteuthis) plei*
(C.F.E. Roper)

PLATE V

24. *Doryteuthis (Doryteuthis) plei*
(R. Hixon)

25. *Doryteuthis (Doryteuthis) plei*
(R. Hixon)

26. *Pickfordiateuthis pulchella*
(C.F.E. Roper)



27. *Sepioteuthis australis*
(M. Norman)

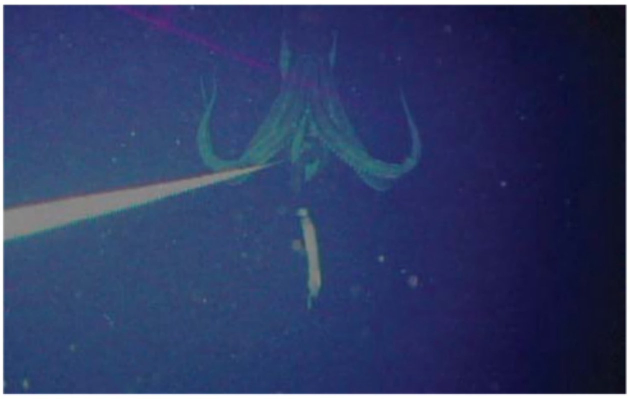
28. *Sepioteuthis lessoniana*
(M. Norman)

29. *Sepioteuthis lessoniana*
(M. Norman)

PLATE VI

30. ***Sepioteuthis sepioidea***
(R. Hanlon)

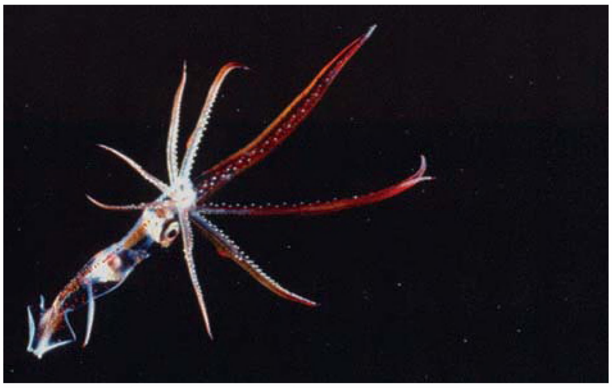
31. ***Sepioteuthis sepioidea***
(R. Hanlon)



a)

33. ***Uroteuthis (Photololigo) edulis***
(I. Soyama)

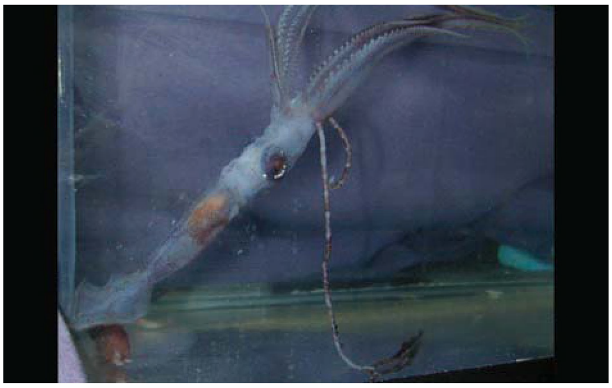
b)



34. ***Chiroteuthis*** **sp.**
(C.F.E. Roper)

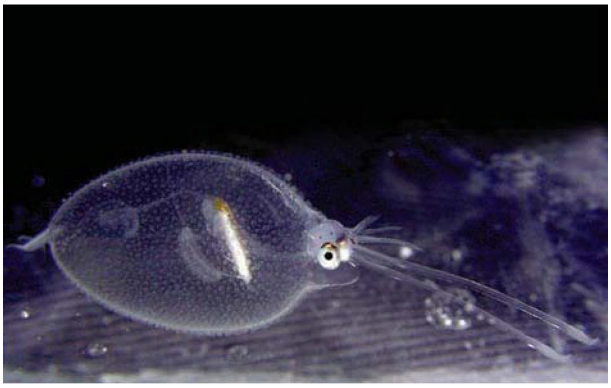
c)

32. ***Architeuthis*** **sp.**
(T. Kubodera)

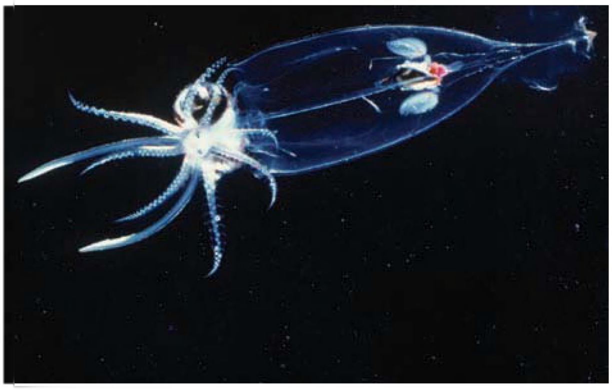


35. ***Chiroteuthis spoeli***
(M. Vecchione)

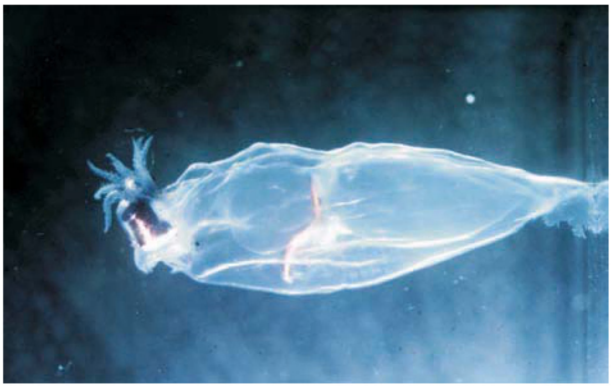
PLATE VII



36. *Cranchia scabra*
(R. Young)



37. Cranchiid squid
(C.F.E. Roper)

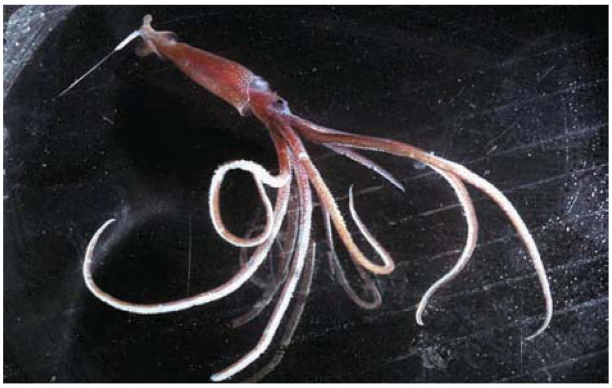


38. *Sandalops melancholicus*
(C.F.E Roper)

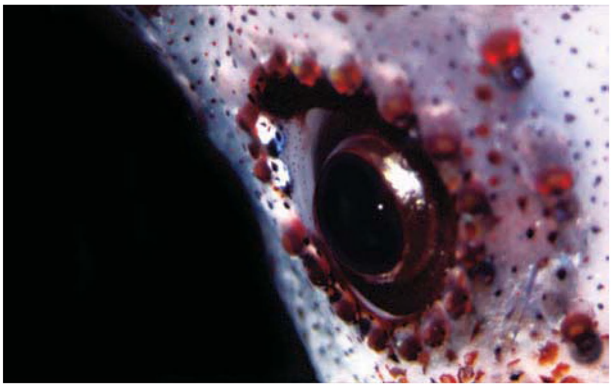
39. *Teuthowenia megalops*
(M. Vecchione)

40. *Abraliopsis* sp.
(C.F.E. Roper)

41. *Histioteuthis corona cerasina*
(C.F.E. Roper & R. Young)



42. *Joubiniteuthis portieri*
(R. Young)

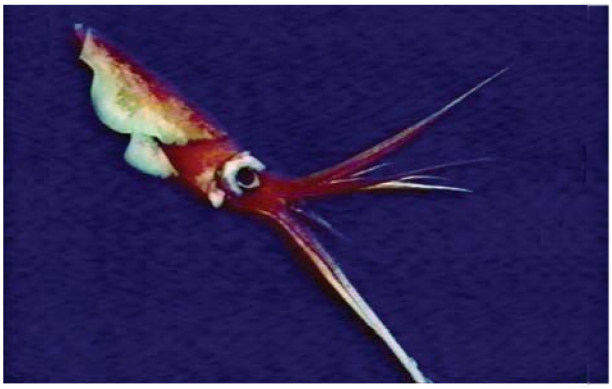


43. *Histioteuthis hoylei*
(C.F.E. Roper & R. Young)

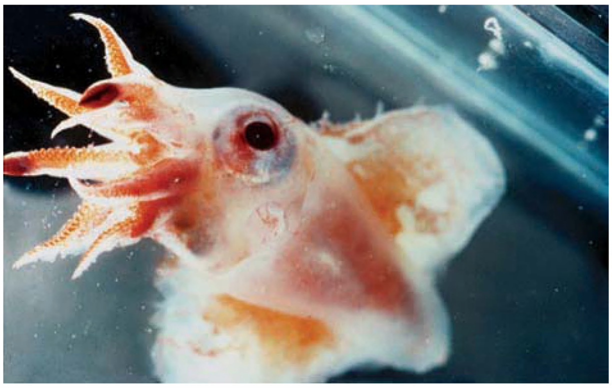
PLATE VIII

44. ***Lycoteuthis*** **sp.**
(C.F.E. Roper)

45. ***Mastigoteuthis*** **sp.**
(C.F.E. Roper)



46. ***Mastigoteuthis hjorti***
(M. Vecchione)



47. ***Taningia danae***
(C.F.E. Roper)

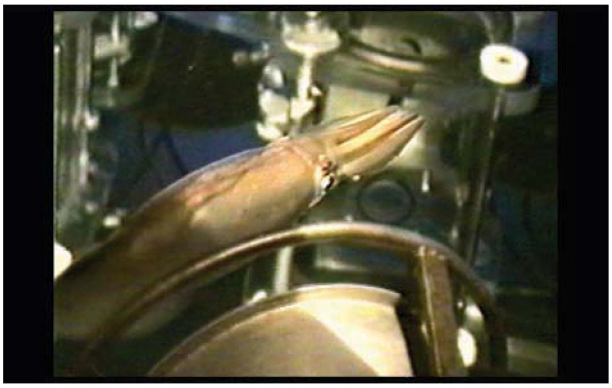
48. ***Taningia danae***
(C.F.E. Roper)

49. Ommastrephid ***Rhynchoteuthion***
(C.F.E. Roper)

50. ***Illex coindetii***
(M. Vecchione)

51. ***Illex coindetii***
(M. Vecchione)

PLATE IX

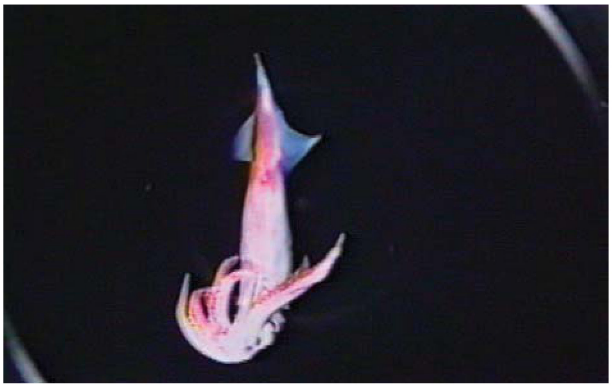


52. *Illex* sp.
(M. Vecchione)

53. *Illex illecebrosus*
(M. Vecchione)

54. *Dosidicus gigas*
(H. Hall)

55. *Ornithoteuthis antillarum*
(M. Vecchione)



56. *Ornithoteuthis antillarum*
(M. Vecchione)

57. *Ornithoteuthis antillarum*
(M. Vecchione)

PLATE X

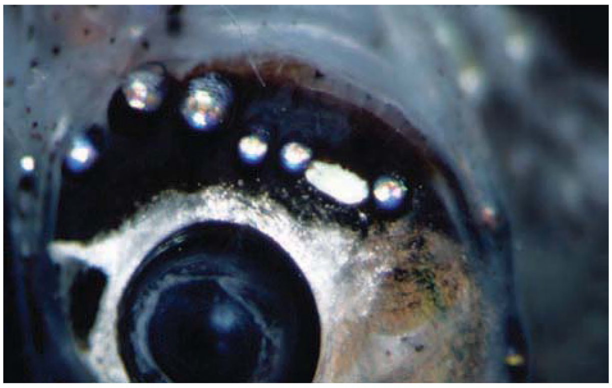

58. *Stenoteuthis oualaniensis*
(R. Young)


59. *Nototodarus hawaiiensiss*
(R. Young)


60. *Onychoteuthis* **sp.**
(R. Young)


61. *Onykia* **sp.**
(R. Young)


62. *Pyroteuthis addolux*
(R. Young)


63. *Pterygioteuthis* **sp.**
(C.F.E. Roper)

This is the second volume of the entirely rewritten, revised and updated version of the original FAO Catalogue of Cephalopods of the World (1984). The present Volume is a multiauthored compilation that reviews 28 families, i.e. (in alphabetical order), *Ancistrocheiridae*, *Architeuthidae*, *Australiteuthidae*, *Bathyteuthidae*, *Batoteuthidae*, *Brachioteuthidae*, *Chiroteuthidae*, *Chtenopterygidae*, *Cranchiidae*, *Cycloteuthidae*, *Enoploteuthidae*, *Gonatidae*, *Histioteuthidae*, *Joubiniteuthidae*, *Lepidoteuthidae*, *Loliginidae*, *Lycoteuthidae*, *Magnapinnidae*, *Mastigoteuthidae*, *Neoteuthidae*, *Octopoteuthidae*, *Ommastrephidae*, *Onychoteuthidae*, *Pholidoteuthidae*, *Promachoteuthidae*, *Psychroteuthidae*, *Pyroteuthidae* and *Thysanoteuthidae*, with 81 genera and the 295 species known and named to the date of the compilation of the volume. It provides accounts for all families and genera, as well as illustrated keys. Information under species accounts includes: valid modern systematic name and original citation of the species (or subspecies); synonyms; English, French and Spanish FAO names for the species; illustrations of dorsal and ventral aspects of the whole animal (as necessary) and other distinguishing illustrations; field characteristics; diagnostic features; geographic and vertical distribution, including GIS map; size; habitat; biology; interest to fishery; local names when available; a remarks section (as necessary) and literature. The Volume is fully indexed and also includes sections on terminology and measurements, an extensive glossary, an introduction with an updated review of the existing biological knowledge on squids (including fisheries information and main catch data for recent years) and a dedicated bibliography. Due to the conspicuous amount of literature addressing many squid species, an appendix is included in the online version, where those references considered most pertinent to the species are listed, by family and species, in alphabetical order by author. Key words, also, are reported

MINISTERO POLITICHE
AGRICOLE E FORESTALI

ISBN 978-92-5-106720-8 ISSN 1020-8682

9 789251 067208