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Biological Services Program

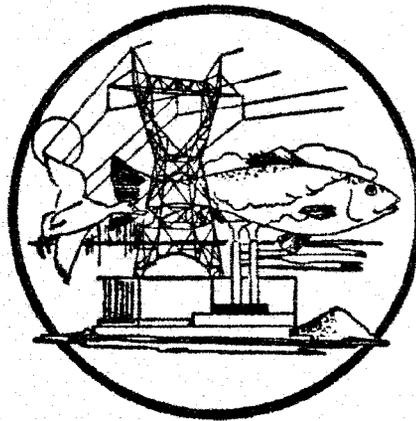
DEVELOPMENT OF FISHES OF THE MID-ATLANTIC BIGHT

AN ATLAS OF EGG, LARVAL AND JUVENILE STAGES

VOLUME

II

ANGUILLIDAE THROUGH SYNGNATHIDAE



Fish and Wildlife Service

U.S. Department of the Interior



Frontispiece: Nesting and courtship behavior in the genus *Gasterosteus*. (Coste, V., 1884: figs. 2-3, Penelope L. Firth, delineator.)

Biological Services Program

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DEVELOPMENT OF FISHES OF THE MID-ATLANTIC BIGHT

AN ATLAS OF EGG, LARVAL AND JUVENILE STAGES

VOLUME II

ANGUILLIDAE THROUGH SYNGNATHIDAE

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**Performed for
Power Plant Project
Office of Biological Services
Fish and Wildlife Service
U.S. Department of the Interior**

Fish and Wildlife Service

U.S. Department of the Interior

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FOREWORD

The demand for electric energy often creates conflicts with the desire to preserve and protect the Nation's fish and wildlife resources. This is particularly true when the use of water for power plants is considered. Power plants require large volumes of water from rivers, lakes, reservoirs, and estuaries. Withdrawal of water for cooling purposes causes the loss of fish eggs, larvae, and juveniles through impingement or entrainment. The discharge of water causes thermal and chemical pollution, and can cause alteration of stream flow patterns and the disruption of the thermal and dissolved oxygen stratification in those water bodies.

The biological consequences of water use by power plants depend upon the species of organisms involved, the mechanical and physiological stresses on the organisms, and the ecological role of the organisms. To assess the impacts of power plants and other habitat modifications on fish populations, it is necessary to identify fish eggs, larvae, and juveniles of different species. However, up to now, descriptions of the developmental stages of fishes have been scattered throughout a large number of sources.

The *Development of Fishes of the Mid-Atlantic Bight* is a reference which compiles descriptions of the egg, larval, and juvenile stages of over 300 fish species, and includes dichotomous keys useful for identifying species. Descriptions of spawning migrations and life habits of adult fishes, their geographic range and distribution, and movements of fish at all life stages are also included.

With this kind of baseline taxonomic information, biologists will be able to assess the management implications of power plant siting and other habitat modifications on aquatic populations and provide information to decision makers. We believe these books are a major step in providing the type of information necessary to incorporate environmental considerations into resource development decisions.

A handwritten signature in cursive script that reads "Lynn A. Greenwalt". The signature is written in black ink and is positioned centrally on the page.

Director, U.S. Fish and Wildlife Service

The Biological Services Program was established within the U.S. Fish and Wildlife Service to supply scientific information and methodologies on key environmental issues which impact fish and wildlife resources and their supporting ecosystems. The mission of the Program is as follows:

1. To strengthen the Fish and Wildlife Service in its role as a primary source of information on national fish and wildlife resources, particularly in respect to environmental impact assessment.
2. To gather, analyze, and present information that will aid decision makers in the identification and resolution of problems associated with major land and water use changes.
3. To provide better ecological information and evaluation for Department of the Interior development programs, such as those relating to energy development.

Information developed by the Biological Services Program is intended for use in the planning and decision making process to prevent or minimize the impact of development on fish and wildlife. Biological Services research activities and technical assistance services are based on an analysis of the issues, the decision makers involved and their information needs, and an evaluation of the state of the art to identify information gaps and determine priorities. This is a strategy to assure that the products produced and disseminated will be timely and useful.

Biological Services projects have been initiated in the following areas:

- Coal extraction and conversion
- Power plants
- Geothermal, mineral, and oil shale development
- Water resource analysis, including stream alterations and western water allocation
- Coastal ecosystems and Outer Continental Shelf development
- Systems and inventory, including National Wetlands Inventory, habitat classification and analysis, and information transfer.

The Program consists of the Office of Biological Services in Washington, D.C., which is responsible for overall planning and management; National Teams which provide the Program's central scientific and technical expertise and who arrange for contracting Biological Services studies with States, universities, consulting firms, and others; regional staff who provide a link to problems at the operating level; and staff at certain Fish and Wildlife Service research facilities who conduct in-house research studies.

CONTENTS

GENERAL INTRODUCTION	1
GLOSSARY	5
Introduction to Volume II	11
Anguillidae—freshwater eels	17
<i>Anguilla rostrata</i> (Lesueur), American eel	18
Muraenidae—morays	33
<i>Gymnothorax funebris</i> Ranzani, Green moray	34
Congridae—conger eels	39
<i>Conger oceanicus</i> (Mitchill), Conger eel	40
Ophichthidae—snake eels	45
<i>Ahlia egmontis</i> (Jordan), Key worm eel	49
<i>Myrophis punctatus</i> Lütken, Speckled worm eel	52
<i>Ophichthus gomesi</i> (Castelnaud), Shrimp eel	58
<i>Ophichthus ocellatus</i> (Lesueur), Palespotted eel	61
<i>Pisoodonophis cruentifer</i> (Goode and Bean), Snake eel	64
Scomberesocidae—sauries	71
<i>Scomberesox saurus</i> (Walbaum), Atlantic saury	72
Belonidae—needlefishes	85
<i>Ablennes hians</i> (Valenciennes), Flat needlefish	87
<i>Strongylura marina</i> (Walbaum), Atlantic needlefish	90
<i>Tylosurus acus</i> (Lacépède), Agujon	96
<i>Tylosurus crocodilus</i> (Peron and Lesueur), Houndfish	102
Exocoetidae—flyingfishes	111
<i>Cheilopogon heterurus</i> (Rafinesque), Atlantic flyingfish	113
Hemiramphidae—halfbeaks	127
<i>Euleptorhamphus velox</i> Poey, Flying halfbeak	128
<i>Hemiramphus brasiliensis</i> (Linnaeus), Ballyhoo	129
<i>Hyporhamphus unifasciatus</i> (Ranzani), Halfbeak	133
Cyprinodontidae—killifishes	141
<i>Cyprinodon variegatus</i> Lacépède, Sheepshead minnow	145
<i>Fundulus confluentus</i> Goode and Bean, Marsh killifish	152
<i>Fundulus diaphanus</i> (Lesueur), Banded killifish	156
<i>Fundulus heteroclitus</i> (Linnaeus), Mummichog	162
<i>Fundulus luciae</i> (Baird), Spotfin killifish	181
<i>Fundulus majalis</i> (Walbaum), Striped killifish	186
<i>Lucania parva</i> (Baird), Rainwater killifish	196
Poeciliidae—livebearers	205
<i>Gambusia affinis</i> (Baird and Girard), Mosquitofish	206
Gadidae—codfishes	219
<i>Enchelyopus cimbrius</i> (Linnaeus), Fourbeard rockling	226
<i>Gadus morhua</i> Linnaeus, Atlantic cod	236
<i>Melanogrammus aeglefinus</i> (Linnaeus), Haddock	260
<i>Microgadus tomcod</i> (Walbaum), Atlantic tomcod	278
<i>Phycis chesteri</i> Goode and Bean, Longfin hake	290
<i>Pollachius virens</i> (Linnaeus), Pollock	292
<i>Urophycis chuss</i> (Walbaum), Red hake	305
<i>Urophycis earlli</i> (Bean), Carolina hake	314

<i>Urophycis regius</i> (Walbaum), Spotted hake	316
<i>Urophycis tenuis</i> (Mitchill), White hake	321
Merlucciidae—merlucciid hakes	327
<i>Merluccius albidus</i> (Mitchill), Offshore hake	328
<i>Merluccius bilinearis</i> (Mitchill), Silver hake	330
Gasterosteidae—sticklebacks	341
<i>Apeltes quadracus</i> (Mitchill), Fourspine stickleback	342
<i>Gasterosteus aculeatus</i> Linnaeus, Threespine stickleback	347
Fistulariidae—cornetfishes	367
<i>Fistularia petimba</i> Lacépède, Red cornetfish	368
<i>Fistularia tabacaria</i> Linnaeus, Bluespotted cornetfish	371
Macrorhamphosidae—snipefishes	377
<i>Macrorhamphosus scolopax</i> (Linnaeus), Longspine snipefish	378
Syngnathidae—pipefishes and seahorses	389
<i>Hippocampus erectus</i> Perry, Lined seahorse	391
<i>Hippocampus obtusus</i> Ginsburg, Offshore seahorse	397
<i>Syngnathus floridae</i> (Jordan and Gilbert), Dusky pipefish	399
<i>Syngnathus fuscus</i> Storer, Northern pipefish	402
<i>Syngnathus louisianae</i> Günther, Chain pipefish	407
<i>Syngnathus pelagicus</i> Linnaeus, Sargassum pipefish	409
BIBLIOGRAPHY	411
INDEX TO COMMON AND SCIENTIFIC NAMES	457

GENERAL INTRODUCTION

As noted by Mansueti and Hardy (1967) in the first edition of Volume I of this series, the early developmental stages of most fishes are either poorly known or completely unknown. Despite the fundamental importance of this knowledge to many aspects of fishery biology and ichthyology, this situation still persists.

OBJECTIVES

The primary purpose of this series is to synthesize the world literature on fishes occurring in the Mid-Atlantic Bight of the United States. The successful accomplishment of this goal serves a number of useful functions, among which are greater ease in identifying young fishes and fish eggs, the systematization of information gaps, and the stimulation of studies in areas where such gaps have been clearly demonstrated. Although some original data have been included in this series, time constraints have kept this to a minimum, primary efforts having been directed toward a comprehensive review of existing literature.

FORMAT

The geographical area considered extends from the northern boundary of New Jersey to the southern boundary of Virginia from tidal freshwater out to the 100 fathom contour (see fig. 1).

Data have been presented on 321 species. Mansueti and Hardy (1967) arranged the species in Volume I in the sequence used by the American Fisheries Society (1960). Although disagreements exist with this arrangement as a phylogenetic sequence it is used here to order the species and families in this series so that the revised Volume I will remain intact. In some cases recent systematic revisions have demanded realignment at familial levels or the updating of generic and specific names.

The series is presented in six volumes as follows: Volume I, Acipenseridae through Ictaluridae, 50 species; Volume II, Anguillidae through Syngnathidae, 48 species; Volume III, Aphredoderidae through Rachycentridae, 52 species; Volume IV, Carangidae through Ehippididae, 52 species; Volume V, Chaetodontidae through Ophidiidae, 52 species; and Volume VI, Stromateidae through Ogcocephalidae, 67 species.

Species accounts are arranged alphabetically within family groupings. Each species account is divided into the following major divisions:

ADULTS—meristics, morphometrics and general description.

DISTRIBUTION AND ECOLOGY—range, habitat and movements of adults, larvae, and juveniles.

SPAWNING—description of season, location, conditions of spawning, and fecundity.

EGGS—description of ripe ovarian, unfertilized or fertilized eggs.

EGG DEVELOPMENT—developmental sequences, physical limiting factors and incubation times.

YOLK-SAC LARVAE—size range, morphology, development and pigmentation.

LARVAE—size range, morphology, development and pigmentation.

PREJUVENILES (not recognized in all volumes)—size range, morphology, development and pigmentation.

JUVENILES—size range, morphology, development and pigmentation.

GROWTH (not given in all volumes)—average and/or representative growth rates, especially preadult growth.

AGE AND SIZE AT MATURITY—average age and size at maturity plus variation if these data are available.

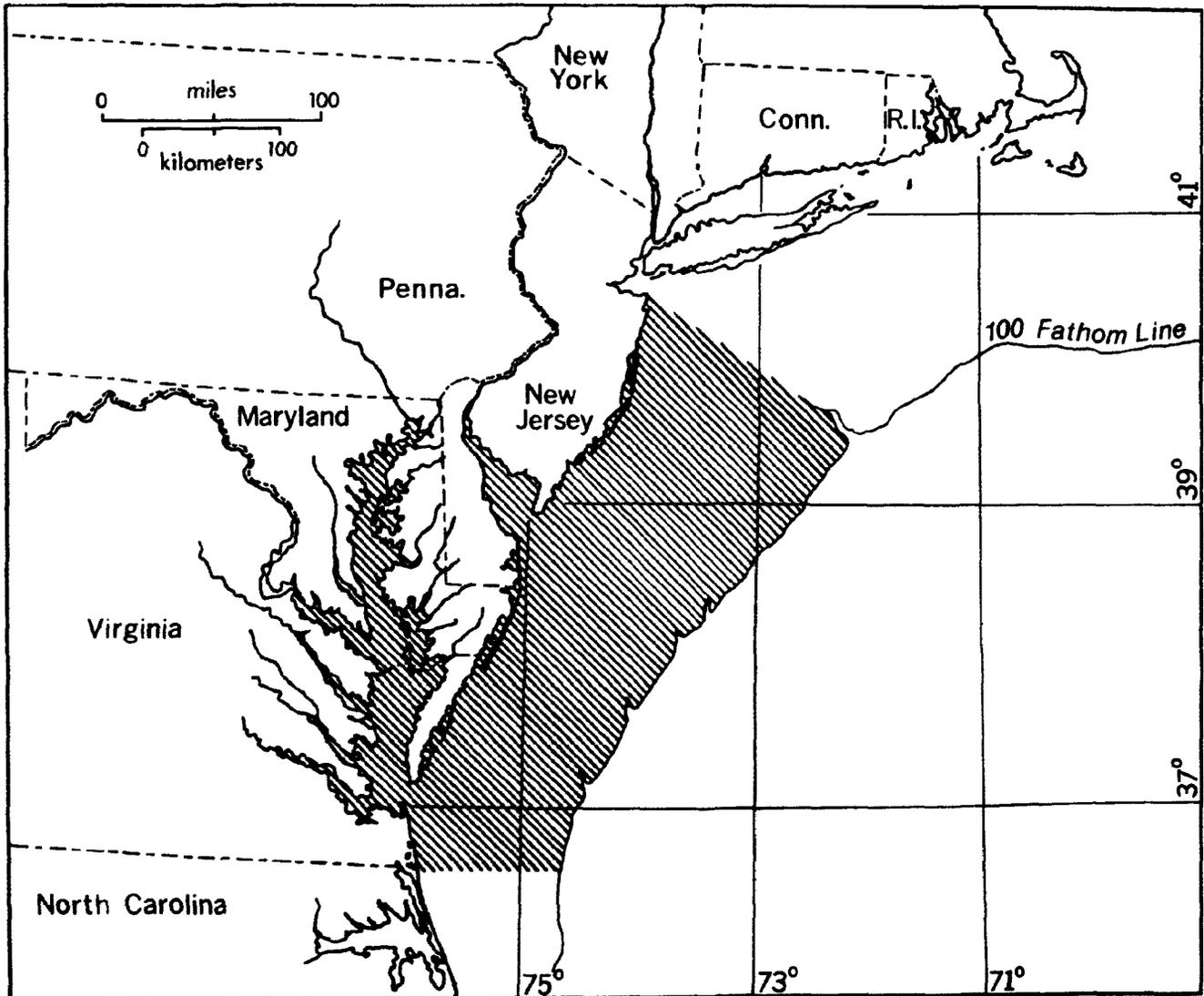


Fig. 1. Map of the Chesapeake Bay and adjacent Mid-Atlantic Bight. Hatching indicates the area considered in this series.

LITERATURE CITED—abbreviated citations to literature consulted for that account. Complete citations in Bibliography.

Superscript numbers in each species account refer to the abbreviated citations given at the end of each account. Complete citations may be found in the bibliography at the end of each volume. In prefaces, introductions, family accounts and figure legends, citations are given by author and date, rather than superscript. Throughout, parenthetical initials follow original unpublished information provided by the person whose initials are given (see preface for full name and address). Each volume has its own bibliography and index. No cumulative bibliography or index has been attempted.

Illustrations are of mixed quality and utility. For the most part they are simply reprinted from the literature. In some cases, however, previously published figures have been redrawn, and a number of original illustrations are in-

cluded. Figure legends cite the artist or delineator. Redrawings are usually of figures which are unique in that they provide the only illustrations of particular features or stages and will not reproduce well or are confusing or inaccurate in detail. Attempts have been made to exclude drawings of misidentified specimens; however, error in judgement is possible. Where available, multiple illustrations of the same stage are included if they show geographic variation or if the authors were unable to determine which illustration provided the most accurate representation. In addition, a number of drawings which have been published in rare or generally unavailable sources have been included primarily for their historic value.

TERMINOLOGY

For the most part, terminology and methods of measuring and counting are those of Hubbs and Lagler (1958); however, these terms are specifically for adult forms and must be modified or replaced by different ones for early developmental stages.

For illustrations of typical developmental stages and larval anatomy see fig. 2.

Definitions and terms for developmental stages vary considerably depending on the investigator and the species worked on. The following terminology has been standardized:

- YOLK-SAC LARVA—stage between hatching and absorption of yolk;
- LARVA—stage between absorption of yolk and acquisition of minimum adult fin ray complement;
- PREJUVENILE—stage between acquisition of minimum adult fin ray complement and assumption of adult body form; used only where strikingly different from juvenile (cf. Hubbs, 1958; *Tholichthys* stage of butterflyfishes, *querimana* stage of mullets, etc.);
- JUVENILE—stage between acquisition of minimum adult fin ray complement and sexual maturity or between prejuvenile stage and adult;
- ADULT—sexually mature.

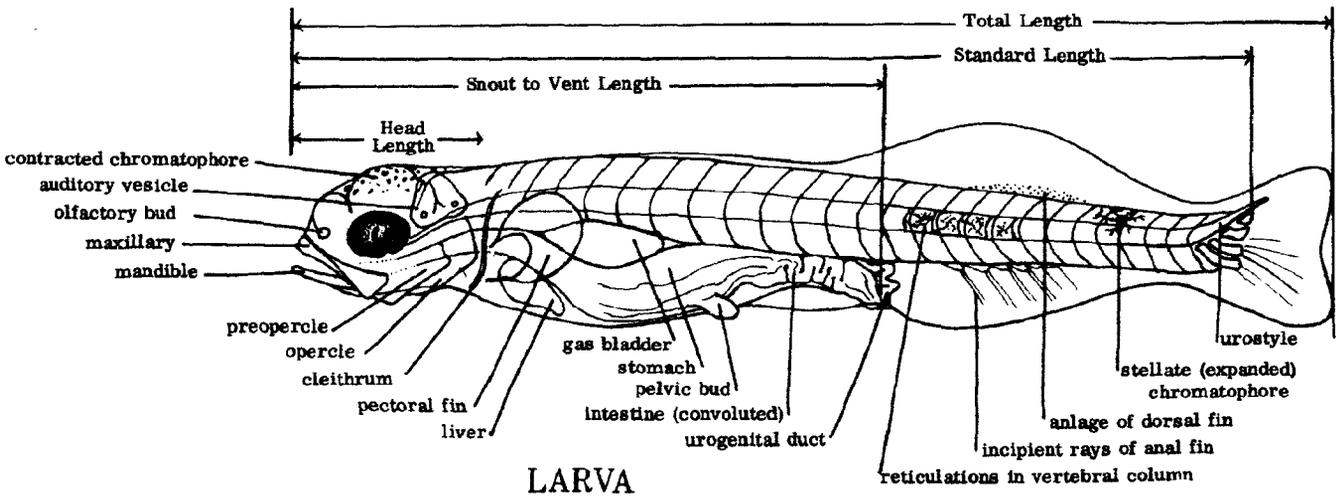
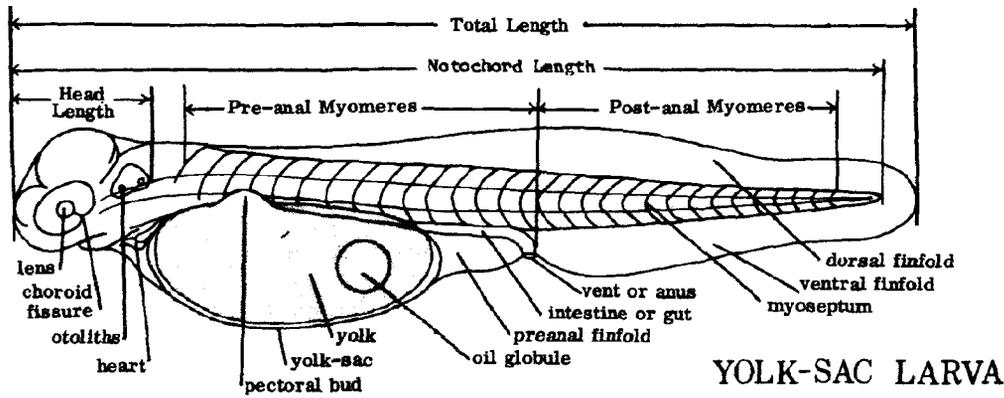
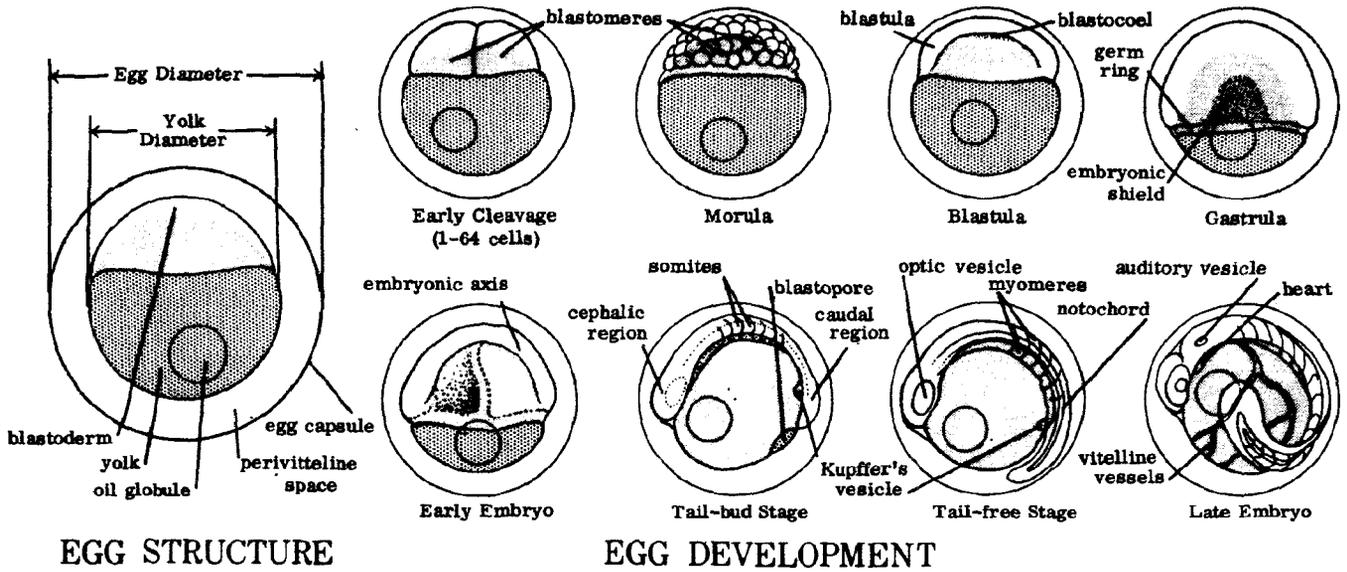


Fig. 2. Diagrammatic representation of morphology and development of egg and larval stages of a typical teleost.

GLOSSARY

A. Abbreviation for anal fin.

abbreviate heterocercal. Tail in which the vertebral axis is prominently flexed upward, only partly invading upper lobe of caudal fin; fin fairly symmetrical externally.

adherent. Attached or joined together, at least at one point.

adhesive egg. An egg which adheres on contact to substrate material or other eggs; adhesiveness of entire egg capsule may or may not persist after attachment.

adipose fin. A fleshy rayless median dorsal structure, located behind the true dorsal fin.

adnate. Congenitally united; conjoined.

adult. Sexually mature as indicated by production of gametes.

anadromous. Fishes which ascend rivers from the sea to spawn.

anal. Pertaining to the anus or vent.

anal fin. Unpaired median fin immediately behind anus or vent.

anal fin origin. Anteriormost point at which the anal fin attaches to the body.

anlage. Rudimentary form of an anatomical structure; primordium.

anus. External orifice of the intestine; vent.

auditory vesicle. Sensory anlage from which the ear develops; clearly visible during early development.

axillary process. Enlarged, accessory scale attached to the upper or anterior base of pectoral or pelvic fins.

BL. Abbreviation for body length.

barbel. Tactile process arising from the head of various fishes.

blastocoel. Cavity of the blastula; segmentation cavity.

blastoderm. *Sensu strictu*, early embryonic tissue composed of blastomeres; more generally, embryonic tissue prior to formation of embryonic axis.

blastodisc. Embryo-forming area of egg prior to cleavage.

blastomeres. Individual cells formed during cleavage.

blastopore. Opening formed by and bordered by the germ ring as it extends over the yolk.

blastula. Stage in embryonic development which represents the final product of cleavage stages, characterized by formation of the blastocoel.

body length. A specialized method of measuring, generally applied only to billfishes, and defined by

Rivas (1956a) as the distance from the tip of the mandible (with jaws closed) to the middle point on the posterior margin of the middle caudal rays.

branched ray. Soft ray with two or more branches distally.

branchial arches. Bony or cartilaginous structures, supporting the gills, filaments and rakers.

branchiostegals. Struts of bone inserting on the hyoid arch and supporting, in a fanwise fashion, the branchiostegal membrane; branchiostegal rays.

buoyant egg. An egg which floats free within the water column; pelagic.

C. Abbreviation for caudal fin.

caeca. Finger-like outpouchings at boundary of stomach and intestine.

catadromous. Fishes which go to sea from rivers to spawn.

caudal fin. Tail fin.

caudal peduncle. Area lying between posterior end of anal fin base and base of caudal fin.

cheek. Lateral surface of head between eye and opercle, usually excluding preopercle.

chorion. Outer covering of egg; egg capsule.

choroid fissure. Line of juncture of invaginating borders of optic cup; apparent in young fish as a trough-like area below lens.

chromatophores. Pigment-bearing cells; frequently capable of expansions and contractions which change their size, shape, and color.

cirrus. Generally small, dermal, flap-like or tentacle-like process on the head or body.

cleavage stages. Initial stages in embryonic development where divisions of blastomeres are clearly marked; usually include 1st through 6th cleavages (2-64 cells).

cleithrum. Prominent bone of pectoral girdle, clearly visible in many fish larvae.

ctenoid scale. Scales with comb-like margin; bearing cteni.

cycloid scale. Scales with evenly curved free border, without cteni.

D. Abbreviation for dorsal fin.

demersal egg. An egg which remains on the bottom, either free or attached to substrate.

dorsal fins. Median, longitudinal, vertical fins located on the back.

- dorsal fin origin.* Point where first dorsal ray or spine attaches to body.
- early embryo.* Stage in embryonic development characterized by formation of embryonic axis.
- egg capsule.* Outermost encapsulating structure of the egg, consisting of one or more membranes; the protective shell.
- egg diameter.* In nearly spherical eggs, greatest diameter; in elliptical eggs given as two measurements, the greatest diameter or major axis and the least diameter or minor axis.
- emarginate.* Notched but not definitely forked, as in the shallowly notched caudal fin of some fishes.
- embryonic axis.* Primitive differentiation of the embryo; an elongate thickening of blastodermal tissue.
- embryonic shield.* Thickened shield-like area of the blastoderm at caudal edge of the germ ring.
- erythrophores.* Red or orange chromatophores.
- esophagus.* Alimentary tract between pharynx and stomach.
- falcate.* Deeply concave as a fin with middle rays much shorter than anterior and posterior rays.
- finfold.* Median fold of integument which extends along body of developing fishes and from which median fins arise.
- FL.* Abbreviation for fork length.
- fork length.* Distance measured from the anteriormost point of the head to the end of the central caudal rays.
- ganoid scales.* Diamond- or rhombic-shaped scales consisting of bone covered with enamel.
- gas bladder.* Membranous, gas-filled organ located between the kidneys and alimentary canal in teleosts; air bladder or swim bladder.
- gastrula.* Stage in embryonic development between blastula and embryonic axis.
- germ ring.* The thickened rim of the blastoderm evident during late blastula and gastrula stages.
- germinal disc.* The blastodisc.
- gill arches.* See branchial arches.
- gill rakers.* Various-shaped bony projections on anterior edge of the gill arches.
- granular yolk.* Yolk consisting of discrete units of finely to coarsely granular material.
- guanophores.* White chromatophores; characterized by presence of iridescent crystals of guanine.
- gular fold.* Transverse membrane across throat.
- gular plate.* Ventral bony plate between anterior third of lower jaws, as in *Amia calva*.
- heterocercal.* Tail in which the vertebral axis is flexed upward and extends nearly to tip of upper lobe of caudal fin; fin typically asymmetrical externally, upper lobe much longer than lower.
- HL.* Abbreviation for head length.
- head length.* Distance from anteriormost tip of head to posteriormost part of opercular membrane, excluding spine; prior to development of operculum, measured to posterior end of auditory vesicle.
- holoblastic.* Type of cleavage in which the entire egg, including the yolk, undergoes division.
- homocercal.* Tail in which the vertebral axis terminates in a penultimate vertebra followed by a urostyle (the fusion product of several vertebral elements); fin perfectly symmetrical externally.
- hypochord.* A transitional rod of cells which develops under the notochord in the trunk region of some embryos.
- hypurals.* Expanded, fused, haemal spines of last few vertebrae which support caudal fin.
- incubation period.* Time from fertilization of egg to hatching.
- interorbital.* Space between eyes over top of head.
- iridocytes.* Crystals of guanine having reflective and iridescent qualities.
- isocercal.* Tail in which vertebral axis terminates in median line of fin, as in *Gadiformes*.
- isthmus.* The narrow area of flesh in the jugular region between gill openings.
- jugular.* Pertaining to the throat.
- juvenile.* Young fish after attainment of minimum adult fin ray counts and before sexual maturation.
- keeled.* With a ridge or ridges.
- Kupffer's vesicle.* A small, vesicular, ventro-caudal pocketing which forms as blastopore narrows.
- larva.* Young fish between time of hatching and attainment of minimum adult fin ray counts.
- late embryo.* Stage prior to hatching in which the embryo has developed external characteristics of its hatching stage.
- lateral line.* Series of sensory pores and/or tubes extending backward from head along sides.
- lateral line scales.* Pored or notched scales associated with the lateral line.
- mandible.* Lower jaw, comprised of three bones: dentary, angular and articular.
- maxillary.* The dorsalmost of the two bones in the upper jaw.
- Meckel's cartilage.* Embryonic cartilaginous axis of the lower jaw in bony fishes.

- melanophores*. Black chromatophores.
- mental*. Pertaining to the chin.
- meroblastic*. Type of cleavage in which only the blastodisc undergoes division.
- micropyle*. Opening in egg capsule through which spermatozoa enter.
- morula*. Stage in development of egg in which blastomeres form a mulberry-like cluster.
- myomeres*. Serial muscle bundles of the body.
- myoseptum*. Connective tissue partitions separating myomeres.
- nape*. Area immediately posterior to occipital region.
- nasal*. Pertaining to region of the nostrils, or to the specific bone in that region.
- NL*. Abbreviation of notochord length.
- notochord*. Longitudinal supporting axis of body which is eventually replaced by the vertebral column in teleostean fishes.
- notochord length*. Straight-line distance from anteriormost part of head to posterior tip of notochord; used prior to and during notochord flexion.
- occipital region*. Area on dorsal surface of head, beginning above or immediately behind eyes and extending backwards to end of head.
- oil globule(s)*. Discrete sphere(s) of fatty material within the yolk.
- olfactory buds*. Incipient olfactory organs.
- optic vesicles*. Embryonic vesicular structures which give rise to the eyes.
- otoliths*. Small, calcareous, secreted bodies within the inner ear.
- P*. Abbreviation for pectoral fin.
- palatine teeth*. Teeth on the paired palatine bones in the roof of the mouth of some fishes.
- pectoral bud*. Swelling at site of future pectoral fin; anlage of pectoral fin.
- pectoral fins*. Paired fins behind head, articulating with pectoral girdle.
- pelagic*. Floating free in water column; not necessarily near the surface.
- pelvic bud*. Swelling at site of future pelvic (ventral) fins; anlage of pelvic fin.
- pelvic fins*. Paired fins articulating with pelvic girdle; ventral fins.
- periblast*. A layer of tissue between the yolk and cells of blastoderm which is observed as a thin border around blastula.
- peritoneum*. Membranous lining of abdominal cavity.
- perivitelline space*. Fluid-filled space between egg proper and egg capsule.
- pharyngeal teeth*. Teeth on the pharyngeal bones of the branchial skeleton.
- postanal myomeres*. The number of myomeres between posterior margin of anus and the most posterior myoseptums.
- preanal length*. Method of measuring often not stated, assumed to be about equivalent to snout to vent length in larvae.
- preanal myomeres*. The number of myomeres between the anteriormost myoseptum and the posterior margin of anus.
- predorsal scales*. Scales along dorsal ridge from occiput to origin of dorsal fin.
- prejuvenile*. Developmental stage immediately following acquisition of minimum fin ray complement of adult and before assumption of adult-like body form; used only where strikingly different from juvenile (*cf.* Hubbs, 1958; *Tholichthys* stage of butterflyfishes, *querimana* stage of mullets, etc.).
- premaxillary*. The ventralmost of the two bones included in the upper jaw.
- primordium*. Rudimentary form of an anatomical structure; anlage.
- principal caudal rays*. Caudal rays inserting on hypural elements; the number of principal rays is generally defined as the number of branched rays plus two.
- procurrent caudal rays*. A series of much shorter rays anterior to the principal caudal rays, dorsally and ventrally, not typically included in the margin of the caudal fin.
- pronephric ducts*. Ducts of pronephric kidney of early developmental stages.
- scute*. A modified, thickened scale, often spiny or keeled.
- sigmoid heart*. The S-shaped heart which develops from the primitive heart tube.
- SL*. Abbreviation for standard length.
- snout to vent length*. Distance from anteriormost part of head to posterior margin of anus; the precise method of measurement often not stated.
- soft rays*. Bilaterally paired, usually segmented, fin supports.
- somites*. Primitive, segmented, mesodermal tissue along each side of notochord.
- spines*. Unpaired, unsegmented, unbranched fin supports, usually (but not always) stiff and pungent.
- standard length*. In larvae, straight-line distance from anteriormost part of head to end of hypural ele-

- ments; not applicable to larvae prior to notochord flexion. (In juveniles and adults measured from most anterior point of snout or upper lip.)
- stomodeum*. Primitive invagination of the ectoderm which eventually gives rise to the mouth.
- tail-bud stage*. Stage of embryonic development characterized by a prominent caudal bulge and marked development of cephalic region.
- tail-free stage*. Stage of embryonic development characterized by separation of the tail from the yolk.
- TL*. Abbreviation for total length.
- total length*. Straight-line distance from anteriormost part of head to tip of tail; all older literature references not stated differently are assumed to be total length.
- urostyle*. Terminal vertebral element in higher teleosts, derived from the fusion and loss of several of the most posterior centra of the more primitive forms.
- V. Abbreviation for the central or pelvic fin.
- vent*. Anus.
- ventral fins*. Paired fins articulating with the pelvic girdle; pelvic fins.
- vitelline vessels*. Arteries and veins of yolk region.
- water-hardening*. Expansion and toughening of egg capsule due to absorption of water into the perivitelline space.
- width of perivitelline space*. Distance between yolk and egg capsule expressed either as direct measurement or a ratio of the egg diameter.
- xanthophores*. Yellow chromatophores.
- yolk*. Food reserve of embryonic and early larval stages, usually seen as a yellowish sphere diminishing in size as development proceeds.
- yolk diameter*. Greatest diameter of yolk; more accurately measurable prior to embryo formation.
- yolk plug*. Yolk within the blastopore.
- yolk sac*. A bag-like ventral extension of the primitive gut containing the yolk.
- yolk-sac larva*. A larval fish characterized by the presence of a yolk-sac.

VOLUME II DEDICATION

This volume is dedicated to Dr. L. Eugene Cronin, former Director of Chesapeake Biological Laboratory, Solomons, Maryland, in recognition of his total and honest devotion to the Chesapeake Bay.

INTRODUCTION TO VOLUME II

This volume contains accounts of the life histories and development of forty-eight species of teleostean fishes occurring in the Mid-Atlantic Bight (Anguillidae through Syngnathidae). It is primarily a compilation of previously published information but also includes some unpublished data and a number of original illustrations. These include the following:

<i>Anguilla rostrata</i> adult	Daniel M. Carver
<i>Conger oceanicus</i> adult	Daniel M. Carver
<i>Pisodonophis cruentifer</i> leptocephalus	Alice J. Lippson
<i>Ablennes hians</i> juvenile	Nancy S. Smith
<i>Strongylura marina</i> eggs, larvae	Peni G. Long
<i>Hemiramphus brasiliensis</i> juvenile	Jerry D. Hardy, Jr.
<i>Hyporhamphus unifasciatus</i> eggs, larvae	Elizabeth R. Peters Jerry D. Hardy, Jr. Nancy S. Smith William L. Dovel
<i>Cyprinodon variegatus</i> larvae	Linda L. Hudson
<i>Fundulus confluentus</i> eggs, larvae	Elizabeth R. Peters Linda L. Hudson
<i>Fundulus diaphanus</i> larvae	Linda L. Hudson
<i>Fundulus heteroclitus</i> larvae	Linda L. Hudson
<i>Fundulus luciae</i> eggs, larvae	Elizabeth R. Peters
<i>Fundulus majalis</i> larvae	Linda L. Hudson
<i>Lucania parva</i> larvae	Linda L. Hudson Nancy S. Smith
<i>Enchelyopus cimbrius</i> juvenile	Nancy S. Smith
<i>Microgadus tomcod</i> eggs, larvae	Jerry D. Hardy, Jr.
<i>Phycis chesteri</i> juvenile	Elizabeth R. Peters
<i>Urophycis tenuis</i> juvenile	Virginia Inst. Mar. Sci.
<i>Apeltes quadracus</i> larvae	William L. Dovel
<i>Hippocampus erectus</i> eggs, larvae	Linda L. Hudson
<i>Syngnathus floridae</i> larvae	Alice J. Lippson

Syngnathus fuscus
larvae

Alice J. Lippson

Original text contributions are indicated by initials as follows:

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 GED George E. Drewry, Chesapeake Biological Laboratory, Solomons, Maryland.
 WLD William L. Dovel, Boyce Thompson Institute, Yonkers, New York.
 MPF Michael P. Fahay, National Marine Fisheries Service, Northeast Fisheries Center, Sandy Hook, New Jersey.
 NRF Neal R. Foster, U.S. Fish and Wildlife Service, Ann Arbor, Michigan.
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 JDH Jerry D. Hardy, Jr., Chesapeake Biological Laboratory, Solomons, Maryland.
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 JAM John A. Musick, Virginia Institute of Marine Science, Gloucester Point, Virginia.
 RRM Robert R. Marak, National Marine Fisheries Service, Narragansett, Rhode Island.
 DGS David G. Smith, Marine Biomedical Institute, Galveston, Texas.
 NSS Nancy S. Smith, St. Petersburg, Florida.
 RLW Robert L. Wisner, Scripps Institute of Oceanography, La Jolla, California.

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I am especially grateful to our artist, Elizabeth Ray Peters, for her outstanding work on this project. Her original drawings of fish eggs and larvae are among the best which I have seen. I thank, also, Joan Ellis, Tamiko Karr, and Donna Davis, students from St. Marys College, for the numerous delineations which

they did as volunteer interns. Celeste Rollins, also a St. Marys student, prepared the figures used in several of the family introductions.

This project would probably not have been possible without the assistance given us by Jack Marquardt, librarian, U.S. National Museum; Leonard Bikowski and Hazel Dawson, of the Library of the U.S. Department of Interior; and Caroline Essex, librarian, Chesapeake Biological Laboratory. I will long remember the patience of these people in dealing with our numerous and often urgent calls for help.

George Drewry, research coordinator, kept the complex machinery of the project running smoothly, and, in its final stages, checked and standardized the bibliographies of this and two other volumes of the series. Julia Clark maintained and organized the reprint library—a task which became especially difficult as the momentum of the project increased. Judy Wiley, Ruth Wilson, and Herbert Harris assisted with the editing of the final manuscript, and Hillary Handwerker made a final check on the bibliographies of all six volumes of the series. The entire manuscript was reviewed and edited by Douglas Martin.

Vina Issacs and Walter Boynton, both former summer students at Chesapeake Biological Laboratory, assisted with library research and editing during the early stages of the development of the project. Ellen K. Sickles reared eggs and larvae of various species of *Etheostoma* while working as a summer aide. Peni G. Lang likewise reared and illustrated young stages of *Strongylura marina*. Linda Hudson, a summer aide in 1974, reared the eggs and larvae of all of the regional cyprinodontid larvae and illustrated most of them. Daniel M. Carver, a more recent summer student, assisted with the literature search, and also prepared a number of illustrations used in this volume. William Dovel supplied preserved tomcod larvae for illustrations, while Tom Peck and Michael Tabery obtained living eggs of this species from the Hudson River.

The patience exhibited by Cynthia Simmonds and Eunice (Sam) Benson in typing and re-typing the numerous manuscripts in this and the other five volumes of the series is almost beyond comprehension. I will always remember and appreciate their help. At times it became necessary to call in additional typists. These included Marjorie Blackwell, Joyce Stinson, Diane Haft, Clovia Hutchins, and Steven Drewry. Without their excellent work we would have probably met even fewer deadlines than we actually managed to meet.

Eurath Hardy, August Selckmann, Jr., and Ronald Bishop spent hundreds of hours in the darkroom when the rest of us were simply too busy to do so. A high percentage of the figures presented in this volume are the results of their volunteer efforts.

Anguilla rostrata

freshwater eels
Anguillidae

FAMILY ANGUILLIDAE

The family Anguillidae, of which there is one genus and about 15 species, occurs in all seas except the eastern Pacific and South Atlantic. Members of the family range north almost to the Arctic Circle and south to New Zealand.

In freshwater eels the body is covered with minute, embedded, cycloid scales; the gill slits are arranged vertically, their upper corners opposite the pectoral fins; and the dorsal fin originates far behind the pectorals.

The American eel, *Anguilla rostrata*, is the only regional member of the group. It is diadromous, moving from fresh and brackish water into the ocean to spawn. Although this species has been assumed to spawn in the vicinity of the Sargasso Sea, the actual spawning area may be much further south. Fertilized eggs have not been identified. The largest ovarian eggs thus far described were 0.6 mm in diameter. In ovarian eggs the yolk appears to be granular.

Leptocephali of the American eel are characterized by 102 to 110 myomeres, a straight gut, and no pigment. In the present volume growth stages are designated as follows:

Leptocephalus, stage I.	Length increasing.
Leptocephalus, stage II.	Length decreasing.
Glass eel, stage I.	Length decreasing.
Glass eel, stage II.	Length increasing.

For a comparison of the leptocephali of this species to those of the other regional fishes, see the key in the introduction to the family Ophichthidae.

Anguilla rostrata (Lesueur), American eel**ADULTS**

D. 183–276, mean 231.44; ⁵³ A. 167–229, ^{26,32} mean 199.12; ⁵³ C. 8–12 (4–6 + 4–6), ²⁶ reported means 9.92, 10.09; ⁵³ P. 14–20, mean 16.73; ²⁹ vertebrae 103–111 ^{22,26,32,80} (although Harden-Jones mentions an undetermined *Anguilla* leptocephalus from Mississippi with a vertebral count of 113); ¹⁹ average vertebrae 107.2; ³⁸ precaudal vertebrae 41–46 (in Virginia waters 41–44); caudal vertebrae 61–68 (in Virginia waters 61–67); ⁵³ branchiostegals 9–13, ^{26,32} mean ca. 11.0. ^{29,45}

Proportions as percent TL (in maximum-size but reproductively inactive males from Lake Sherman, Michigan): Head length 12.3–12.7, predorsal length 32.2–33.3, preanal length 41.8–42.0, pectoral length 7.5, interorbital width 2.5–2.6, horizontal diameter of eye 2.6–2.9, preorbital distance 2.3–2.7. Proportions as percent head length: interorbital width 20.3–20.6, horizontal diameter of eye 20.6–23.4, preorbital distance 18.8–21.4. Horizontal diameter of eye as percent of interorbital width (based on a number of specimens larger than minimum maturity size): in females 38.5 to ca. 89, in males ca. 80–100. ⁶⁷

Proportions as percent TL (based on silver eels migrating from Chesapeake Bay): Preanal length, males 39.4–43.8, females 36.6–45.2; predorsal length, males 29.1–35.6, females 30.8–36.7; head length, males 11.2–14.1, females 10.5–13.8. As percent of head length, gape length, males 16.7–26.9, females 19.7–32.1. As percent of gape length, horizontal diameter of eye, males 42–100, females 34.2–68.8.

Proportions as percent TL (based on 1 males and 11 females migrating in oceanic waters): Preanal length, males 42.3, females 40.8–44.8; predorsal length, males 33.8, females 32.8–35.6; head length, males 13.9, females 11.8–13.7. As percent of head length, gape length, males 21.7, females 21.2–27.9. As percent of gape length, horizontal diameter of eye, males 57.5, females 40.8–59.0. ⁷¹

Body elongate, serpentine, ^{6,54} round anteriorly, compressed posteriorly ⁶² (but in beginning of stage much fatter than juveniles); ⁷¹ snout depressed, broad, blunt; mouth large, slightly oblique; ⁶² gape extended to posterior margin of eye; ⁴³ lower jaw equal to or slightly longer than upper; ³¹ gill openings well separated, lateral and ventral; branchiostegals long; teeth in bands on jaws

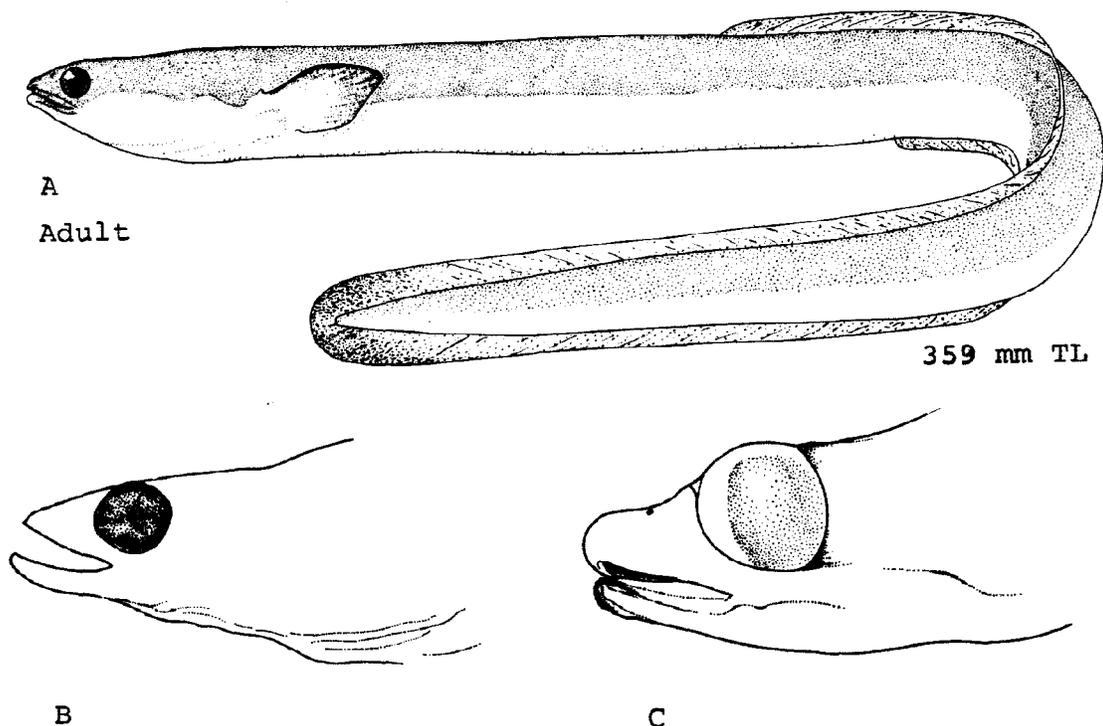


Fig. 3. *Anguilla rostrata*, American eel. A. Adult, 359 mm TL. B. Old male, eyes enlarged. C. Maximum eye development. (A, Original drawing, Daniel M. Carver. B-C, Vladykov, V. D., 1973: figs. 1–2, Elizabeth Ray Peters, delineator.)

and vomer.^{14,43}

Scales small, cycloid,⁴³ placed at right angles to each other,⁵ embedded,³³ and often difficult to see without magnification.⁵ Lateral line well-developed,³³ accentuated.^{71,77} Dorsal, caudal, and anal continuous; dorsal origin far behind pectorals, nearer vent than gill openings; ^{6,31,43,69} pectorals (in very large but apparently reproductively inactive males) pointed rather than rounded; ⁶⁷ ventrals absent; ⁵⁴ skin conspicuously thickened.¹⁰²

Pigmentation: Vladykov described mature eels at the time of descending streams as having a metallic sheen, the back and sides almost black or bronze with purple reflections, and the pectoral fins black.⁶⁸ Edel, using laboratory specimens in which ovulation was artificially induced, noted that, in maturing females "the flanks were an intense copper color; the dorsal surface was dark but not black . . . the ventral surface which began as silvery-white became darkly mottled."⁷³ Wenner found migrating eels in the ocean which were silver and had the dorsal aspect of the pectoral fins and the caudal fin darkly pigmented.^{53,78} It is possible that there is a transition from bronze to silver as the spawning migration progresses (JDH). As maturity progresses the eye develops a coloration termed "retinal gold."⁷⁷

Maximum length: Females 1275 mm; ⁵⁹ males 521 mm to possibly 752 mm.⁶⁷

DISTRIBUTION AND ECOLOGY

Range: Coastal areas and, presumably, open ocean from Labrador and Newfoundland ^{5,11} to Trinidad and the Guianas ¹⁹ (although apparently known only from Panama in Central America); ⁶⁸ also Greenland ^{25,47,52} and Bermuda,³⁸ and the entire Caribbean.^{33,51} Throughout the Great Lakes ^{20,52} and up the Mississippi drainage as far as South Dakota.⁵² West to the Rocky Mountains.²⁰ Elvers have been collected in Denmark,⁷⁹ and a single adult has been recorded from northern Spain.^{30,41,65} Attempted introductions in California have failed; ^{23,46} introduced individuals have survived in Saskatchewan, Canada, for at least 10 years,³⁴ and in Sherman Lake, Michigan, for 35–40 years.⁶⁷

Area distribution: Found throughout Chesapeake Bay ⁶² and in coastal waters of New Jersey,⁷⁰ Maryland, Delaware,⁶⁴ and Virginia.⁶²

Habitat and movements: Adults—initially in freshwater lakes and rivers, and in brackish estuaries or coastal marine waters; as maturity progresses migrate to deep offshore waters (JDH). Temperature range, 8–12 C for migrating offshore individuals,⁷¹ possibly as high as 15 C in the spawning area.⁴⁵ Maximum recorded depth, 82.3 meters,⁷¹ but presumably reaches much greater depths if Vladykov's estimate of spawning at ca. 486.5 meters is correct.⁶⁸

Medcof has noted that mature or maturing eels sometimes lie in inverted "U" 's over submerged or exposed stems of water plants; and sometimes form free floating or submerged balls which may be up to 2 meters in diameter. An eel ball 0.5 meters in diameter was estimated to contain up to 30 individual eels.⁷³

Catadromous, migrating from fresh and brackish water to the vicinity of the Sargasso Sea in the Atlantic Ocean (JDH). In Canadian waters the downstream migration is generally thought to last from late July ⁷³ to mid-November,⁶⁸ although it is possible that some individuals (possibly the males) begin migrating as early as April or May.^{30,48} Bigelow and Schroeder ⁵² estimate that the seaward migration (interpreted here as the freshwater phase of the migration) lasts 1 or 2 months. Eales ⁵⁴ estimated a total of 2 or 3 months for arrival in the spawning area. Eels have been noted migrating from the Chesapeake Bay in November ⁷¹ and from South Carolina from August through December.⁷⁶ There is evidence to suggest that eels from throughout the range all arrive in the spawning area at the same time and in the same state of reproductive development.⁵³ Migrating freshwater eels may move through deep grass and shallow ditches. Downstream movements are most prevalent at night, particularly on warm, dark, stormy nights; ^{12,31,54} Winn, *et al.*, for example, noted migrations near Charleston, South Carolina only between 1800 and 2300 hours, and only after heavy rains. They noted also that large runs occurred between full and new moon (the third and fourth lunar quarters). Under these conditions some yellow eels show tendency to migrate with the silver eels. Migrating males are much smaller than migrating females, varying from 280–400 mm in total length.⁷⁶ Adult eels presumably die after spawning.^{13,29}

Leptocephali—oceanic waters. The geographic limits within which leptocephali have been collected are:

Northernmost. Lat. 47° 16' N, long. 40° 56' W.⁸¹
 Southernmost. Lat. 17° 55' N, long. 64° 48' W.³⁸
 Westernmost. Long. 84° 23' W, lat. 20° 38' N.⁸¹
 Easternmost. Long. 40° 56' W, lat. 47° 16' N.⁸¹

The northernmost western North Atlantic specimen is from Crank Banks, Canada.⁶⁸ Some of the leptocephali found near Bermuda transform and colonize brackish ponds in Bermuda.^{29,44} Specimens 39 to 53 mm long have been recorded near Bermuda in July and August; ³⁷ leptocephali are common along the Florida coast from January through summer ¹⁶ and specimens 18–58 mm long have been taken in the Straits of Florida from April 2 to August 28.²⁵ Leptocephali reach lengths of 60–65 mm in December and January.⁵²

Initially move passively with current,⁵⁴ becoming strong and active when they approach transformation.³⁷ Tucker feels that Schmidt's 15 mm leptocephali may have drifted 300 to possibly 1200 miles from the spawning area.²⁹

Migrate to the coast of North America in 1^{9,44,54} or 2 years.⁵⁸

From surface^{35,52,54} to 1829 meters. Tåning obtained specimens 39.5–53.0 mm long from 914.4 to 1829 meters.³⁷ Other depth records are: Specimens 22 to 40 mm long at 25 meters;^{38,44} metamorphosing leptocephali at 250 meters in Gulf of Mexico.¹⁶ Leptocephali are apparently more easily collected at night³⁷ (presumably at surface, JDH).

Glass eels—coastal and offshore waters (JDH), also streams.⁴⁸ The transformation probably occurs when the young pass through the edge of the Gulf Stream.²⁵ Glass eels have been observed offshore at Georges and Browns Banks.⁵² Specimens as small as 48 mm reported in Chesapeake and Narragansett bays;¹² a 47 mm specimen recorded from roots of water hyacinths in Florida.¹⁵ Vladykov pointed out that total lengths of ascending “elvers” increase from southern to northern localities.⁵⁹

From surface⁵² to possibly 21.9 or 27.4 meters.⁶⁰

Move shoreward, arriving in Delaware Bay and northeastern United States in March and in Nova Scotia in April.⁶⁸

Elvers—coastal marine waters (usually in association with eel grass),⁵⁴ tidal flats,¹² tidal marshes, harbors, barrier beach ponds,³⁴ large coastal rivers,⁶ creeks,⁶³ streams⁵⁵ (although seldom in cold streams), and warm, shallow lakes.⁵⁴ Apparently only females ascend to freshwater, males remain in estuarine waters.^{9,13,57} Recorded from detritus covered bottom and in turbid water.⁶⁴ Specimens less than 150 mm long generally in shallow water near shore; larger individuals in deeper water of creek channels.⁶³

Minimum recorded temperature, minus 0.8 C.¹²

Ascend streams in immense numbers (thus hundreds caught in a four-inch aquarium net).^{10,56} Time, duration, and extent of upstream movement varies from year to year and in different localities (JDH). In Florida “elvers” evident in mid-January, but probably spend autumn in coastal waters, possibly buried in bottom.²⁵ Arrive on Carolina coast around last of April;⁶ in Maryland in April;⁵¹ and in Long Island from early April to late May.³⁹ Jeffries recorded elvers from the Rhode Island area as early as January 3, and pointed out that a small percent of elvers reach temperate estuaries several months in advance of main spring-summer arrivals.¹² Arrivals recorded at Woods Hole, Massachusetts, from mid-February to mid-June,⁸ in Gulf of Maine in April,⁷ and in Canada in April and May.^{55,68} Eales, working in Canada, suggested that the upstream migration may last from “only a few days” to a maximum of one month;⁷ Smith, however, observed upstream movements lasting from mid-May through September (a period of nearly five months) in New Brunswick.⁵⁵

Swim near surface when ascending streams;²⁰ climb rocks to surmount obstacles;^{18,31} also move through underground channels (including water pipes),⁵⁴ and leave streams during exceptionally heavy rains. May hide in gravel in streams,⁵⁵ and recorded hiding in moss in inverted position over water.³

Juveniles—tidal water (sometimes up to tide line)¹⁷ in river channels; streams, particularly at obstructions in riffle areas, log jams, under overhanging banks, and in swampy areas; creeks; spring “boils;” underground streams in caves; marshes; ponds; lakes; and roadside ditches. Recorded over mud and sandy stone bottom; particularly abundant in heavily vegetated areas.^{49,50,54}

Able to withstand abrupt salinity changes.³⁶

Movements generally restricted while in headwaters of rivers, thus Gunning and Shoop noted a maximum movement of only 137.2 m in 10 to 13 months.⁴⁹ Vladykov, however, recorded a movement of 200 miles in 5 years and 11 months.⁶⁶ When experimentally displaced may return to rivers as far as 50 miles away.⁶¹ In Canadian waters some immatures may migrate downstream with adults.⁷³

Sometimes burrow in mud with only head protruding,³⁶ also hide in holes, or drape themselves over vegetation.⁵⁴ Hibernate in mud at depths of ca. 150–200 mm.^{1,39,51,63,68} Hibernation sites apparently equipped with a ventilation hole.⁵⁴ May leave water at night, particularly during heavy rains, and crawl about on land;^{3,31,51} and sometimes stranded on land by receding water.⁴² Can survive up to 48 hours without water.^{39,68}

SPAWNING

Location: Indefinite. Generally stated as between Bermuda (or southwest of Bermuda) and the West Indies,^{9,12} or in the vicinity of the Sargasso Sea between latitudes 20° and 30° N and longitudes 60° and 75° W.^{10,27} Smallest leptocephali (less than 10 mm) collected at 22° 14' N, 67° 22' W. Vladykov has suggested that the true spawning area may be much further south than previous data would suggest.³⁰

Season: Possibly from January^{25,29} to July.⁸¹

Depth: Brunn⁴⁵ suggests that spawning in Atlantic species of *Anguilla* takes place above the thermocline at depths no greater than 500 meters. Estimates of spawning depth in *A. rostrata* vary from 200 to 700 meters^{10,19,54,68} but such estimates may not be reliable.⁷⁴

Temperature: Estimated 15–16 C,^{10,45} but these figures are apparently not based on actual observations.⁷⁴

Salinity: 35²⁸–37 ppt,¹⁰ apparently not based on actual observations.⁷⁴

Fecundity: 413,000 to 2,561,000 based on counts from specimens migrating from Chesapeake Bay.⁵³ A count of 9,000,000 in a specimen from Long Island⁴⁰ may not be reliable (JDH). Estimates of 10,000,000 to 20,000,000^{10,31,54} are apparently not based on actual counts on this species.⁷⁴

EGGS

Location: Assumed to be pelagic, floating in the upper to intermediate water layers,^{52,55} but statement without direct supporting evidence (JDH).

Ovarian eggs: Mostly spherical (although smaller developing eggs cuboidal) with centrally located nucleus, and inclusions resembling yolk granules of *Brevoortia*.⁵⁵ Egg diameters of eels leaving Chesapeake Bay in November varied from 0.25–0.45 mm with an average of 0.356 mm.⁷¹ Other ovarian egg size ranges in apparently migrating eels are: Newfoundland 0.109–0.214 mm, $\bar{x}=0.165$ mm;⁷² south of Cape Cod 0.12–0.27 mm, $\bar{x}=0.17$ mm;⁷¹ off northeastern United States, 0.17–0.37 mm, $\bar{x}=0.27$.⁵³ Growth of eggs was observed in four Canadian females between November and December. The diameters of these eggs have been reported as 0.33–0.45 mm (maximum size per female),²¹ and 0.20–0.35.^{30,45} There are indications that eels leave Chesapeake Bay later in the year and with the gonads more fully developed than in fishes from more northern localities (thus assuring that all eels will arrive in the spawning area at the same time and in the same state of reproductive development).⁵³ Maximum size of ripening eggs of *A. rostrata* obtained through hormone injection, 0.6 mm. Eggs larger than 0.5 mm arc described as “loose” (presumably in the coelom).³⁰

Presumably ripe, unfertilized eggs. Diameter 0.59–1.25 mm, average 1.06; transparent; slightly ellipsoidal; a number of relatively large, various-sized oil globules.⁷⁵

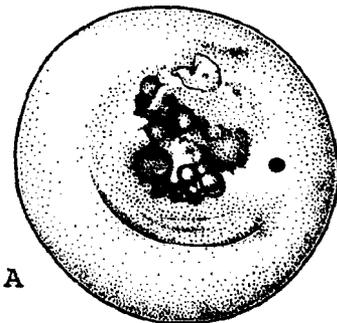


Fig. 4. *Anguilla rostrata*, American eel. A. Advanced ovarian egg, 1.25 mm in greatest diameter. (A, Edel, R. K., 1975: fig. 1, Elizabeth Ray Peters, delineator.)

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

Undescribed except for comments by Eldred and Raney that recently hatched larvae are 7–9 mm long and that the hatchlings may be ca. 6 mm long.^{10,28}

STAGE I, LEPTOCEPHALUS

Size range described, 10.5–69.0 mm.⁸¹

Total myomeres, at 10.5 mm, 104–110;²⁴ at 18–58 mm, 102–110 (a specimen within this size range had 99 myomeres but was obviously malformed,^{10,25} while another specimen of unspecified length had 101 myomeres⁸¹). Preanal myomeres, at 10.5 mm, 63; at 14.25–15.75 mm, 64; at ca. 22 mm, 68;²⁴ at 43.9–45.5 mm, 68–69;^{10,19} at 47–49 mm, 65–68;¹¹ at 50 mm, 70;²⁷ at 51.5 mm, 71.³⁷ In specimens of unspecified stage or size, preanal myomeres 64–74.⁸¹ Postanal myomeres, at 10.5 mm, 41–47;²⁴ at 43.9–45.5 mm, 36;^{10,27} at 47–49 mm, 40;¹¹ at 50 mm, 34.²⁷ In specimens of unspecified stage or size, minimum postanal myomeres, 31.⁸¹ Predorsal myomeres, at 43.9, 61;²⁷ at 45.5 mm, 62.¹⁰ Myomeres between dorsal and anal origin, at 43.9, 8;²⁷ at 45.5 mm, 6;¹⁰ at 47–49 mm, 8;¹¹ at 50 mm, 9. Branchiostegal rays undeveloped at 43.9 mm, 11 at 50 mm.²⁷

Morphometric data is presented in Tables 1 and 2.

TABLE 1. Proportions as percent TL (derived from morphometric data presented by Eldred)^{16,27}

	43.9 mm	45.5 mm	50.0 mm
Total length	43.9 mm	45.5 mm	50.0 mm
Preanal length	72.9%	73.4%	74.0%
Predorsal length	65.4	68.1	65.0
Postanal length	27.1	26.6	26.0
Head length	9.3	8.8	8.4
Depth at pectoral base	6.6	6.6	6.2
Maximum depth (level of renal-portal vein)	17.3	17.1	16.8
Depth at anus	16.0	16.4	14.4

TABLE 2. Proportions as percent HL (derived from morphometric data presented by Eldred)^{16,27}

	4.1 mm	4.0 mm	4.2 mm
Head length	4.1 mm	4.0 mm	4.2 mm
Snout length	26.9%	27.5%	26.2%
Horizontal diameter of eye	22.0	19.8	23.8

Eye diameter greater than snout length at 9–10 mm;²⁸ at 47–49 mm, 1.33 times in snout length.¹¹

At 10.5 mm body somewhat more slender than in more advanced stages.²⁴

At 50 mm body moderately elongate, compressed except for head, maximum depth at midpoint of body; eye slightly oval and with narrow fleshy margin; upper jaw slightly protuberant; gape not extended to posterior

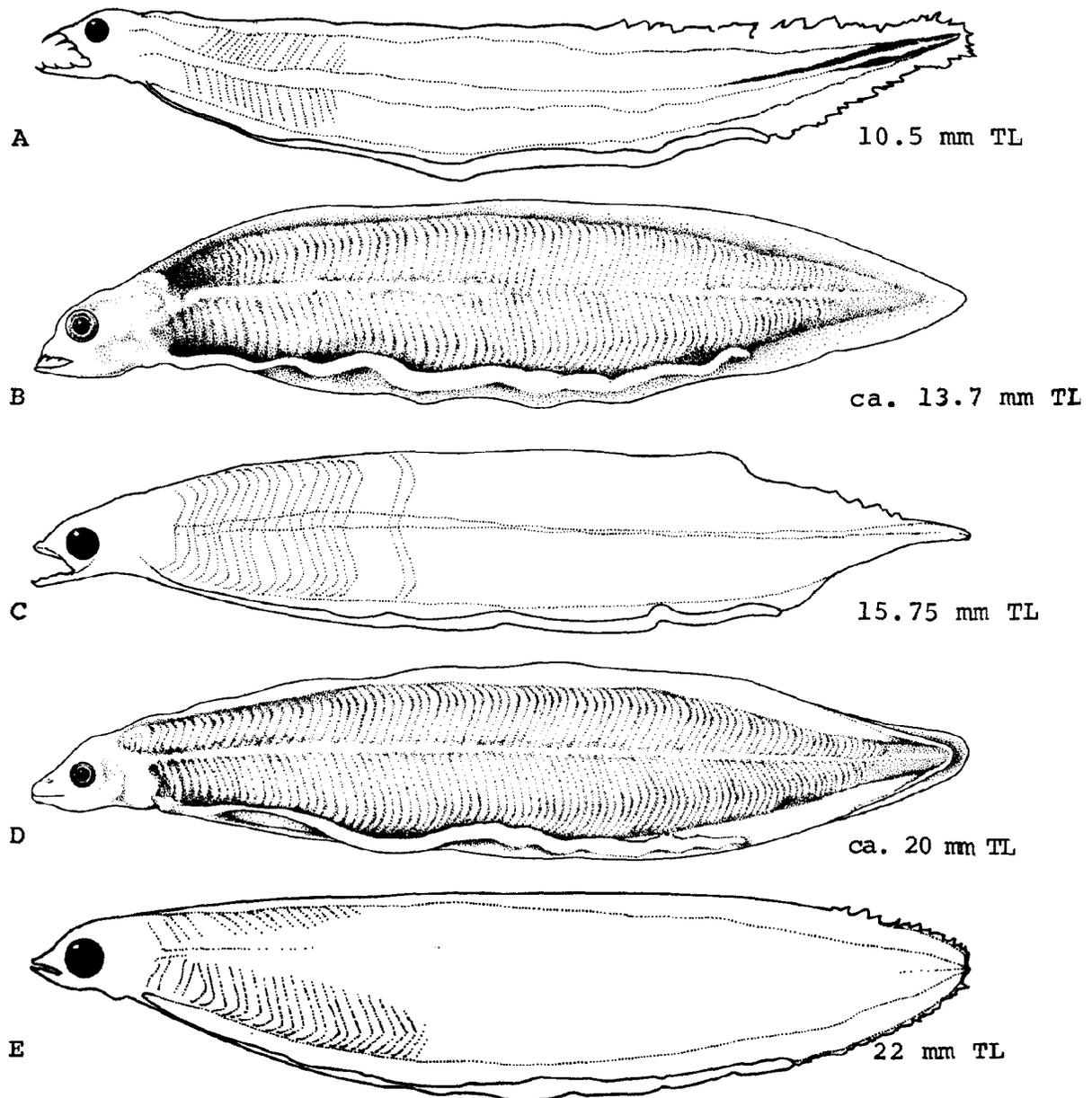


Fig. 5. *Anguilla rostrata*, American eel. A. Stage I leptocephalus, 10.5 mm TL. B. Stage I leptocephalus, ca. 13.7 mm TL. Note reduction in size of teeth, and convolutions of gut. C. Stage I leptocephalus, 15.75 mm TL. D. Stage I leptocephalus, ca. 20 mm TL. E. Stage I leptocephalus, 22 mm TL. (A, C, E, Schmidt, J., 1916: figs. 5, 6, 7, Elizabeth Ray Peters, delineator. B, D, Vladykov, V. D., 1955: unnumbered plate, Elizabeth Ray Peters, delineator.)

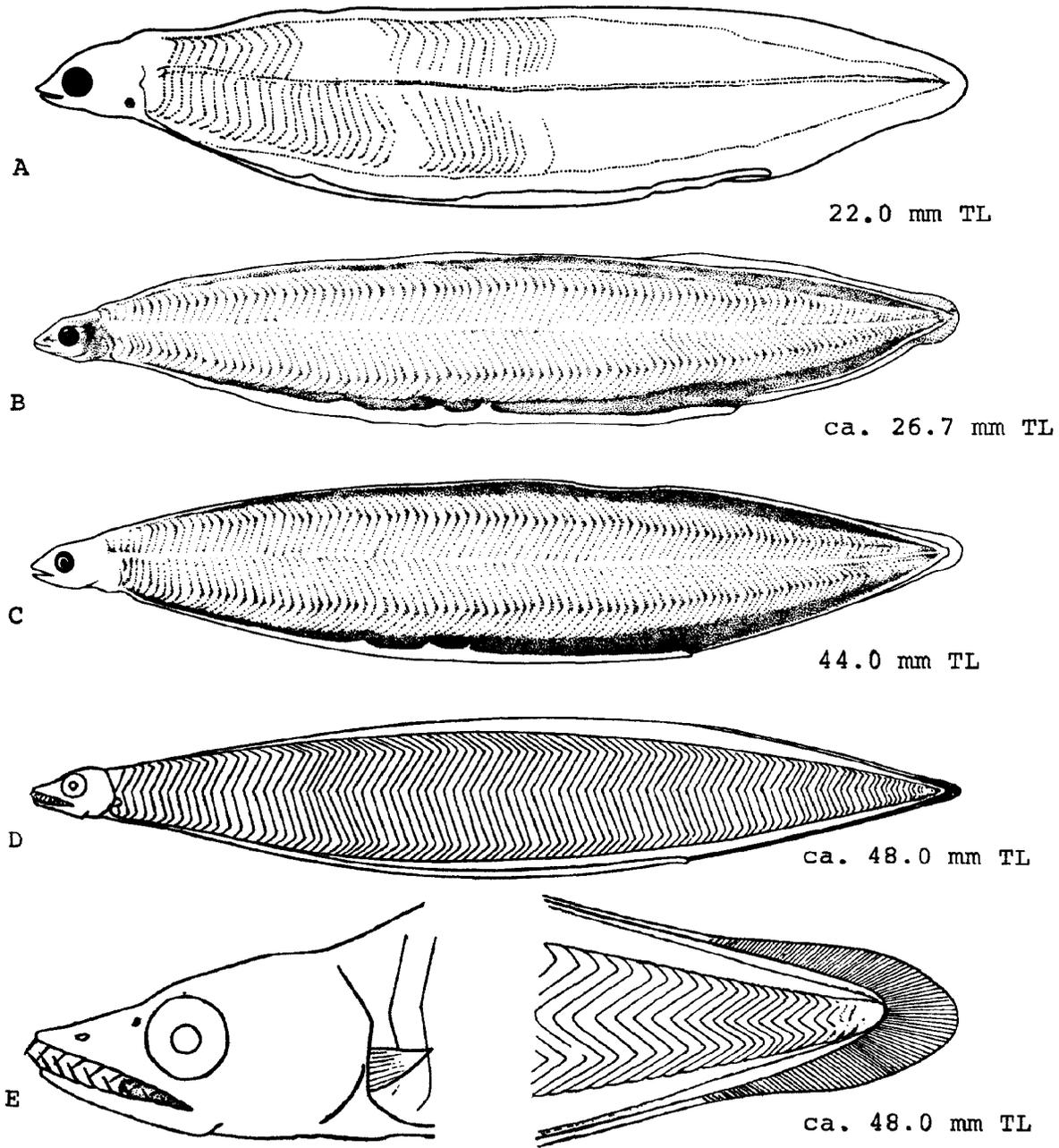


Fig. 6. *Anguilla rostrata*, American eel. A. Stage I leptocephalus, 22.0 mm TL. B. Stage I leptocephalus, ca. 26.7 mm TL. C. Stage I leptocephalus, 44.0 mm TL. D. Stage I leptocephalus, ca. 48.0 mm TL. E. Detail of head and caudal region of previous specimen. (A, C, Schmidt, J., 1916: pl. 4, figs. 1, 2, Elizabeth Ray Peters, delineator. B, Vladykov, V. D., 1955: unnumbered plate, Elizabeth Ray Peters, delineator. D, E, Eigenmann, C. H., and C. H. Kennedy, 1901: figs. 1, 1a, 1b.)

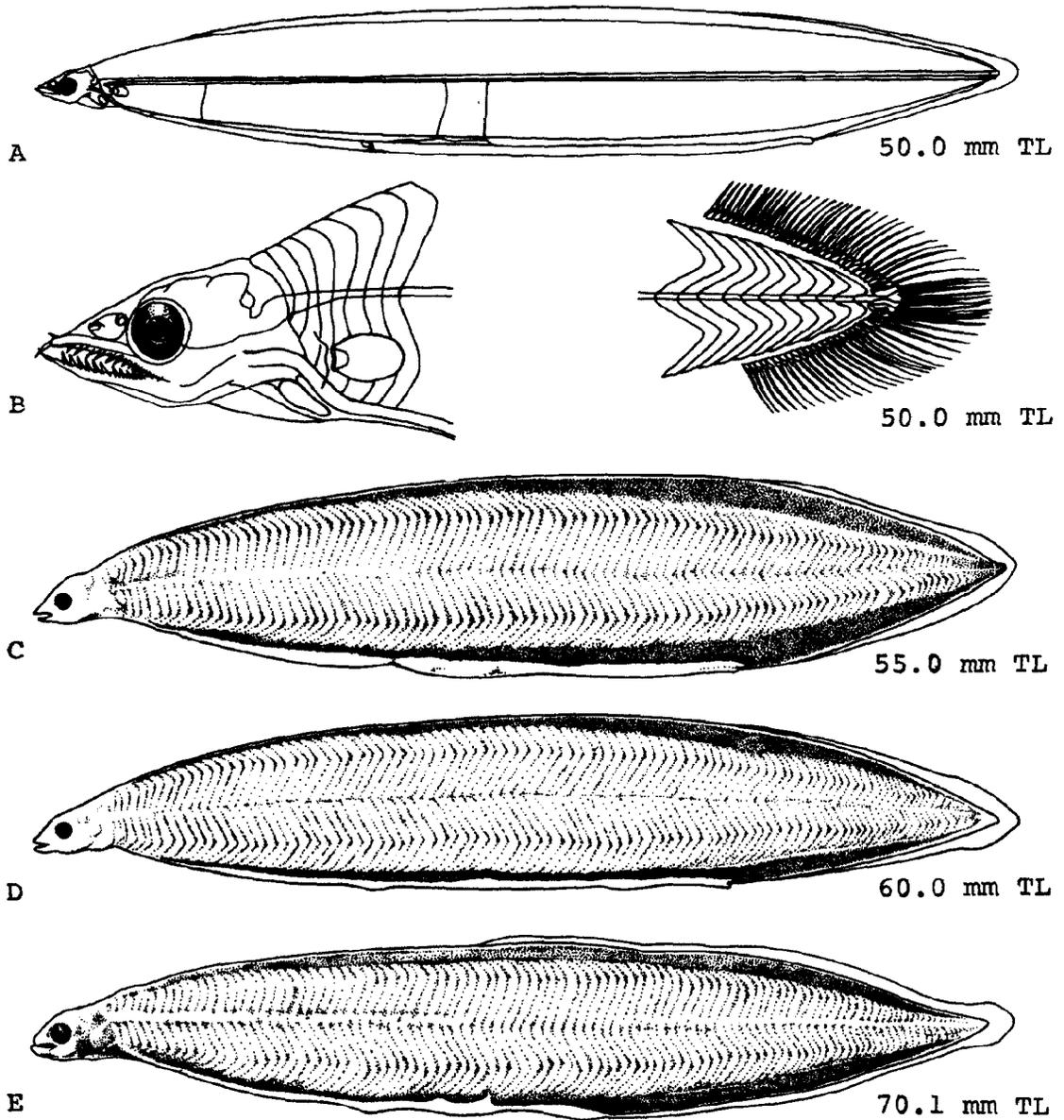


Fig. 7. *Anguilla rostrata*, American eel. A. Stage I leptocephalus, 50.0 mm TL. B. Detail of head and caudal region of previous specimen. C. Stage I leptocephalus, 55.0 mm TL. D. Stage I leptocephalus, 60.0 mm TL. E. Stage II leptocephalus, 70.1 mm TL. Note conspicuous decrease in length of gut. (A, B, Eldred, B., 1968: fig. 1. C, D, Schmidt, J., 1916: pl. 4, figs. 3, 4, Elizabeth Ray Peters, delineator. E, Vladykov, V. D., 1955: unnumbered plate, Elizabeth Ray Peters, delineator.)

margin of eye; nasal capsule small, oval; anterior nostril slightly tubular, at midpoint between tip of snout and anterior margin of eye; posterior nostril in front of eye.²⁷

Dental formula: at 10.5 mm $\frac{1+3}{1+3}$; at 14.25 mm $\frac{1+4}{1+3}$; at 15.75 mm $\frac{1+5}{1+4}$; at ca. 22 mm $\frac{1+6}{1+5 \text{ or } 6}$; ²⁴ at 43.9 mm $\frac{1+1+VIII+6}{1+VII+2}$; ²⁷ at 45.5 mm $\frac{1+1+V+7}{1+VIII+2}$; ¹⁶ at 50 mm $\frac{1+1+VI+8}{1+VII+4}$.

Teeth in a 50 mm specimen described as very acute, 16 in left side of upper jaw (1 small tooth projecting from dorsal surface of snout, 1 long fang at tip of snout followed by series of 6 large and 8 small teeth); 12 in left side of lower jaw (1 large curved tooth at tip followed by a series of 7 large and 4 small teeth).²⁷ Schmidt reports a maximum of 20 teeth on each jaw.²⁴

In specimens of unspecified size or stage, first major blood vessel at myomere 16–20 (average 17.3), second major blood vessel at myomere 36–43 (average 40.0), third major blood vessel at myomere 42–46 (average 44.5).⁸¹ First major artery at myomere 17 between sizes of 43.9 and 50.0 mm; renal artery at myomere 38–42 at 43.9–45.5 mm, 40–42 at 50 mm; renal-portal vein at myomere 44–45 at 43.9–45.5 mm, 45–46 at 50 mm; anterior margin of gall bladder at myomere 32–34 at 43.9–45.5 mm, 34 at 50.0 mm; liver between myomeres 12 and 33–36 at 43.9–45.5 mm, between 12 and 70 at 50.0 mm; gut long, straight, and narrow, extending to myomere 70 at 50 mm.^{16,27,28}

At ca. 44 mm incipient rays in anal and dorsal fin; at 47–49 mm vertical fins well-developed, broad. Dorsal at 61st myomere at 50 mm.²⁷ At 44 mm caudal fin bifid,²⁴ at 45.5 mm 1+3+2+2 rays,¹⁶ at 50 mm total 11.²⁷ Pectorals lacking at 45.5 mm,¹⁶ developed but with or without rays at 49–50 mm.^{11,27} Penultimate hypural divided at ca. 22 mm, hypurals fully developed at 44 mm. Urostyle slightly oblique at 15.75 mm.²⁴

Pigmentation: At 10.5–14.25 mm few stellate melanophores in finfold near tip of tail; at 15.75 mm an additional 8 melanophores on caudal part of finfold; at ca. 44–50 mm caudal pigment no longer evident, eye pigmented.^{24,27}

STAGE II, LEPTOCEPHALUS

Size range, 71 to ca. 58 mm.⁶⁸

In a specimen 59.5 mm long, total myomeres, 105; pre-anal myomeres, 66; predorsal myomeres, 60; postanal myomeres, 39; myomeres between dorsal and anal origin, 6.¹⁶

At 59.5 mm, preanal length, 41.5 mm; predorsal length,

39.0 mm; postanal length, 18.0 mm; head length, 5.0 mm; snout length, 1.6 mm; horizontal diameter of eye, 0.9 mm; postcranial depth, 2.5 mm; depth at pectoral base, 3.6 mm; maximum depth (measured at level of renal-portal vein), 11.0 mm; depth at anus, 10.2 mm.¹⁶

At 71 to ca. 58 mm, body still essentially leptocephalous-like; at ca. 64–65 mm body depth greatly reduced. Head initially as in stage I leptocephalus; rounded by end of stage.⁶⁸ At 59.5 mm teeth $\frac{1+V+8}{1+VI+3}$ (one side);¹⁶ teeth lacking in slightly more advanced specimens 57–58 mm long.

At 59.5 mm first artery at myomere 16, renal artery at 39, renal-portal vein at 43; anterior margin of liver at myomere 10, posterior margin at 34; anterior margin of gall bladder at myomere 33.

Caudal rays (at 59.5 mm) 1+4+2+2.¹⁶

Pigmentation: Apparently lacking (JDH).

STAGE I, GLASS EEL

Size range, ca. 60⁴⁸–48 mm.¹²

Body rounded,¹⁰ teeth apparently lacking.

Pigmentation: Unpigmented,⁴⁸ more or less transparent.¹⁰

STAGE II, GLASS EEL

Size range, 48¹²–ca. 65 mm.⁷⁴

At 49.5–52.0 mm total myomeres, ca. 103–109; preanal myomeres, ca. 35–37; postanal myomeres, 68–72; predorsal myomeres, 26–29; myomeres between dorsal origin and anal origin, 7–10. Pectoral rays, 16; total dorsal, caudal, and anal rays, 203–258; total vertebrae (excluding last hourglass-shaped centrum), 103–109; precaudal vertebrae, 41–46; caudal vertebrae, 60–67.²² At 49.5–52.2 mm, branchiostegal rays, 11–12.²⁷

Morphometric data is presented in Tables 3 and 4.

Body rounded,¹⁰ slightly compressed throughout stage; lower jaw projecting beyond upper; anterior nostril tubular; posterior nostril round with slightly raised rim; eye rounded; adult teeth forming throughout stage.

At 52.0 mm dorsal origin 4.5 mm in front of anus; caudal fin rays indistinct; pectoral rays long.²⁷

Pigmentation: Little pigment developed at time of arrival inshore.¹²

At 52 mm few faint chromatophores on dorsal surface of snout and on head behind eye, a few small chromatophores in caudal region, a series of large deep chromatophores on spinal cord from pectoral base to caudal

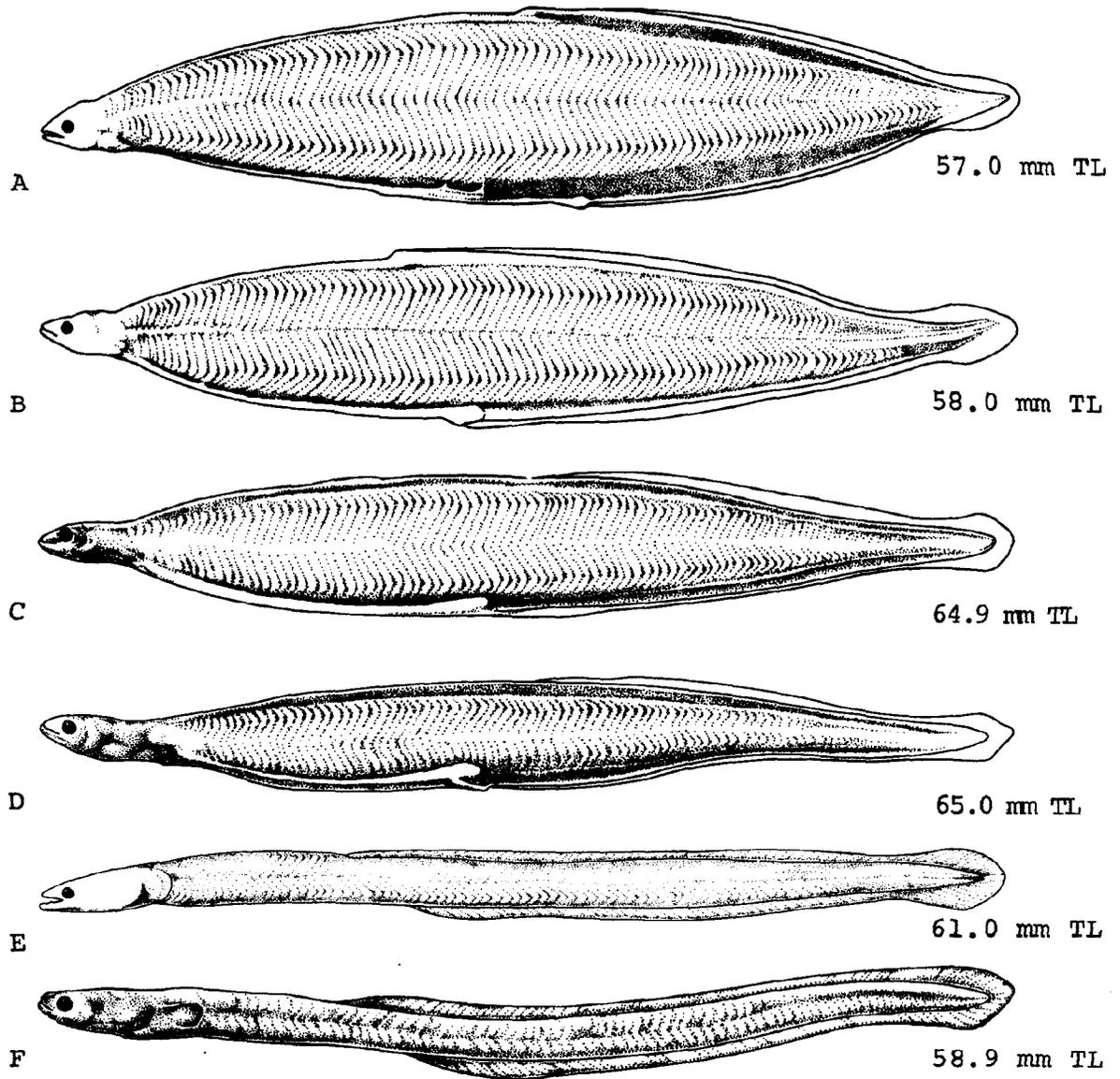


Fig. 8. *Anguilla rostrata*, American eel. A. Stage II leptocephalus, 57.0 mm TL. B. Stage II leptocephalus, 58.0 mm TL. C. Stage II leptocephalus, 64.9 mm TL. Although larger than the previously figured specimen, development of the body is more advanced. D. Stage II leptocephalus, 65.0 mm TL. E. Glass eel, stage I, 61.0 mm TL. F. Glass eel, stage I, 58.9 mm TL. (A, B, E, Schmidt, J., 1916: pl. 4, figs. 5-7, Elizabeth Ray Peters, delineator. C, D, F, Vladykov, V. D., 1955: unnumbered plate, Elizabeth Ray Peters, delineator.)

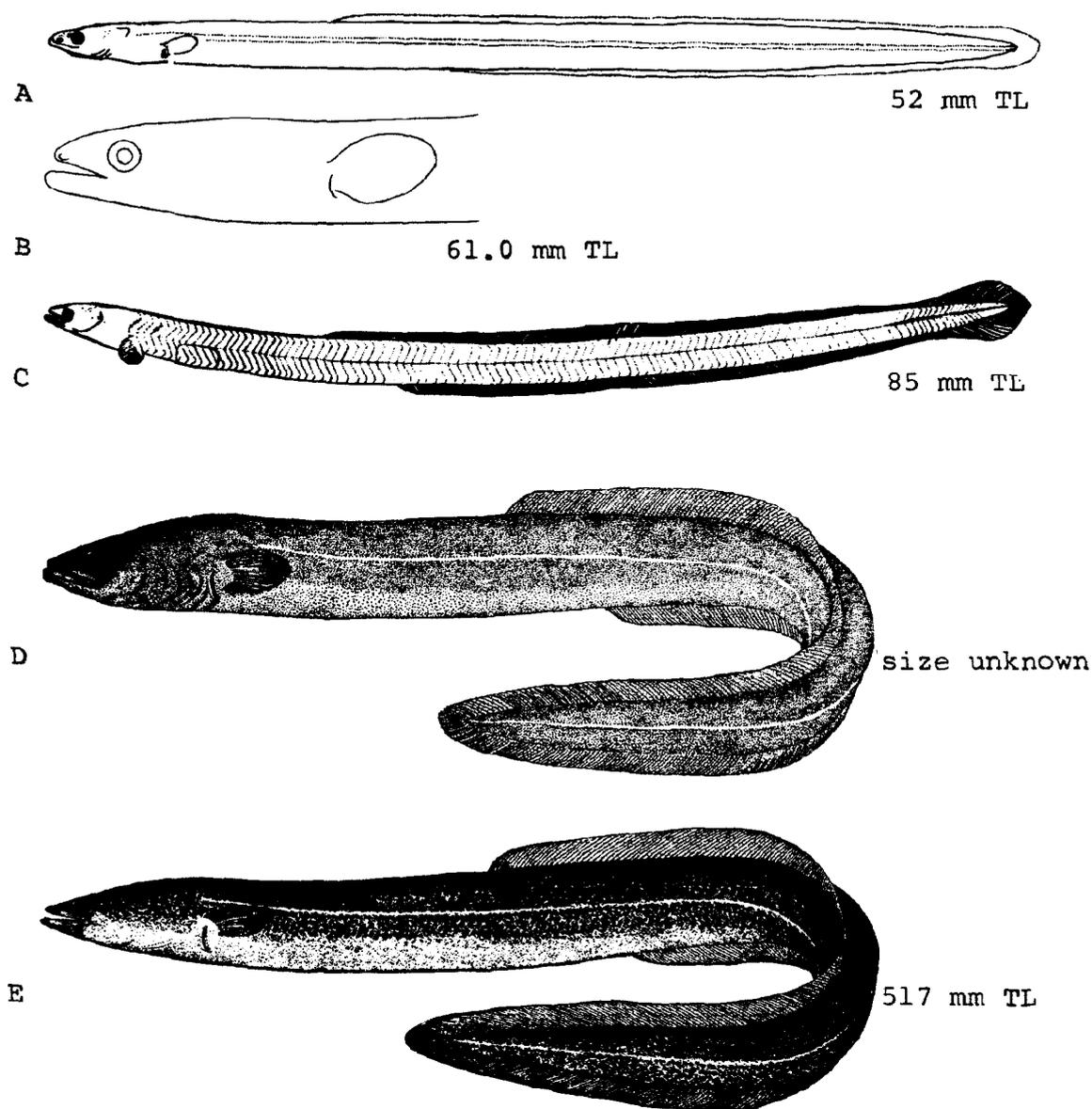


Fig. 9. *Anguilla rostrata*, American eel. A. Glass eel, stage I, 52 mm TL. B. Glass eel, stage uncertain, 61.0 mm TL. C. Elver, 85 mm TL. D. Juvenile, size unknown. Note small eye and rounded pectoral fin. E. Juvenile, 517 mm TL, eye small, pectoral fin somewhat elongate. (A, Eldred, B., 1968: fig. 1. B, Ege, V., 1939: fig. 30. C, Lippson, A. J., and R. L. Moran, 1974: 30. D, Scott, W. B., and E. J. Crossman, 1973: 624. E, Jordan, D. S., and B. W. Evermann, 1896-1900: 143.)

TABLE 3. Proportions as percent TL (derived from morphometric data presented by Eldred)²⁷

Total length	49.5 mm	50.0 mm	50.5 mm	51.5 mm	52.0 mm	52.2 mm
Preanal length	38.4%	38.0%	38.6%	36.9%	39.4%	29.5%
Predorsal length	26.1	30.0	31.3	29.7	30.8	31.8
Postanal length	61.6	62.0	61.4	63.1	60.6	60.5
Head length	11.1	11.0	8.1	11.7	11.5	11.5
Postcranial depth	1.3	3.6	4.4	3.7	3.9	3.8
Depth at pectoral base	4.1	4.0	6.1	3.9	3.9	3.8
Maximum depth (renal-portal vein)	4.1	4.0	3.4	3.3	4.2	4.8
Depth at anus	3.6	4.0	3.2	3.3	4.0	4.6

TABLE 4. Proportions as percent HL (derived from morphometric data presented by Eldred)²⁷

Head length	5.5 mm	5.5 mm	4.1 mm	6.0 mm	6.0 mm	6.0 mm
Snout length	20.0%	18.2%	26.8%	17.7%	16.7%	19.2%
Horizontal diameter of eye	18.2	12.7	24.4	15.0	16.7	11.7

tip.²⁷ In a "large elver" (but apparently a glass eel with pigment just developing) cranial pigmentation similar to cerebral nerve cord spot described for European eel.¹²

ELVERS

Minimum size ca. 65 mm.⁷⁴

Longest pectoral ray 6.0 times in HL in "young."⁶²

Scales first evident at ca. 160 mm at mid-body and in caudal region. Scales not fully formed in these regions until ca. 200 mm. Anterior scales not evident until ca. 175 mm.⁴⁸

Pigmentation: Fully pigmented at 65–90 mm,⁷⁴ brown and much like the adults as they ascend streams.^{10,12}

JUVENILES

Maximum size, males ca. 280 mm or larger, females ca. 460 mm or larger (based on approximate minimum size at maturity).

Body elongate, snake-like.^{6,54}

Proportions as percent TL (average values based on presumed immature females): Preanal length, 42.73–43.90; preanal length minus HL, 29.79–30.10; distance from dorsal origin to anus, 8.80–9.63; predorsal length minus HL, 20.23–21.01; head length 12.90–13.78.

Gape length as percent head length (average values, presumed immature females): 25.88–27.23.⁴¹

Proportions as percent TL (extreme values, presumed immature males): Head length, 12.0–12.6; predorsal distance, 30.3–33.0; preanal distance, 40.8–41.7; pectoral fin length, 4.2–5.0; interorbital width, 1.9–2.0; horizontal diameter of eye, 1.6–2.0; preorbital distance, 1.9–2.1.

Proportions as percent HL (extreme values, presumed immature males): Interorbital width, 14.7–16.7; horizontal diameter of eye, 12.5–16.7; preorbital distance, 15.6–17.3.

Horizontal diameter of eye as percent interorbital width (extreme values, presumed immature males), 81.3–100.0; in males of less than 299 mm (thus less than or near to minimum maturity size), 62.5–83.3; in females less than 499 mm (thus less than or near to minimum maturity size), 45.5–93.6.

Horizontal diameter of eye as percent interorbital distance (extreme values, presumed immature males), 72.2–106.7.⁶⁷

Horizontal diameter of eye as percent of gape (presumed juveniles, sex unknown), 30.7–59.1, \bar{x} 41.8.⁵³

Depth as times in HL (presumed juveniles, sex unknown), 1.65–2.65.⁶²

Pectoral fin rounded, not pointed.⁶⁷

Pigmentation: "Half grown" eels, predominately yellow or green.⁶¹ Otherwise brown, dark brown, or olive brown above; sides tinged with yellow or yellow-green; lower sides brown; venter white, dirty yellowish white, golden, or dirty yellow.^{6,31,52,62}

AGE AND SIZE AT MATURITY

Age at maturity, variously estimated from 5 to possibly 18 years.^{9,10,55,58}

Minimum length at maturity, males ca. 280 mm, females ca. 457 mm,⁵² although one author states that females are "frequently" mature at lesser sizes.⁵⁴

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Gymnothorax funebris

morays

Muraenidae

FAMILY MURAENIDAE

The muraenids, of which there are two subfamilies, 12 genera, and about 100 species, occur in tropical, subtropical, and, rarely, temperate waters (the regionally rare species, *Gymnothorax funebris*, has been recorded as far north as Canada). These secretive, nocturnal eels are almost exclusively restricted to reefs or rocky areas within the 46 meter isobath and are rarely if ever found in the open sea.

Morays may be recognized by the following characteristics: the anterior nostril is tubular and the posterior nostril is high on the head above or slightly in front of the eye; the gill openings are noticeably small and roundish; the jaws are usually equipped with long, depressible canine teeth; there are two branchial pores; the fourth branchial arch is strengthened and supported by pharyngeal jaws; there are lateral line pores on the head, but not on the body; the body is somewhat compressed; scaleless; pectoral fins are absent; and, in some genera such as *Uropterygius*, the dorsal and anal fins are vestigial. Many morays reach maximum lengths of 4 or 5 feet, but some species grow to extreme lengths of 10 feet.

The eggs of muraenids are generally not well known. *Muraena helena* produces extremely large, pelagic eggs (diameter 5.5 mm) in which the yolk is granular and there are no oil globules. In spite of several recent statements that morays may lack a leptocephalous stage, leptocephali of a number of species have been described. In these the intestine lacks "loops" and occupies 40 to 65% of the standard length; the tail is broadly rounded. Pigment is usually present. The pectoral buds may be very poorly developed and presumably transitory.

Eldred (1970) described several leptocephali which she attributed to *Gymnothorax funebris*—the only representative of the family in the Mid-Atlantic Bight. Her figures and descriptions are included in the present volume, although David G. Smith (personal communication) has questioned their identity on the basis of the reported myomere count (131–136) compared to the known vertebral count for *G. funebris* of 139–145.

Gymnothorax funebris Ranzari, Green moray**ADULTS**

Teeth $\frac{\text{ca. } 32}{26}$,² vertebrae 139-145 (DGS).

Head 7 times in TL.²

Body elongate,² somewhat rounded in cross-section anterior to vent, moderately compressed posterior to vent (FDM); head conical; mouth terminal; nasal pits circular, the anterior ones almost terminal, the posterior ones just in front of eyes. One or more long depressible canines in midline of upper jaw, about halfway between snout

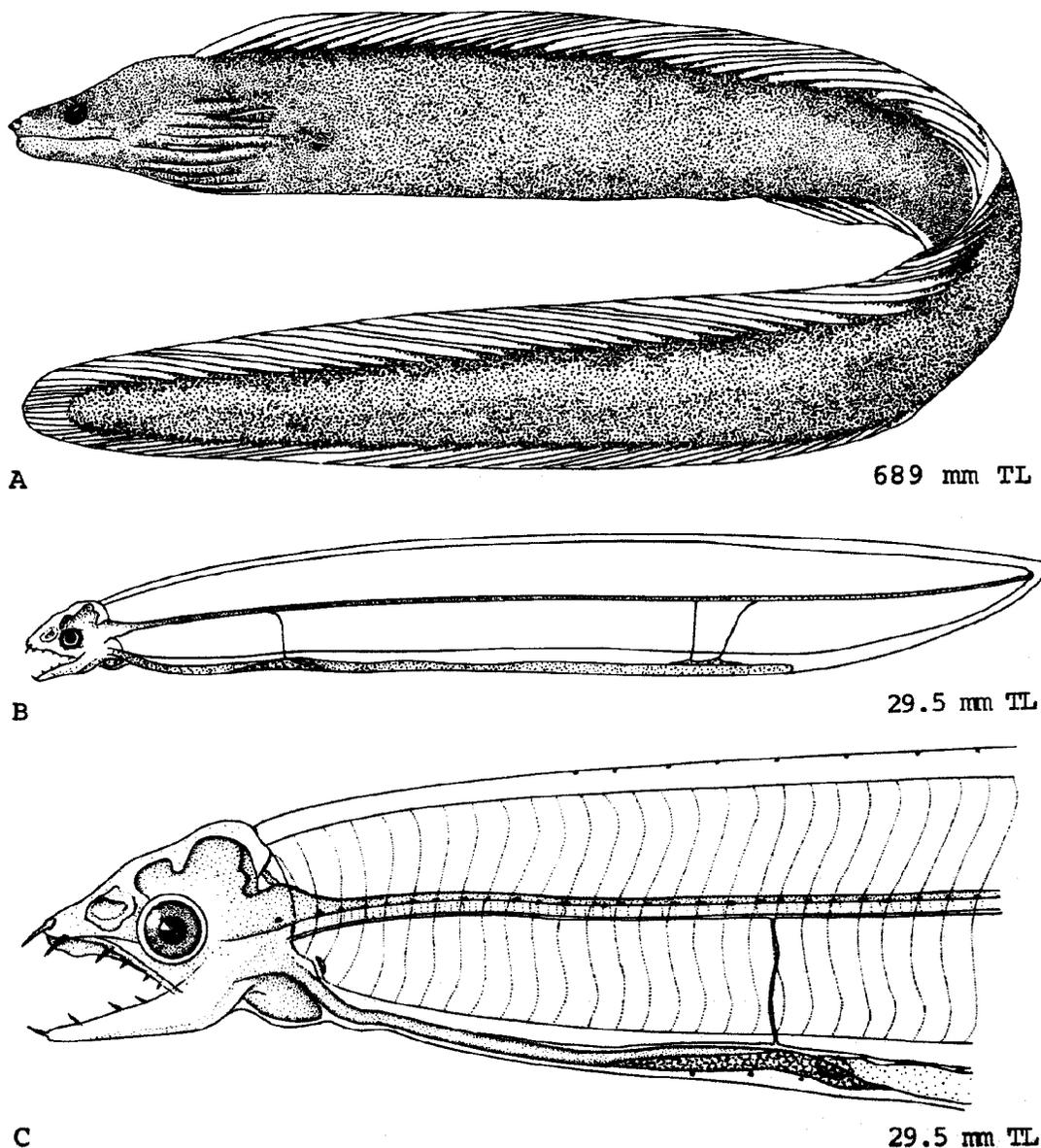


Fig. 10. *Gymnothorax funebris*, Green moray. A. Adult, 689 mm TL. B. *Leptocephalus*, 29.5 mm TL. C. Same as B, detail of head and anterior part of body. (A, Böhlke, J. E., and C. C. G. Chaplin, 1968: 84, Tamiko Karr, delineator. © Academy of Natural Sciences of Philadelphia. Used with permission of authors and publishers. B, C, Eldred, B., 1970: fig. 1, Daniel M. Carver, delineator.)

and eye; 2 rows of smaller teeth on vomer, with ca. 8 teeth in each row. Gill openings short, oblique. Body and fins covered with thick leathery skin. Dorsal fin origin slightly in front of gill opening. Pectoral and pelvic fins absent.^{2,8,9,12}

Pigmentation: Body bright green to brown, olive brown, or slate gray; ^{2,8,9,12} green color due to yellowish mucous layer overlaying skin,⁵ this layer lost in preservation or with rough handling (FDM); throat paler. Body sometimes slightly mottled; head sometimes with dark horizontal lines on lower parts. Dorsal and anal fin reported both with ^{2,8,9,12} and without dark longitudinal lines.⁵

Maximum length: 1893 mm.¹¹

DISTRIBUTION AND ECOLOGY

Range: In the Atlantic, Canada to Rio de Janeiro, Brazil; Bermuda; Cape Verde Islands. Also reported from the eastern Pacific.^{2,4,11}

Area distribution: Coast of New Jersey.³

Habitat and movements: Adults—coral reefs,⁷ rocky shorelines,⁵ sometimes in caves and cracks;¹⁰ also reported from tidal creeks; ⁵ over bottoms of dead coral, sand and mud,⁶ occasionally taken on grass beds where hard substrate is present (FDM). Maximum depth, 12 m; ⁵ minimum depth, 20 cm (FDM).

Leptocephali—recorded from waters of Florida Straits; reported salinity range 37.0–38.5 ppt; reported temperature range 28.0–28.5 C.¹

Eelers and/or juveniles—inshore in Puerto Rico in April,¹³ or year round but sporadic (FDM).

SPAWNING

No information.

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LEPTOCEPHALI

Size range described, 10.8–29.5 mm, the largest specimen thought to be transitional.

Total myomeres 131–136; preanal myomeres 75–77; post-anal myomeres 56–59. Teeth $\frac{1+II-III+1-4}{1+I-III+1-2}$.¹

Proportions as percent TL: Preanal length 74; maximum depth (at anus) 13; head length 6.¹

Eye with narrow, fleshy margin. Dorsal fin origin at myomeres 54–57; myomeres between dorsal and anal origin +13–23. Caudal fin rays undeveloped. A small pectoral fin evident,¹ this lost later (JDH). Twenty-three myomeres before anus; anterior margin of liver between myomeres 13 and 16; posterior margin of liver between myomeres 22 and 23; anterior margin of gallbladder between myomeres 20 and 22; first major vertical artery at myomere 18–20; renal artery at myomere 63–68; renal portal vein at myomere 69–73.¹

Pigmentation: At 25 mm a series of chromatophores along dorsal midline between myomeres 10 and 54; a second series along dorsal surface of intestine past liver; and a third series along ventral surface of spinal cord. Two conspicuous single chromatophores: one deep in myelencephalon and one below gill opening. Scattered chromatophores on palate and on ray bases of dorsal and anal fins. Eyes pigmented.¹

ELVERS

No information.

JUVENILES

Minimum size, unknown.

Pigmentation: Olivaceous or dark brownish gray,¹¹ uniform.⁵

AGE AND SIZE AT MATURITY

No information.

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Conger oceanicus

conger eels
Congridae

FAMILY CONGRIDAE

The family Congridae, which contains three subfamilies and about 38 genera and 100 species, occurs only in the Atlantic and Pacific oceans. The only regional representative of the family (*Conger oceanicus*) has been recorded as far north as Nova Scotia. Members of the family are generally limited to shallow, coastal waters. In the Atlantic, they typically occur over sandy bottoms near grass beds and reefs.

In this family the pectoral fins may be well-developed (as in Congrinae) or minute or absent (as in Heterocongrinae). Congridae are scaleless. The lateral line is present; the nostrils are lateral and in front of the eyes; the anterior nostril is developed as a short tube; the mouth is usually almost horizontal.

Little is known of the spawning of *Conger oceanicus* except that it apparently moves offshore to spawn. *Conger conger* ceases feeding before spawning; its teeth are lost. There are radical changes in the shape of the head, the bones become soft and gelatinous, and the eyes of the males become greatly enlarged. The fish die after spawning.

Offshore spawning migrations may be typical of a number of congrid eels. Females of *Ariosoma bowersi* become egg-bound in captivity, swell to enormous dimensions, and eventually explode. This results from the presence of a calcareous plug in the oviduct which, presumably, may not form if the females are exposed to increased pressure in offshore waters.

Congrid leptocephali may have from 106-242 myomeres (140 to 151 in the regional species), and the gut, which lacks swellings, may extend almost to the end of the body. Leptocephali of some members of the family have narrow eyes beneath which there is a distinct patch of choroid tissue. In the subfamily Congrinae (to which *Conger oceanicus* belongs) there is usually a prominent pigment patch beneath the eye and pigment ventrally below the gut. Characteristics for distinguishing congrid leptocephali from other regional *leptocephali* are presented in a key in the introduction to the section on Ophichthidae.

Schmidt (1931b) pointed out that the eggs and larvae identified by Eigenmann (1902) as *Conger oceanicus* were, in fact, those of an ophichthid eel. The specific identity of this series, based on eggs collected off New England, is still unknown.

Conger oceanicus (Mitchill), Conger eel**ADULTS**

D. 273; A. 187; P. 16–18;¹² branchiostegal rays 9;¹⁵ total vertebrae ca. 135¹²–149²⁰ (but note higher larval myomere counts below); precaudal vertebrae 50–51; caudal vertebrae 85–96; lateral line pores 39–44; compressed teeth in upper jaw 27–65, in lower jaw 28–59.¹²

Head 6.37–7.30 times in TL; depth 2.3–2.85 times in head.² Length of head as thousandths of TL, 130–180.¹²

Body elongate, round anteriorly, compressed posteriorly.² Upper jaw usually projected beyond lower;¹ two rows of teeth, the innermost conical; premaxillary tooth patch wider than long.¹² Skin scaleless. Eyes oval.¹ Lateral line complete.² Origin of dorsal less than 50 percent of pectoral fin length behind tip of pectoral.¹²

Pigmentation: Grayish brown, bluish gray or nearly black above, sometimes with reddish tinge; sides paler; dingy white below. Dorsal fin light blue centrally, dusky at base, and with black outer edge; anal pale, edged with black; pectorals blue gray, tipped with bluish white or pale blue.^{1,2,13}

Maximum length: Possibly to ca. 2034 mm.¹

DISTRIBUTION AND ECOLOGY

Range: Coastal waters from Nova Scotia¹³ to Mississippi;¹² also the West Indies based on collections of larvae.¹ Records from Brazil^{9,11} are questioned (JDH).

Area distribution: Lower Chesapeake Bay north to Worcester County, Maryland and mouth of Potomac River;^{2,4,6,26} coastal waters of New Jersey and Delaware.^{7,12}

Habitat and movements: Adults—waters of the continental shelf, sometimes entering harbors, sounds, shallow bays, and river mouths along coast;^{1,11,17,19} minimum salinity, 22.3 ppt;²¹ maximum depth, 475 m.¹² Possibly moves offshore in winter or during spawning season.^{1,5}

Leptocephali—coastal and estuarine waters from Nova Scotia to Chesapeake Bay;^{1,3,13} in northern latitudes inshore (and sometimes washed on beaches) from May to August;^{8,10,18,22,30} minimum salinity, in water which varied annually from 3 to ca. 19 ppt,¹⁴ also in estuarine water with average of 26 ppt.³⁰

Elvers and/or juveniles—recently transformed individuals from Fire Island Inlet, Long Island in August.²⁷

SPAWNING

Location: Possibly offshore in New England;^{1,5,20} also

thought to spawn in the West Indies.¹

Season: Possibly summer in New England;^{1,5} leptocephali collected as early as late May in Long Island²² and mid-July in Nova Scotia;¹³ in aquaria adults ripen in all months except October and November.²⁰

Fecundity: Unknown (counts attributed to this species^{24,25} are based on *Conger conger*²³).

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LEPTOCEPHALI

Maximum length attained, 160 mm. Specimens 75²⁹–98 mm³⁰ long have apparently shrunk from maximum size and begun transformation.

Total myomeres 140¹–151;⁸ preanal myomeres 74; post-anal myomeres 72;²⁹ myomeres before dorsal (at 96.5 mm) 52.⁸

At 96.5 mm TL head 4.6 mm, eye 1.7 mm, body width 6.6 mm.⁵

Eye oval, pectoral fins formed at 96.5 mm.⁸

Pigmentation: At 93.0 mm TL a crescentic pigment patch under eye.³¹ At 96.5 mm, in life, perfectly transparent, eye brilliant gold; after preservation, a row of about 85 minute dots along side of body, ca. 100 similar dots along ventral surface, numerous small dots at bases of anal and dorsal rays.⁸ In an apparently more advanced specimen 75 mm long pigment differentiation along outer edge of fins.²⁹

ELVERS

No information.

JUVENILES

Size range described ca. 107¹⁸–150 mm.¹²

At ca. 113 mm body elongate, tapering posteriorly to a

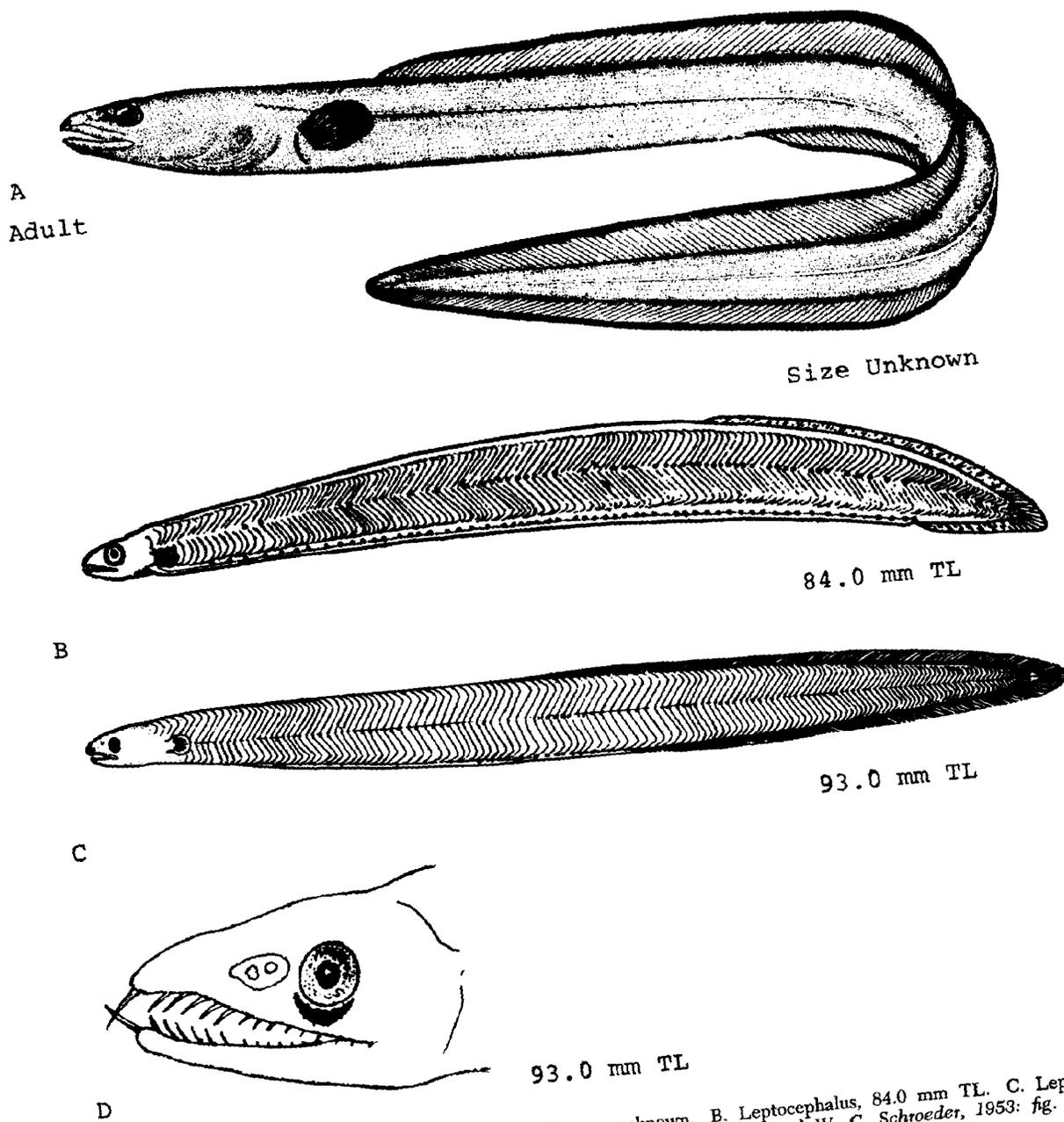


Fig. 11. *Conger oceanicus*, Conger eel. A. Adult, size unknown. B. *Leptocephalus*, 84.0 mm TL. C. *Leptocephalus*, 93.0 mm TL. D. Detail of head of B. (A, B, Bigelow, H. B., and W. C. Schroeder, 1953: fig. 70. C, D, Lippson, A. J., and R. L. Moran, 1974: 30.)

point, very compressed.¹⁶

At ca. 150 mm number of teeth less than in adult.¹²

Pigmentation: At ca. 113 mm translucent, vertebral column and ribs visible, small spots on margin of dorsal and anal fins and along lateral line.¹⁶

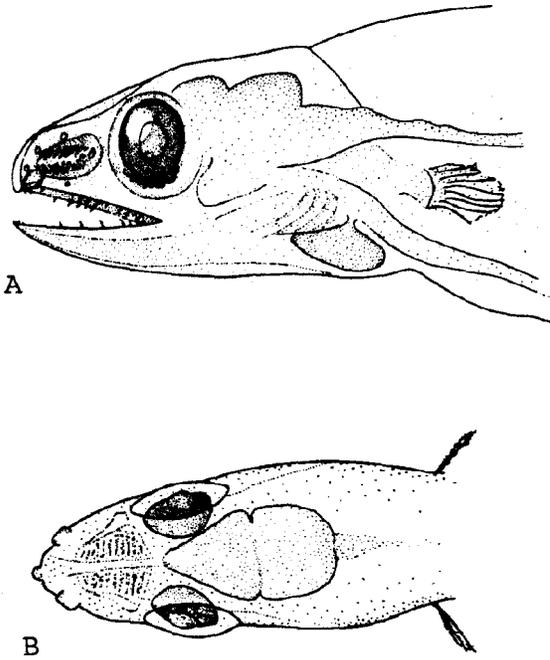


Fig. 12. *Conger oceanicus*, Conger eel. Head of transforming leptocephalus, 93.5 mm TL. A. Lateral view. B. Dorsal view. (A, B, Original illustrations, Daniel M. Carver.)

AGE AND SIZE AT MATURITY

No information.

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Ahlia egmontis
Myrophis punctatus
Ophichthus gomesi
Ophichthus ocellatus
Pisoodonophis cruentifer

snake eels
Ophichthidae

FAMILY OPHICHTHIDAE

Members of this family are most easily distinguished from other eels by the position of the posterior nostril which either pierces the upper lip or lies along the inner margin of the lip within the mouth. In addition, they are characterized by their attached tongue and by the presence of a distinct jugostegalia in the throat formed by overlapping of the branchiostegal rays. Most ophichthid eels lack pectoral fins, and some have no fins at all. Two subfamilies are recognized: Ophichthinae (snake eels) and Echelinae (worm eels). Snake eels lack scales and an external fin around the tip of the tail, their tail tip is strong and spike-like, and, typically, they have striking and sometimes very bright color patterns. In worm eels there is a fringe-like fin around the tip of the tail, and the color patterns are plain.

Ophichthid eels, of which there are, according to recent estimates, approximately 200 to 270 species and 31 to 60 genera, occur in tropical and temperate waters throughout the world.

Five ophichthid eels or their leptocephali have been recorded in the Mid-Atlantic Bight. Nothing is known of the actual spawning of these species except for the comment by Cohen and Dean (1970) that, in *Ahlia*, a seaward migration in late fall and early winter may be related to the onset of sexual maturation.

Two of the regional species are known to produce pelagic eggs. In one of these (*Pisoodonophis*) the eggs are relatively large (ca. 2.2 to 2.6 mm in diameter) and have a segmented yolk containing one to many oil globules.

Ophichthid leptocephali all have more or less well-developed gut swellings and/or convolutions. They can be distinguished from leptocephali of other regional eels in a number of ways. Leptocephali of the freshwater eel (*Anguilla*) lack pigment and have a reduced number of myomeres (102-110 in *Anguilla*, 114-165 in the five regional ophichthids). In leptocephali of *Conger* the gut is straight, and there is a characteristic crescent pigment patch beneath the eye which is lacking in both snake eels and worm eels. The leptocephalus of *Gymnothorax funebris* can be distinguished from all regional ophichthids leptocephali by its straight gut, and from all but *Myrophis punctatus* by the absence of distinct subcutaneous spots below the mid-lateral line on the tail.

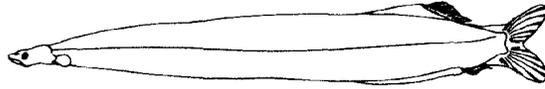
Although all ophichthid leptocephali probably go through a period of length decrease during their development, this has been clearly demonstrated in only one of the regional species, *Myrophis punctatus*. In the present review these growth stages are designated as follows:

Leptocephali	
Stage I	Length increasing.
Stage IIa	Length decreasing.
Stage IIb	Length decreasing.
Elvers	Length increasing.

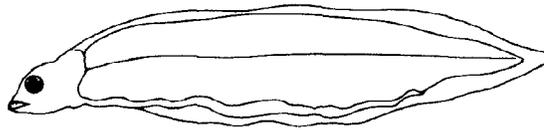
A key to leptocephali of Mid-Atlantic Bight fishes:

- 1A. More than 100 myomeres 2
- 1B. Less than 90 myomeres; anus far back on body; distinct dorsal, anal, and caudal fins formed during development of leptocephali .

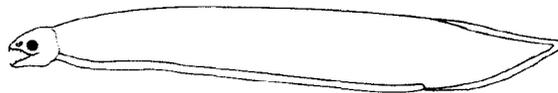
Order Clupeiformes:
Elopidae and Albulidae
(see volume I).



- 2A. Total myomeres 114 or more 3
- 2B. 102-110 myomeres, preanal myomeres 63-74, preanal length 60-74 percent TL, no pigment on body, gut without "loops" or swellings *Anguilla rostrata*



- 3A. Gut straight, lacking swellings or "loops" 4



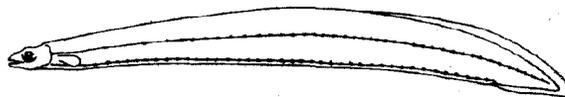
- 3B. Gut with 3-11 distinct swellings or "loops" 5



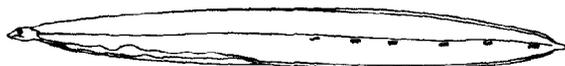
- 4A. Total myomeres 131-136; preanal myomeres 75-77; pectoral fin rudimentary, never well-developed; no pigment below eye *Gymnothorax funebris*



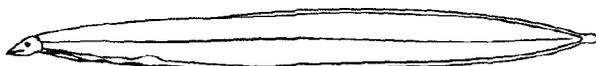
- 4B. Total myomeres 140-151, preanal myomeres 74, pectoral fin well-developed by end of stage, usually a crescent-shaped pigment patch below eye *Conger oceanicus*



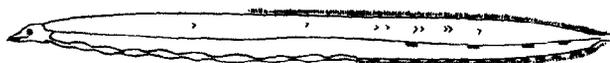
- 5A. Gut with less than 8 swellings or "loops" 6
- 5B. Gut with 8 or more swellings or "loops" 7
- 6A. 4 to 6 gut swellings, 4-7 subcutaneous spots below midline on tail, total myomeres 147-165, preanal myomeres 65-73 *Ahlia egmontis*



- 6B. 3 gut swellings, the third most prominent; no subcutaneous spots ventral to midline on tail, total myomeres 138-150, preanal myomeres 52-63 *Myrophis punctatus*



- 7A. A series of conspicuous, evenly spaced, linear pigment clusters separated by unpigmented gaps ventrally beyond anus and, in later stages, this pigment associated with developing anal fin; pigment present on a few myosepta between mid-lateral line and dorsal ridge (but not shown in all illustrations in present account); 8 or 9 prominent spots on gut; total myomeres 114-162; preanal myomeres 66-75 *Pisoodonophis cruentifer*



- 7B. No pigment ventrally beyond anus, or a single chromatophore at base of each anal fin ray 8



- 8A. Gut with 8 weak swellings, ventral gut pigment restricted to first 2 swellings, total myomeres 139-150, preanal myomeres 66-79 *Ophichthus gomesi*



- 8B. Gut with 9 weak swellings, gut pigmented ventrally throughout its length, total myomeres 126-142, preanal myomeres 62-78 *Ophichthus ocellatus*



Ahlia egmontis (Jordan), Key worm eel**ADULTS**

(The following based on a sample of about 20 specimens.) Preanal fin vertebrae 63–66, predorsal vertebrae 65–70, total 157–162 (JEB) or 152.¹³

Proportions as percent TL: Head 9.2–9.6, body 42.3–44.4, trunk 32.6–34.8, tail 55.5–57.6, snout 1.6–1.9, eye 0.5–0.6, depth 2.4–2.5, upper jaw 2.4–2.5, lower jaw 2.2–2.3.⁷ Distance from snout to dorsal 2.1–2.5 times in TL, depth 2.6–3.0 times in head,⁹ eye 1.3–2.3 times in snout.¹⁰

Body slender, compressed;¹⁰ head small, moderately pointed, anterior nostril in a short tube; lower jaw considerably shorter than upper; gape extended beyond eye;⁶ eye relatively small, but apparently increasing in

size during spawning season as in *Anguilla*.² Dorsal origin above or slightly behind anus;^{4,10} caudal and pectoral fins developed⁵ (in specimens 215–270 mm long, pectorals short and broad, about as long as snout and broader than gill slit).⁹

Pigmentation: Variable. May be almost uniformly pale, may have upper half finely peppered with dark dots, may be bicolored (upper half dark, lower half light) in trunk region with tail uniform throughout, or may be entirely brown except for ventral surface of trunk region.⁴ Pigment also described as yellowish, brownish^{5,10} or olive green above, bright golden yellow to yellowish olive below. Fins light yellowish.¹¹

Maximum length: 381 mm.⁴

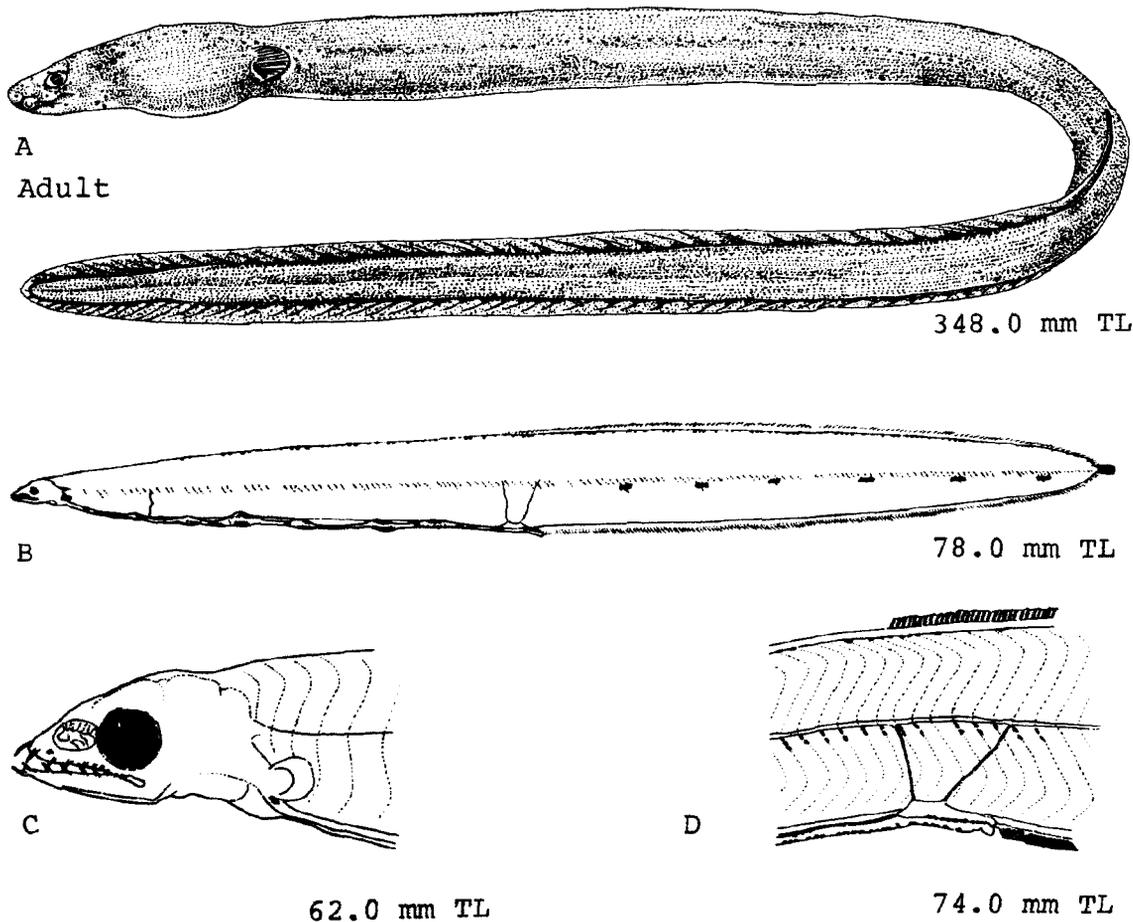


Fig. 14. *Ahlia egmontis*, Key worm eel. A. Adult, 348.0 mm TL. B. Leptocephalus, 78.0 mm TL. C. Detail of head of leptocephalus, 62.0 mm TL. D. Region of anus, 74.0 mm TL specimen. (A, Böhlke, J. E., and C. C. G. Chaplin, 1968: 100. © Academy of Natural Sciences of Philadelphia, used with permission of authors and publishers, redrawn by Tamiko Karr. B-D, Fahay, M. P., and C. L. de Gorgue, MS.)

DISTRIBUTION AND ECOLOGY

Range: From just south of Martha's Vineyard, Massachusetts¹ (based on leptocephali) to Maceió, Brazil;³ also the Bahamas⁴ and the West Indies.¹¹

Area distribution: A single leptocephalus from the coast of New Jersey.¹

Habitat and movements: Adults—primarily a shallow water species² (although apparently move seaward at certain times of year⁸) found over hard bottoms⁵ and reefs;⁴ specifically recorded from canals, natural channels, tidal creeks, protected bays, eel grass beds,² and over fine white sand;⁷ may burrow in substrate;² nocturnal, often swimming at surface at night. Apparently move seaward on ebb tide in late fall and early winter, and this movement may be associated with spawning.^{2,8}

Recorded depth range, 6 or 7 cm² to 37 m.⁹ Temperature range 26.5–31.0 C. Maximum recorded salinity, 35.5–35.7 ppt.¹

Leptocephali—oceanic; recorded temperature range 20–28.7 C.¹

Elvers and/or juveniles—no information.

SPAWNING

Location: Probably pelagic⁴ in deep water beyond the continental shelf of North America, and in the Caribbean.¹

Season: Unknown, except for comment that seaward movement in late fall and early winter is probably associated with spawning.^{2,8}

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LEPTOCEPHALI

Size range described 56¹–85 mm TL.¹²

Total myomeres 147–165, preanal myomeres 65–73,¹ post-anal myomeres 89–93;¹² maxillary dental formula 0–1 + II–V + 0–7.¹

Relative preanal length decreases from 53% TL at 56.0 to 48% at 82.0 mm.¹

Body long, slender, tapering from very slender head to behind alimentary canal.¹² Dorsal fin origin at myomere 63–70. Gut swollen at 4–6 places (although usually 4); first gut swelling at about myomere 17; third gut swelling pronounced; fourth and fifth and sixth (if present) low and indistinct. Anterior margin of liver at myomere 13–18, posterior margin at myomere 21–32. First major artery joins aorta at myomere 16–24, renal artery at myomere 62–66, renal-portal vein at myomere 68–71. Opisthonephros located over gut, and with 2 peaks on dorsal aspect.¹

Pigmentation: In specimens 56.0–82.0 mm TL nearly

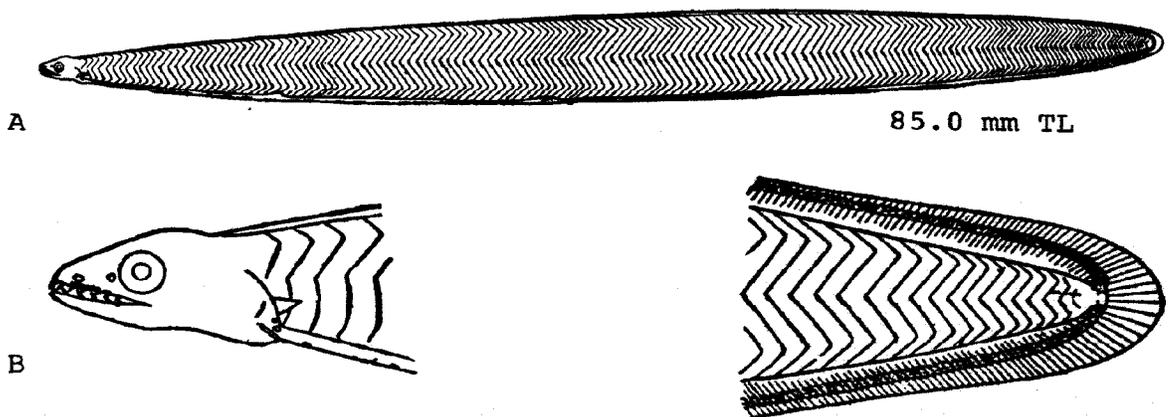


Fig. 15. *Ahlia egmontis*, Key worm eel. A. Leptocephalus, 85.0 mm TL. B. Detail of head and caudal region of A. (A, B, Eigenmann, C. H., and C. H. Kennedy, 1901: fig. 14.)

every myoseptum with a series of dashes just ventral to midline; 4-7 subcutaneous spots below midline, on tail; gut pigmented on dorsal and ventral aspects at level of each swelling and on dorsal aspect near anus; a series of spots along dorsal edge of body; anal base with a single spot at base of each ray; few small spots on gular region and snout.¹

In another series of specimens 75-85 mm long pigment essentially similar to above but additional pigment as follows: a series of 3 or 4 chromatophores along edge of upper jaw half way between its tip and the eye; a conspicuous chromatophore near pectoral base; chromatophores developed on dorsal, anal, and caudal; and a series of spots above posterior part of spinal cord.¹²

JUVENILES

Minimum size described, 60 mm.

Body more worm-like than in larger specimens (in a 60 mm specimen depth only 2.0 mm).

Pigmentation: At 60-65 mm transparent when freshly captured, finely punctulate with dark dots on dorsal

surface when preserved.⁹ A 159 mm specimen described as yellowish brown.¹¹

AGE AND SIZE AT MATURITY

No information.

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Myrophis punctatus Lütken, Speckled worm eel**ADULTS**

Vertebrae (based on myomere counts of young) 138–150.^{1,16,17,19,30} Head 3.0²⁸–3.5 times in trunk, 5.5 times in tail.²¹ Depth of body at gill opening 2.75²⁸–3.3 times in head,²¹ 25–35 in TL (MPF). Distance from dorsal origin to anus 1.9–2.6 times in trunk.³

Body worm-like, slender, compressed or rounded,² upper jaw projected,¹⁴ snout somewhat broader than long,²⁴

gape extended beyond eyes.²⁹ Posterior nostril large, located at rim of gape; anterior nostril tubular, near lateral profile and a short distance from end of snout.³ Eye ellipsoid.¹³ Teeth small, pointed; teeth on upper jaw usually in 2, rarely 3, irregular rows; premaxillary teeth usually 5 in number and in an arched row; palatal teeth in 2 or 3 rows.³ Tongue attached.¹³

Vertical fins high (MPF); origin of dorsal fin halfway

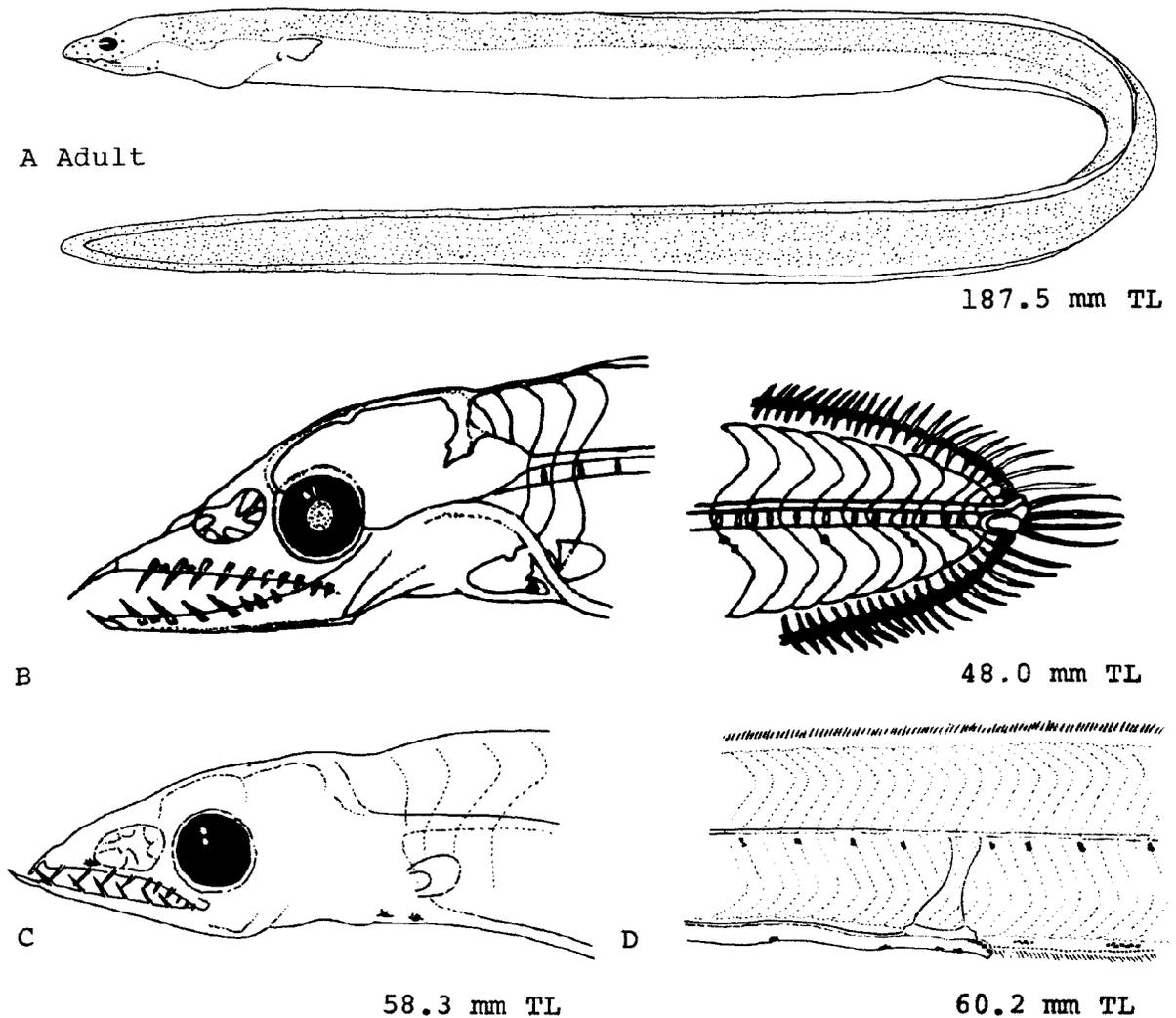


Fig. 16. *Myrophis punctatus*, Speckled worm eel. A. Adult, 187.5 mm TL. B. Stage I leptocephalus, 48.0 mm TL. C. Detail of head of 58.3 mm TL leptocephalus. D. Region of anus, specimen 60.2 mm TL. (A, Böhlke, J. E., and C. C. G. Chaplin, 1968: 100. © Academy of Natural Sciences of Philadelphia, used with permission of authors and publishers, redrawn by Tamiko Karr. B, Eldred, B., 1966: fig. 1. C, D, Fahay, M. P., and C. L. de Gorgue, MS.)

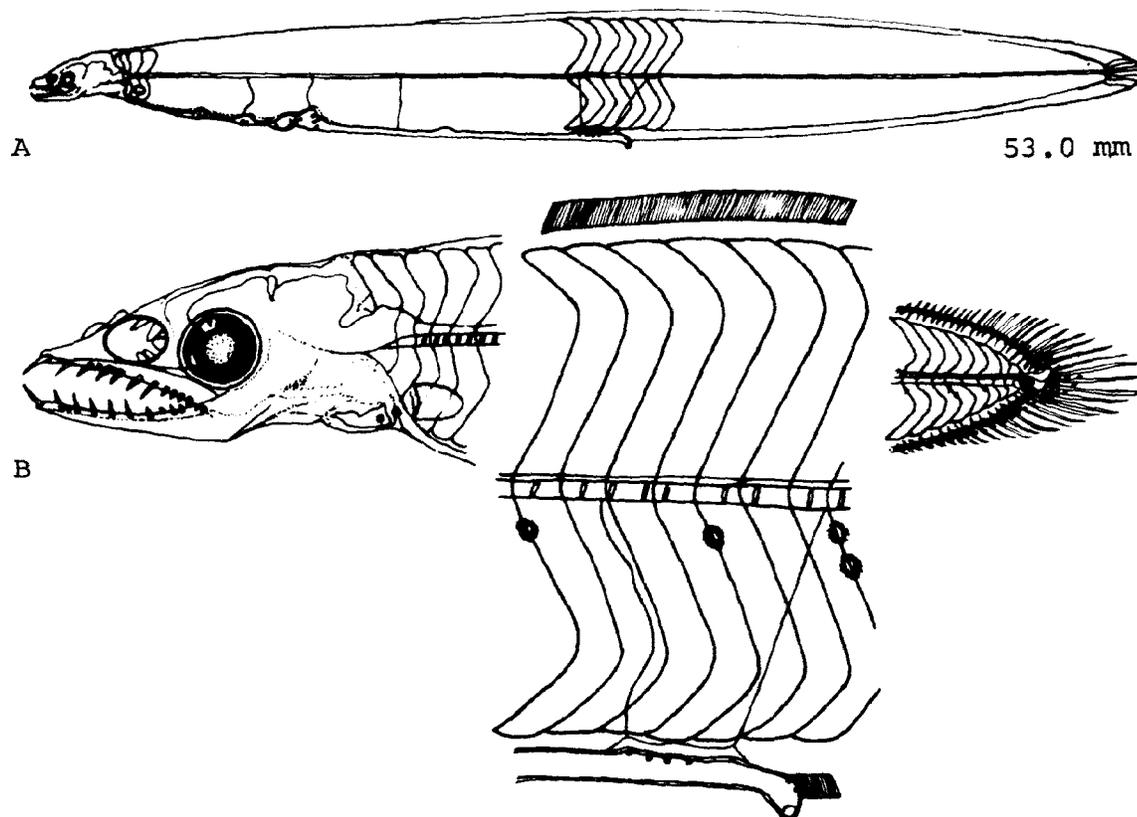


Fig. 17. *Myrophis punctatus*, Speckled worm eel. A. Stage I leptocephalus, 53.0 mm TL. B. Detail of head, midbody and caudal region of previous specimen. (A, B, Eldred, B., 1966: fig. 2.)

between gill opening and anus; ² pectoral base wide (MPF).

Pigmentation: Brownish or yellowish; anterior lower half nearly uniform in color; dorsal surfaces covered with tiny dark specks, with speckled pattern covering most of sides posteriorly.³ Iris pale.¹³

Maximum length: 426 mm.³

DISTRIBUTION AND ECOLOGY

Range: Chesapeake Bay, Maryland² to Rio Goyanna, Brazil; also Bermuda,⁴ the West Indies,³ and the west coast of Africa.¹³

Area distribution: A single specimen from Chesapeake Bay, off Calvert County, Maryland² (the inclusion of this species among the Potomac River ichthyofauna²⁵ is questioned, JDH).

Habitat and movements: Adults—a coastal species (JDH) sometimes entering bays²³ and tidal creeks,⁶ usually over soft mud;^{1,3,8,28} sometimes over dead coral and sand; minimum depth less than 1.2 m; ⁶ maximum depth, 88

m;¹² temperature range 16–33 C; euryhaline,²⁶ salinity 17–37 ppt.¹¹ Move to surface at night; ¹ in some areas move in and out on flood and ebb tides each day; ¹⁵ in Louisiana inshore in spring and fall; ⁹ in Florida move seaward on night ebb tides in late fall and winter.²³

Leptocephali—coastal, in both offshore and inshore waters (JDH), sometimes entering shallow bays; found at surface at night; temperature range 12.2–26.0 C; ¹ salinity range 0.0²²–39.5 ppt. Leptocephali recorded offshore in January, February, March, June, November, and December; inshore in January, February, March, October, November, and December.^{1,27}

Elvers and/or juveniles—elvers recorded both inshore and offshore; initially planktonic,¹ but cease planktonic existence between March and May,³² burrowing then into mud; also reported along grassy shores,¹ at surface at night.¹¹ Reported inshore from December through May, occasionally offshore in March¹ and August.³⁰

SPAWNING

Location: Offshore,¹ probably beyond the 46 m contour.²⁶

Season: Probably fall and winter, "larvae" recorded from October through March, but most prevalent in December and January.¹

Note: *Spawning males may acquire larger eyes and pectoral fins.*⁶

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LEPTOCEPHALI (STAGED)

Stage I (size increasing): Size range 48¹–80 mm.²⁶

D. 337. A. 233. Total myomeres 138–147 (average 141); preanal myomeres 54–59 (average 55); postanal myomeres 82–91 (average 86); myomeres between D. and A. 21–26 (average 23). Dorsal origin at myomere 30–35 (average 32); anterior margin of liver at myomere 12–14 (average 13), posterior margin at myomere 21–27 (average 24); first major artery at myomere 18–22 (average 19), 2nd at 24–27 (average 25), 3rd at 28–36 (average 32); major renal artery at 49–55 (average 51); renal-portal vein at 54–59 (average 56).¹

Proportions as percent SL at ca. 60–80 mm, dorsal 70–74, anal 55–56.²⁶

Body long, flattened, tapering to maximum depth just behind anus. Snout described as thin and pointed,¹ or blunt. Eye distinctly oval in 71 mm specimen,² otherwise apparently round.¹ Gape to posterior edge of pupil.² Gill slits small, oblique. Leptocephali up to 59.8 mm with unseparated nasal capsule. Teeth in upper jaw 0–1 + 0–VI + 0–11; in lower jaw 0–1 + III–IV + 0–4.¹ Anterior-most lower tooth almost horizontal.² Pectoral fins small, rounded, located at 3rd myomere; pectoral rays developed in a specimen 59.8 mm long,¹ although absent in other specimens up to ca. 80 mm long.²

Pigmentation: Transparent throughout stage. Lateral pigment spots variable (MPF); in some descriptions lateral series of paired brown chromatophores under the level of the vertebral column²⁶ beginning "behind head"² or at beginning of level of liver and continuing to tail

and comprised of 1 or 2 large chromatophores over every 3rd¹ to 6th myoseptum; the total series consisting of ca. 36–40 pairs of spots. In some specimens the last 4–6 spots broken into clusters of smaller dots.²⁶

Stage IIa (size decreasing): Size range 79.0–ca. 50.0 mm.¹

Total myomeres 138–148 (average 142); preanal myomeres 53–59 (average 55); postanal myomeres 83–90 (average 86); myomeres between dorsal and anal 20–26 (average 23); branchiostegals, when present, 5–7.¹

Dorsal origin at myomere 30–37 (average 32); first major artery at myomere 17–21 (average 19), 2nd at myomere 22–30 (average 25), 3rd at myomere 29–36 (average 34); major renal artery at level of myomere 48–53 (average 51); renal-portal vein at myomere 53–59 (average 58); anterior margin of liver at myomere 11–15 (average 13), posterior margin at myomere 23–26 (average 24).¹

Depth ca. 11 times in length at 74 mm.⁷

Body long, flattened. Nostrils well differentiated, the anterior ones becoming tubular. Teeth absent.¹ At 74 mm gape extending beyond eyes, lower jaw shorter than upper.⁷

Pigmentation: Transparent throughout stage. At 74 mm a lateral series of spots on myocomma, each spot consisting of 1 or 3 chromatophores; one or two chromatophores below pectoral; six prominent spots along alimentary canal with a few chromatophores scattered between them; a few spots along anal and caudal bases, and along bases of last dorsal rays; few chromatophores evident on head.⁷ In "transition stage" ventral pigment spots tend to extend horizontally into longitudinal stripes; lateral spots somewhat enlarged.²⁶

Stage IIb (size decreasing): Size range 62–ca. 45 mm. (Shrinkage of ca. 15–25 mm, average 19 mm, or ca. 26% SL, occurs during metamorphosis and transformation may take as little as 18 hours or less.)²⁶

Total myomeres 138–146 (average 142); preanal myomeres 49–59 (average 52); postanal myomeres 85–93 (average 88); myomeres between dorsal and anal 19–25 (average 21); branchiostegal rays 4–7 and present in most specimens. Pectoral base at myomere 3–7; anterior margin of liver at myomere 11–14 (average 12), posterior margin at 23–25 (average 24); dorsal origin at myomere 29–37 (average 31). Head with series of mucous pores; snout rounded, blunt, extending beyond lower jaw. Anterior nostril near tip of snout, broad-based, tubular, and with pointed tab on upper part; posterior nostril on rim of gape just anterior to end and below margin of eye. Teeth absent.¹

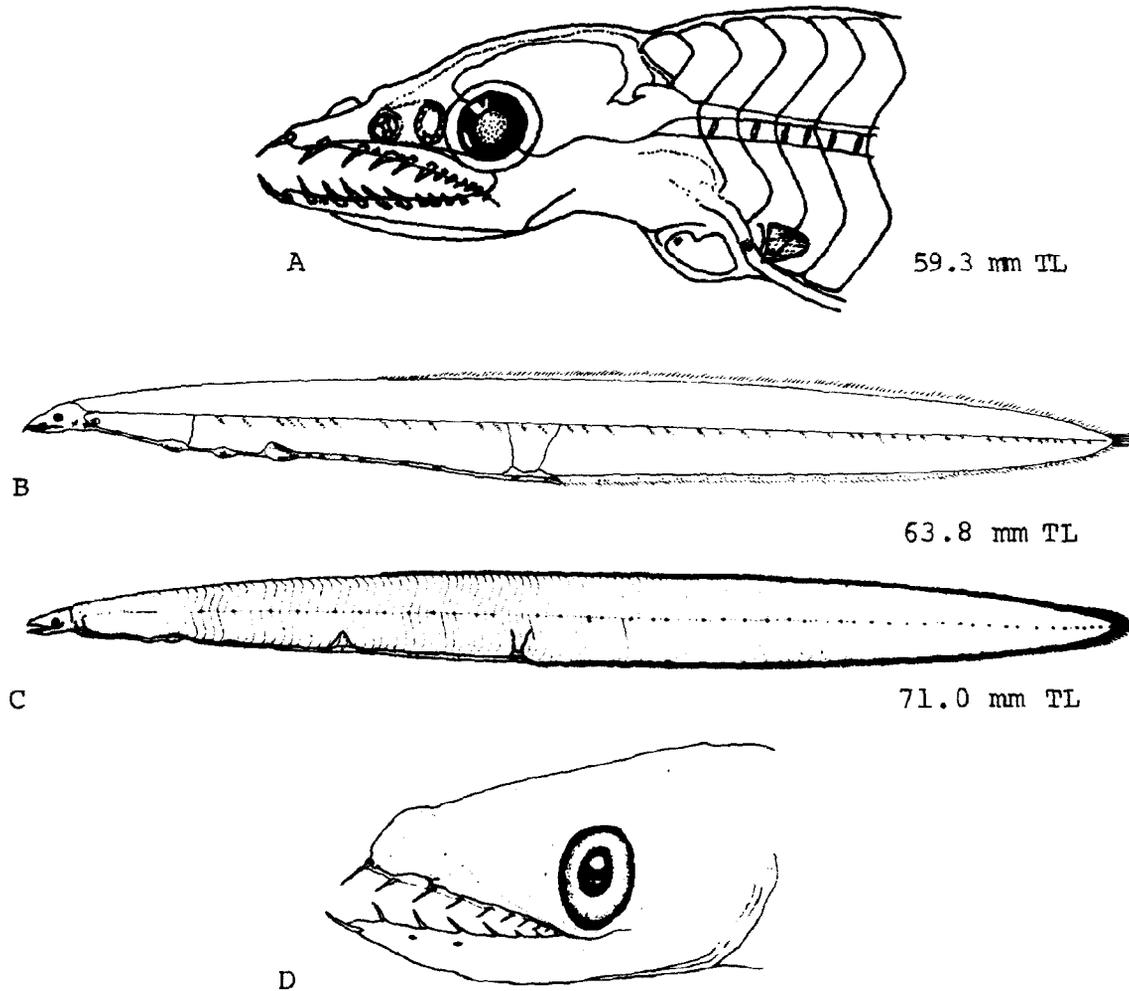


Fig. 18. *Myrophis punctatus*, Speckled worm eel. A. Stage I leptocephalus, detail of head of specimen, 59.3 mm TL. B. Stage I leptocephalus, 63.8 mm TL. C. Stage I leptocephalus, 71.0 mm TL. D. Detail of head of previous specimen. (A, Eldred, B., 1966: fig. 3a. B, Fahay, M. P., and C. L. de Gorgue, MS. C, D, Cooper, J. E., and M. P. Fahay, 1974: 32.)

Pigmentation: Opaque, otherwise undescribed.¹

LEPTOCEPHALI (UNSTAGED)

22.5–78.2 mm TL, substages not distinguished.

Total myomeres 138–150, preanal myomeres 52–63.

Maxillary dental formula 0–1 + III–VIII + 3–7.³⁰

Preanal length as percent TL: At 23.8 mm, 69%; at 78.2 mm, 44%.³⁰

Anterior margin of liver at myomere 10–16, posterior margin at myomere 19–27; first major artery at myomere 13–20; renal artery at myomere 48–54; renal-portal vein

at myomere 54–60; origin of dorsal fin at myomere 30–37. Three gut swellings, the third most pronounced. Opisthonephores short, located over end of gut, and with two peaks on dorsal surface.³⁰

Pigmentation: No subcutaneous spots ventral to midline posterior to vent; myosepta sporadically pigmented along midline; gut pigmented on ventral aspect of first and second bulges, on dorsal and ventral aspects of third bulge, intermittently along straight portion of intestine.³⁰

At ca. 40 mm linear clusters of large spots between myomeres and anal fin base; at ca. 50 mm (and until time of metamorphosis) an additional row of smaller spots, one at base of each anal ray.³⁰

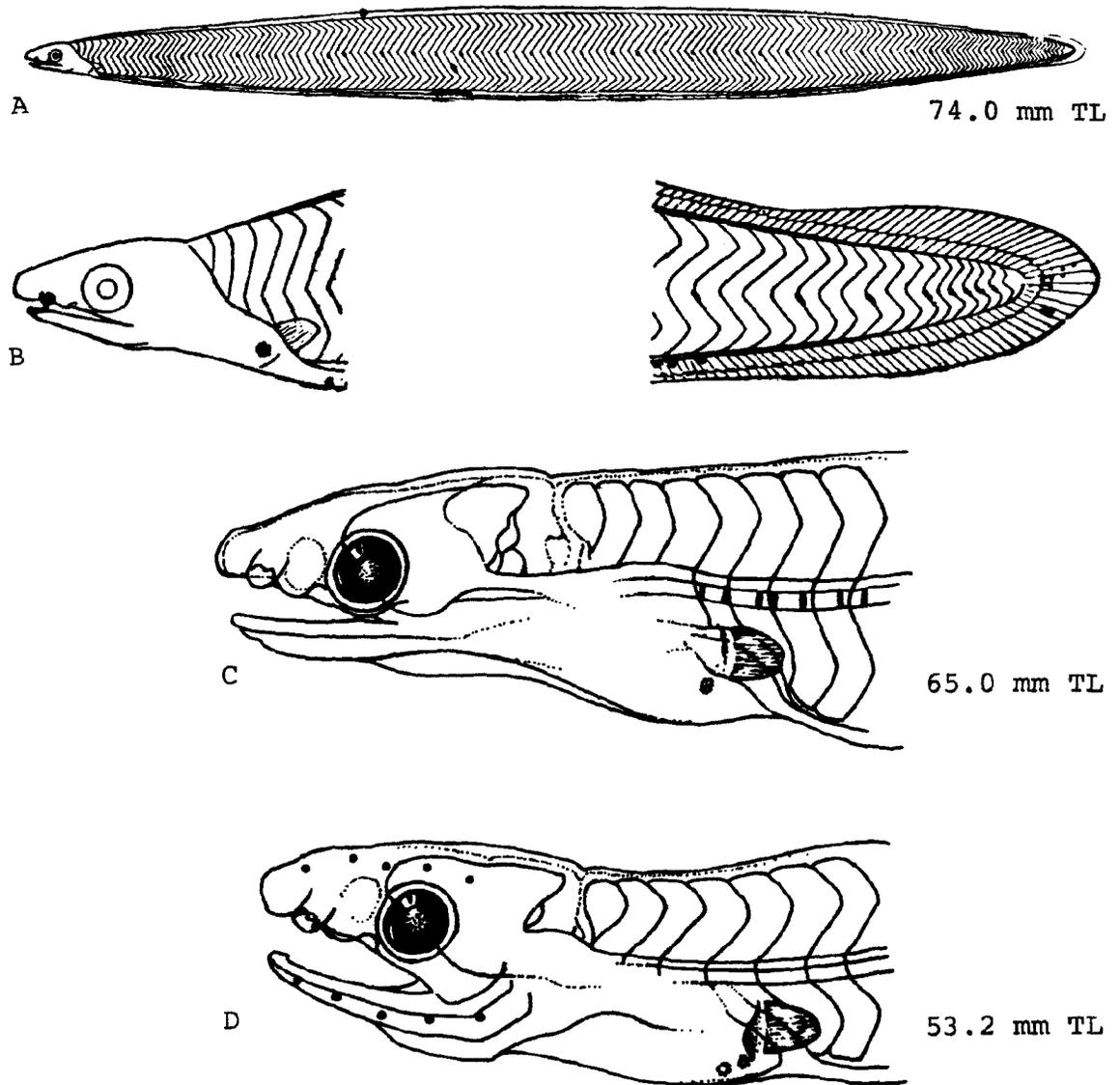


Fig. 19. *Myrophis punctatus*, Speckled worm eel. A. Stage IIa leptocephalus, 74.0 mm TL. B. Detail of head and caudal region of previous specimen. C. Detail of head of stage IIa leptocephalus, 65.0 mm TL. D. Detail of head of stage IIb leptocephalus, 53.2 mm TL. (A, B, Eigenmann, C. H., and C. H. Kennedy, 1901: 90. C, D, Eldred, B., 1966: figs. 3b, 3c.)

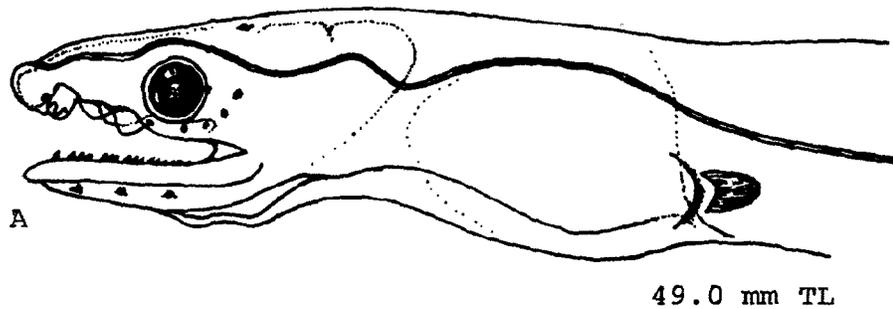


Fig. 20. *Myrophis punctatus*, Speckled worm eel. A. Elver, 49.0 mm TL. (A, Eldred, B., 1966: fig. 3d.)

ELVERS

Size range 39–59 mm.¹

Average branchiostegals, 6.¹

“Newly transformed” anal fin base length typically 55–56% SL, occasionally 39–40% (these later may represent either abnormally developing individuals or another species).²⁶

Adult teeth developed.¹

Pigmentation: No information.

JUVENILES

Size range described 121¹–146.³

Total vertebrae 138–145, preanal vertebrae ca. 45–53, postanal vertebrae ca. 86–93.¹

Distance from dorsal origin to vent 2.0–2.4 times in trunk.³ Proportions as percent TL in specimen 103 mm long: Head length, 9.7; snout length, 1.73; eye diameter, 0.75; snout to anal distance, 38.4; snout to dorsal distance, 23.5; pectoral length, 1.2; body depth, 2.4.²⁴

Dorsal origin slightly more posterior in “young” than in adults.¹³

Pigmentation: A 120 mm specimen described as light olive-green with fine punctations above, lighter below.²¹

AGE AND SIZE AT MATURITY

No information.

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Ophichthus gomesi (Castelnu), Shrimp eel**ADULTS**

Vertebrae 141.¹⁴

Proportions as percent TL: Head 10.8–11.7, body 34.9–40.2, tail 59.7–63.5, trunk 26.2–28.0, depth 4.0–5.0⁹ (depth also given as 20–30 times in length⁶), snout 1.8–2.8, upper jaw 3.8–4.9, lower jaw 3.1–4.5, eye 1.1–1.3.⁹ Head 2.8 times in trunk; head and trunk 2 times in tail;¹⁰ lower jaw 2.8–3.2 times in head;¹⁷ pectoral fin 2 1/5 to 2 3/5 times in head.⁸

Conspicuous pores on head and jaws;⁸ upper jaw overhanging lower.⁷ Two to 4 rows of teeth on jaws and vomer; in specimens 320–420 mm long, 2 rows on jaws, the inner one slightly smaller, in specimens 600 mm and longer 4 somewhat irregular rows; arch of premaxillary tooth rows often converging at symphysis to form V-shaped row;^{7,13} vomerine teeth convergent posteriorly.⁶ Caudal fin absent;⁷ origin of dorsal fin above or in advance of tips of pectoral fins.¹³

Pigmentation: Yellowish,¹³ brownish yellow,⁷ light brown,⁶ olive brown,⁸ or dark gray above⁹ grading to white,⁶ yellowish white,⁹ or yellow below.¹⁰ Dorsal pigment actually comprised of numerous brown points on yellow ground color. Pores on head rimmed with black;⁶ lower jaw with dusky markings. Dorsal and anal fins translucent⁸ and edged with black. Pectoral fin dusky,⁶ dark along upper edge,⁸ sometimes yellowish brown.⁹

Maximum length: Ca. 914 mm.⁷

DISTRIBUTION AND ECOLOGY

Range: Massachusetts to Rio Grande do Sul, Brazil;^{15,18} also Cuba and Puerto Rico.^{6,8}

Area distribution: A single leptocephalus recorded from the coast of New Jersey.¹⁹

Habitat and movements: Adults—found over bottoms of sand,⁷ mud,⁹ rock or shell⁵ near coast; recorded in bays³ and harbors¹¹ and sometimes associated with rocks,⁹ jetties, and docks;¹ apparently sometimes concentrated in deep holes in otherwise shallow areas;¹¹ may swim at surface.¹⁵ Recorded depth range, in water 13¹ to 73 m deep.¹⁵ Temperature range, 15.0² to ca. 28.9 C (maximum based on July average temperature).¹² Salinity range 0.3² to ca. 27.8 ppt (maximum based on July average salinity).¹²

Leptocephali—smallest larvae (30.0 mm) off North Carolina; larger larvae (up to 70.0 mm) southward over continental shelf to Florida, yolk-sac larvae probably transported north by Gulf Stream, but larvae then

sheared off by Carolina coastal current and carried southward.¹⁶

Elvers and/or juveniles—very small young at outlets of bays.⁵

SPAWNING

Season: Apparently in spring and summer¹⁶ (adults captured in mid-July appeared to be recently spent¹⁵).

EGGS

Unfertilized eggs: Ca. 1.0 mm in diameter, pale yellow.¹⁵

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LEPTOCEPHALI

Size range described, 14.5–98.4 mm TL.

Total myomeres 139–150; preanal myomeres 62–79; post-anal myomeres 79; maxillary dental formula 0-1 + I-VIII + 1-10.¹⁶

Greatest depth 10.33 times in length; eye 1.6 in snout, about 5 in head.¹⁷ Relative preanal length decreases from 79% TL at 18.0 mm to 54% TL at 95.0 mm.¹⁶

Body gradually tapering from head to behind anus; head pointed; jaws equal; caudal pointed; origin of rayed dorsal 4 myomeres in front of anal;¹⁷ dorsal finfold origin at myomere 60–69. Gut with 8 weak swellings. Opisthonephros long, lying along dorsal aspect of gut. Anterior margin of liver at myomere 10–14, posterior margin at myomere 21–27. First major artery joins aorta at myomere 7–21, renal artery at myomere 55–79, renal-portal vein at myomere 61–79 (renal artery and renal-portal vein relatively close together).¹⁶

Pigmentation: Through size range described, all but first few myosepta with pigmented dashes just ventral to midline; ventral gut pigment restricted to first two swellings; dorsal gut pigment a cluster of spots over each swelling; four to five subcutaneous spots ventral to midline posterior to vent; a pigment spot at base of each anal ray in specimens larger than 57.0 mm; a spot near tip of lower jaw, another on upper jaw but not near

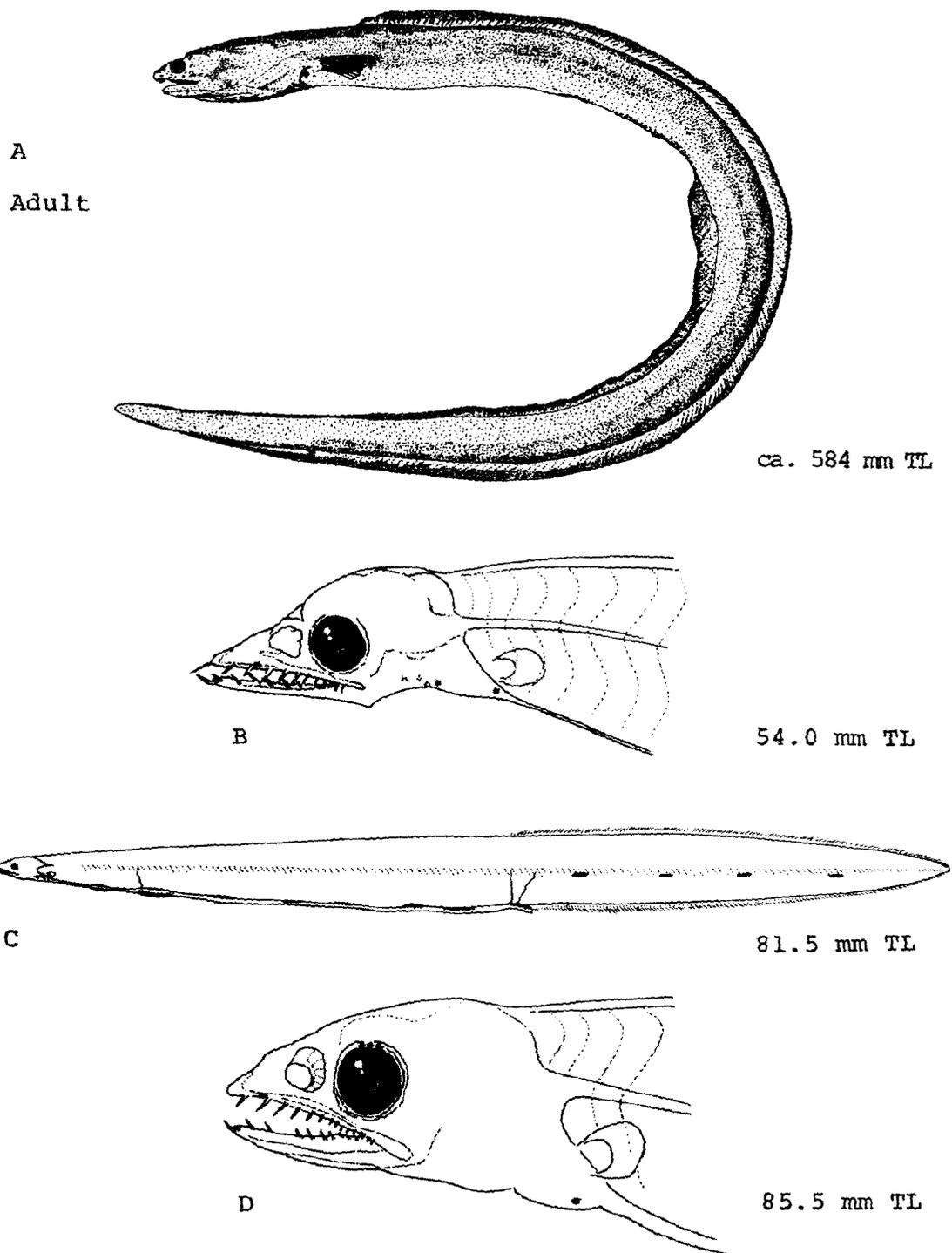


Fig. 21. *Ophichthus gomesi*, Shrimp eel. A. Adult, ca. 584 mm TL. B. Detail of head of 54.0 mm TL specimen. C. *Leptocephalus*, 81.5 mm TL. D. Detail of head of 85.5 mm TL specimen. (A, Randall, J. E., 1968: fig. 29. TFH Publications. Used with permission of publisher. Redrawn by Tamiko Karr. B-D, Fahay, M. P., and C. L. de Gorgue, MS.)

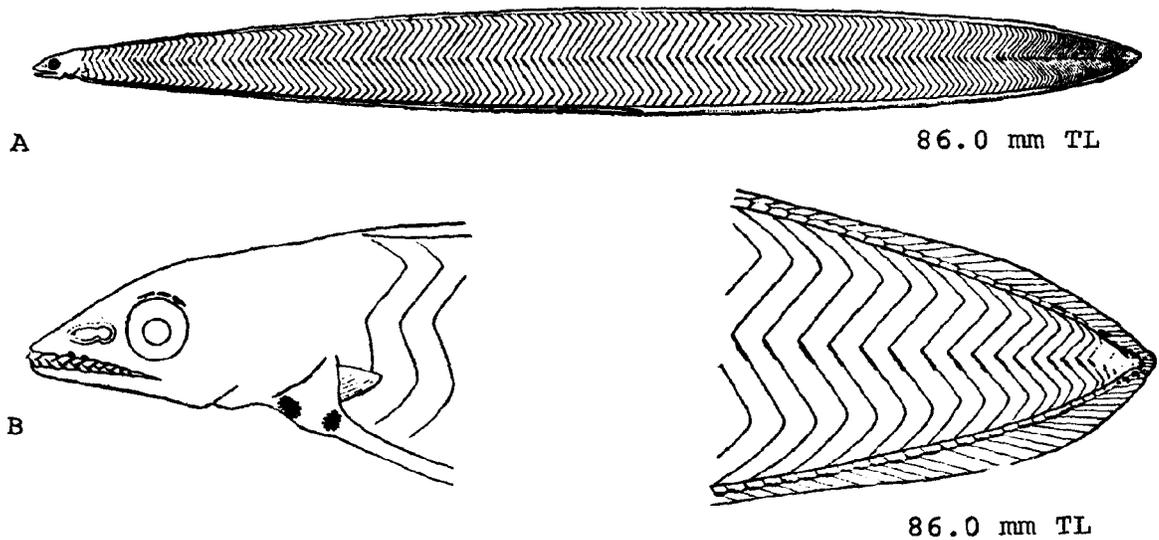


Fig. 22. *Ophichthus gomesi*, Shrimp eel. A. Leptocephalus, 86.0 mm TL. B. Detail of head and caudal section of A. (A, B, Eigenmann, C. H., and C. H. Kennedy, 1901: fig. 9.)

tip; few spots in gular region.¹⁶

In a specimen 86 mm long, pigment similar to above, but additional pigment as follows: several chromatophores at base of caudal, two at base of dorsal near tail, and 3-4 over eye.¹⁷

ELVERS

No information.

JUVENILES

Minimum size described, 211 mm.

At 211-238 mm jaw teeth in 2 rows, but outer row of mandibular teeth incomplete posteriorly.¹⁸

AGE AND SIZE AT MATURITY

No information.

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Ophichthus ocellatus (Lesueur), Palespotted eel

ADULTS

Vomerine teeth, ca. 15; ⁴ vertebrae, 134.⁸

Proportions as percent TL: Trunk 35.5–37.4, tail 49.7–51.9, head 12.4–13.1, depth 3.7–5.8, predorsal length 16.5–18.5, snout 2.2–2.4, eye 1.2–1.8.⁵ Average length of pectoral fin 34.3% HL in males, 33.3% in females.¹¹ Lower jaw 2.2–2.6 times in head.⁷

Upper jaw projected.³ Teeth rather large; teeth in inner

row of lower jaw, except for a short distance anteriorly, smaller than those in outer row and variable in number from a nearly complete row to few; vomerine teeth usually in a single row, but sometimes two small teeth, side by side, in front of anteriormost tooth; anterior 2–5 vomerine teeth usually enlarged and disjunct from outer teeth.⁷ Dorsal origin variable, from over tip of pectoral to over one fin length beyond pectoral ¹³ (possibly these data include specimens of *O. retropinnis*, MPF); caudal fin absent.³

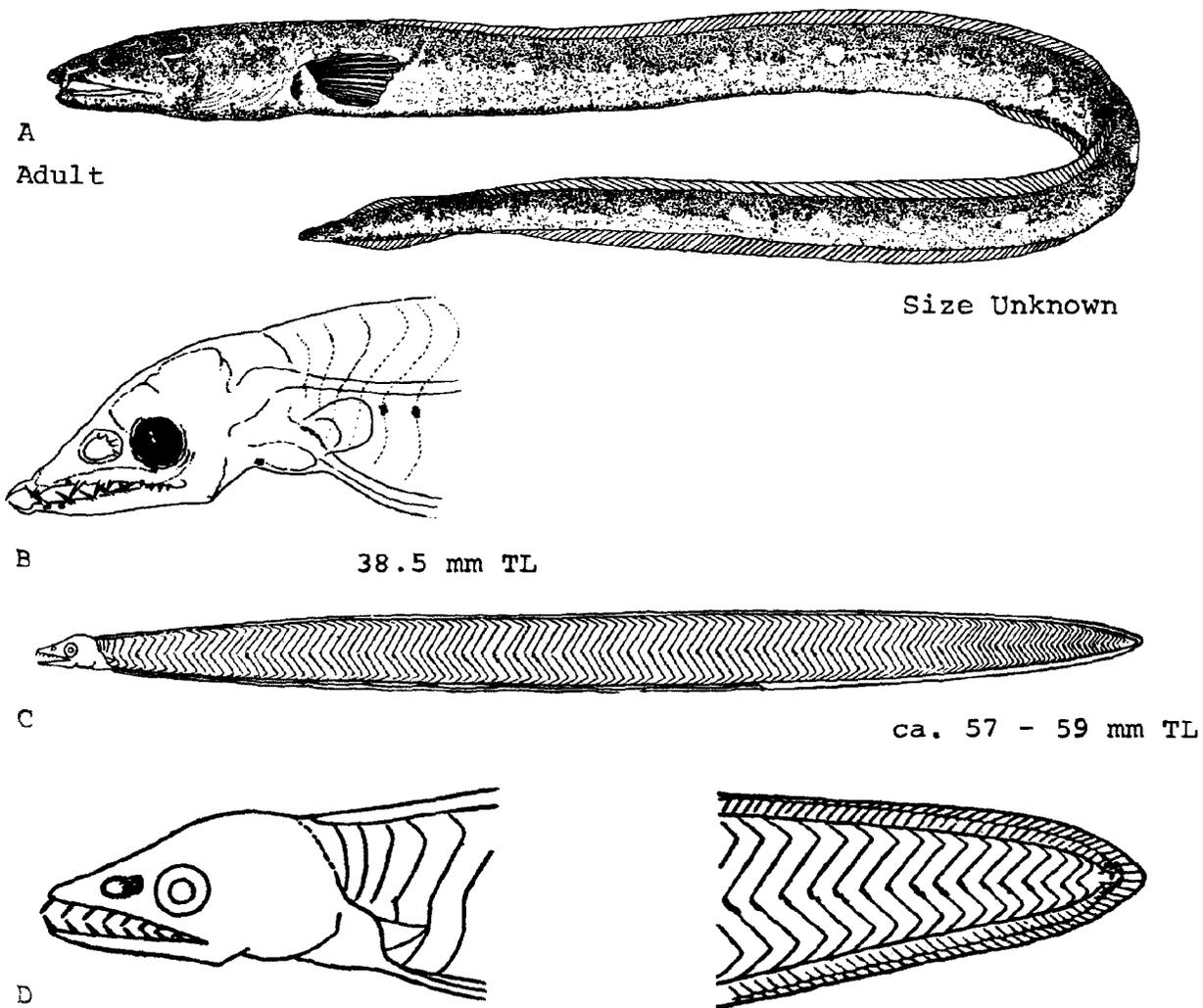


Fig. 23. *Ophichthus ocellatus*, Palespotted eel. A. Adult, size unknown. B. Detail of head of 38.5 mm leptocephalus. C. Leptocephalus ca. 57–59 mm TL. D. Detail of head and caudal region of C. (A, Jordan, D. S., and B. W. Evermann, 1896–1900: fig. 169, Tamiko Karr, delineator. B, Fahay, M. P., and C. L. de Gorgue, MS. C, D, Eigenmann, C. H., and C. H. Kennedy, 1901: fig. 5.)

Pigmentation: Basic color variable, generally brown³ or yellowish brown above,⁵ yellow⁷ or white below. Sides with series of 18³ to 21¹¹ white spots running along entire length of fish.⁷ Jaws, throat, and chin dusted with brown dots;⁴ nuchal region often with a whitish rather narrow stripe anteriorly and a few irregularly scattered spots;⁷ sides of head yellow; a longitudinal row of white dots on each side of head and a transverse one across top of head;⁵ pores on head and lower jaw often marked with small brown spots.⁷ Dorsal fin light colored with narrow dark edge, anal light yellow, pectoral dusky.⁴

Maximum length: Possibly to ca. 1830 mm, although identity questioned;³ otherwise 815 mm TL.⁵

DISTRIBUTION AND ECOLOGY

Range: Adults from North Carolina to Brazil, including the Gulf of Mexico and the West Indies;^{4,5,6,10} larvae north to Hudson Canyon (off New York).

Area distribution: Leptocephali recorded just south of Chesapeake Bay, and close to the 183 m line off New Jersey.¹

Habitat and movements: Adults—typically over hard bottom,³ but also recorded over mud.⁵ Depth range 9⁷–146 m.³

Leptocephali—some individuals drift south in the Carolina coastal current, while others are carried north by the Gulf Stream.¹

Elvers and/or juveniles—no information.

SPAWNING

Season: Presumably at least 3 times a year, early winter, spring and early fall.¹

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LEPTOCEPHALI

Size range described, 11–87 mm TL.

Total myomeres 126–142, preanal myomeres 62–78,¹ post-anal myomeres 56–58.⁹ Maxillary dental formula 0–1+II–VII+3–9.¹

At 42–59 mm greatest depth 13 times in TL; head ca. 1.25 times in greatest depth; eye 2 times in snout, 5.5 times in head.⁹ Preanal length decreases from 81% TL at 19.0 mm to 59% TL at 77.5 mm.¹

Body nearly uniform in depth from head to beyond end of alimentary canal. Snout pointed, profile straight or

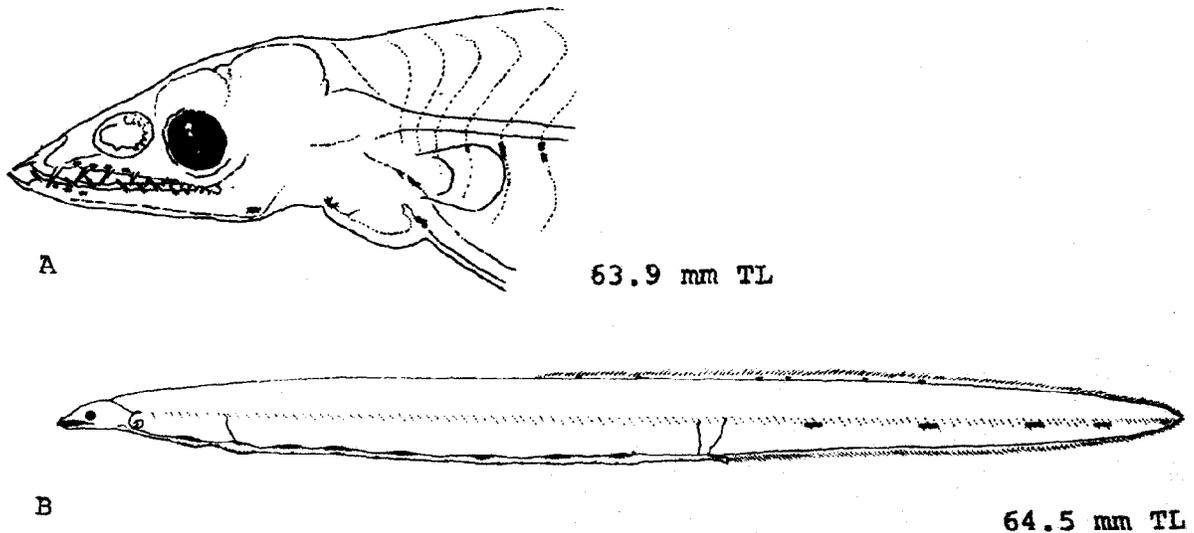


Fig. 24. *Ophichthus ocellatus*, Palespotted eel. A. Detail of head of 63.9 mm leptocephalus. B. Leptocephalus, 64.5 mm TL. (A, B, Fahay, M. P., and C. L. de Gorgue, MS.)

slightly depressed over eye. Anterior nostril about half-way between eye and tip of snout. At 42–59 mm pectoral fins well-developed;⁹ dorsal fin origin at myomere 47–59. Gut with 9 weak swellings. First major artery leaves aorta at myomere 10–18, renal artery at myomere 57–63, renal-portal vein at 63–69. Anterior margin of liver at myomere 8–12, posterior margin at 19–22. Opisthonephros elongate.¹

Pigmentation: In specimens 11–28 mm TL every myoseptum, except several of first few, with pigmented dashes just ventral to midline; gut pigmented ventrally with an accumulation of spots under first 2 swellings and sparsely on remaining length; gut pigmented dorsally with an accumulation of spots on each swelling; specimens over 45 mm with an additional two spots between first two swellings; four to six subcutaneous spots ventral to midline posterior to vent; anal base pigment absent in specimens less than 30 mm TL, sparse in specimens 33–35 mm TL, and with a single spot at base of every ray in specimens larger than 36 mm TL; pigment along dorsal edge of body in some specimens; 2 or 3 spots on lower jaw; 1 to 4 spots on upper jaw below bases of teeth; few gular spots present in all specimens.¹

In another series of specimens 42–59 mm long, one or two chromatophores at margin of upper jaw; a series of 9 pigment spots above alimentary canal; no pigment spots at base of anal and dorsal fins; a few chromatophores at base of tail; a spot at upper surface of end of spinal cord; a series of ca. 4 spots in tail just beneath notochord; myomeres with 1–3 inconspicuous chromatophores below mid-lateral line.⁹

ELVERS

No information.

JUVENILES

Specimen described, 58 mm.

Preanal vertebrae 53, total vertebrae 137.¹

Preanal distance 45% TL. Dorsal origin at vertebrae 14 and behind pectoral origin by distance equal to 2.5 times length of pectoral fin.¹

Pigmentation: At 58 mm leptocephalous pigment no longer evident, head and body straw colored with an overlying scattering of dark spots.¹

AGE AND SIZE AT MATURITY

No information.

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Pisoodonophis cruentifer (Goode and Bean), Snake eel**ADULTS**

Total vertebrae 145-152, preanal vertebrae 61-62, post-anal vertebrae 84-90.⁶

Depth 35-47 (MPF),⁵ head 12 times in TL; eye 10 times in head.⁸

Body moderately elongate (MPF), more or less cylindrical, robust;⁴ head snake-like, constricted behind;⁹ snout conical, depressed,¹⁰ bluntly rounded;⁵ mouth ca. 1/3 length of head; upper jaw projected;⁸ gape extended considerably beyond eye;⁵ gill openings lunate.⁸ Teeth very small, more or less compressed, short, robust, strong, pointed, biserial anteriorly on both jaws and vomer, slightly larger and more or less triserial on premaxillaries. Lateral line distinct, median.⁴ Origin of dorsal a short distance behind tip of pectorals; anal origin far behind dorsal origin;⁵ vertical fins low; pectoral fins narrow

based (MPF); tip of tail hard, pointed;⁵ no caudal rays.

Pigmentation: Uniform olive brown,⁴ light brown or brownish yellow, or dorsal surfaces with alternating black and white mesh-like pattern;⁸ large individuals darker than smaller;⁵ inside of mouth white; dorsal fin pale to whitish, with anterior margin dark olive or brownish; anal fin pale to whitish; pectoral fin olive buff, darker along upper border.⁴

Maximum length: Ca. 416 mm.²

DISTRIBUTION AND ECOLOGY

Range: Reported from Cape Breton, Nova Scotia, but record based on specimen from swordfish stomach; otherwise Gulf of Maine to vicinity of Cape Henry, Virginia.²

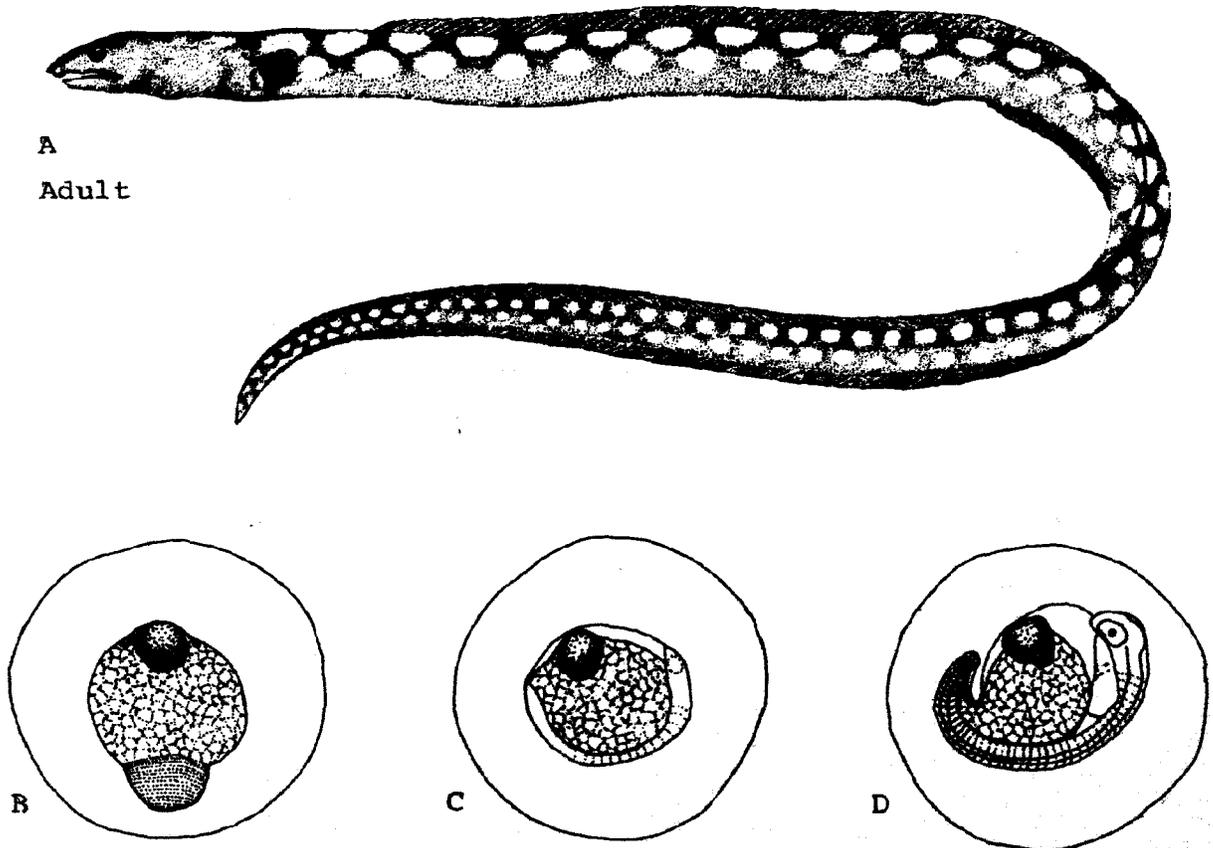


Fig. 25. *Pisoodonophis cruentifer*, Snake eel. A. Adult, size unknown. B. Egg at early stage of development. C. Embryo about two-thirds around yolk; eyes, somites forming. D. Tail-free embryo. (A, Leim, A. H., and W. B. Scott, 1960: 162. B-D, Richardson, S. L., 1974: fig. 1.)

Area distribution: Coast of New Jersey; ^{1,4} off mouth of Chesapeake Bay. ^{5,6}

Habitat and movements: Adults—depth range 44 to 448 m; ⁵ once thought to bore into flesh of larger fish, ⁸ but this has been questioned. ¹¹

Leptocephali—specimens less than 10 mm SL at surface in Norfolk Canyon; larger leptocephali 74 to 111 km off mouth of Chesapeake Bay. ⁶

Elvers and/or juveniles—no information.

SPAWNING

Location: Eggs 74–148 km off Virginia over continental shelf. ⁶

Season: Eggs July 4 to September 12. ⁶

Fecundity: No information.

EGGS

Location: Pelagic, usually at surface in water having temperature of 20–32 C and salinity of 23–35 ppt. ⁶

Fertilized eggs: Diameter 1.78–2.89 mm (averages 2.24 and 2.63 mm); egg membrane smooth; yolk segmented; perivitelline space very large; one to many oil globules varying in diameter from 0.33–0.44 mm (averages 0.37–0.38 mm). ⁶

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

Hatching length probably 5.5 mm ± 0.5 mm SL; largest examined 5.8 mm SL. ⁶

At 5.8 mm SL preanal length 76% SL. ⁶

Jaws not fully formed at hatching. ⁶

Pigmentation: No pigment at hatching (MPF).

LEPTOCEPHALI

Size range described, 5.9 mm SL ⁶ to 83.5 mm TL. ¹² Specimens 75–82 mm long are near transformation. ⁷

Total myomeres 114 ⁶–162 (in a series of 59 specimens ranging from 13.0–83.5 mm TL those from north of Delaware Bay had 145–162 myomeres with an average of 154 while those from south of Delaware Bay had 142–156 myomeres with an average of 148) ¹² with an apparent increase with increasing length; ⁶ preanal myomeres 66 ⁷–75; ¹² postanal myomeres 50+ to possibly as high as 84, increasing with increasing length. ⁶

Proportions as percent SL at 34.2 mm SL: Preanal length 63. ⁶ Proportions as times in length at 75–82 mm TL: Depth 11.5, head 14.3. ⁷ Preanal length changes from 75% TL in specimens under 20 mm to 53% TL at 83.5 mm. ¹²

At 75–82 mm body elongate, band-shaped, tapering gradually to about midway between anus and tip of tail; head rounded, conical; nostrils separated from each other by distance equal to diameter of eye; gill slits very nearly vertical. ⁷ Lower jaw about equal to upper in a specimen 6.7 mm SL; much longer than upper in a specimen 6.9 mm SL. Teeth well-developed at 6.9 mm SL; ⁶ maxillary dental formula 1 + II–VII + 2–9; ¹² leptocephalous teeth still evident at 82 mm. ⁷ Anterior margin of liver at myomere 8–12; posterior margin at myomere 20–27; first major artery joins aorta at myomere 8–18; last two major blood vessels join aorta at myomere 55–65 and at myomere 62–70. ¹² Dorsal and anal fins evident at sizes greater than 19 mm; ⁶ dorsal origin at myomere 44–57; ¹² pectorals apparently absent at 6.7 mm SL, present at 6.9 mm SL. Gut strongly looped, with nine peaks. ¹²

Pigmentation: At 6.7 mm SL (or smaller) to 10.0 mm SL, 8 prominent pigment patches on gut. At 7.0 mm SL or longer a single pigment spot over esophagus. At 10 mm SL or larger, 9 pigment spots along gut, the 9th posterior to the rest. At 10 mm SL 1–5 pigment patches ventrally between anus and tip of tail, and a similar series dorsally near tip of tail. By 12.9 mm SL dorsal pigment row on tail migrated to position just above notochord and ventral row just below vertebral column. At 20 mm SL or larger additional pigment patches ventral to gut, a mid-lateral row of pigment just below notochord, lower jaw pigmented. At 20 mm SL up to 8 pigment patches on outer edge of anterior segment of dorsal finfold. At 22.9 mm SL similar pigment in ventral finfold. At 30 mm SL melanophores developed on midbrain. At 32.1 mm SL a row of spots on posterior segment of dorsal finfold. Pigment spots on gut distribution as follows in relation to myomeres: ⁶

Pigment patch (anterior to posterior)	Myomere at which it occurs
1	9–11 (\bar{x} 10)
2	16–19 (\bar{x} 17)
3	22–27 (\bar{x} 24)
4	28–34 (\bar{x} 31)
5	36–41 (\bar{x} 39)
6	43–49 (\bar{x} 45)
7	50–58 (\bar{x} 53)
8	59–65 (\bar{x} 62)
9	66–72 (\bar{x} 68)

At 75–82 mm a spot near end of jaw, one behind eye, and one on nape; sides with 3 irregular rows of melanophores, the ventralmost restricted to caudal region; pigment also along dorsal and anal fin and above and below gut. ⁷

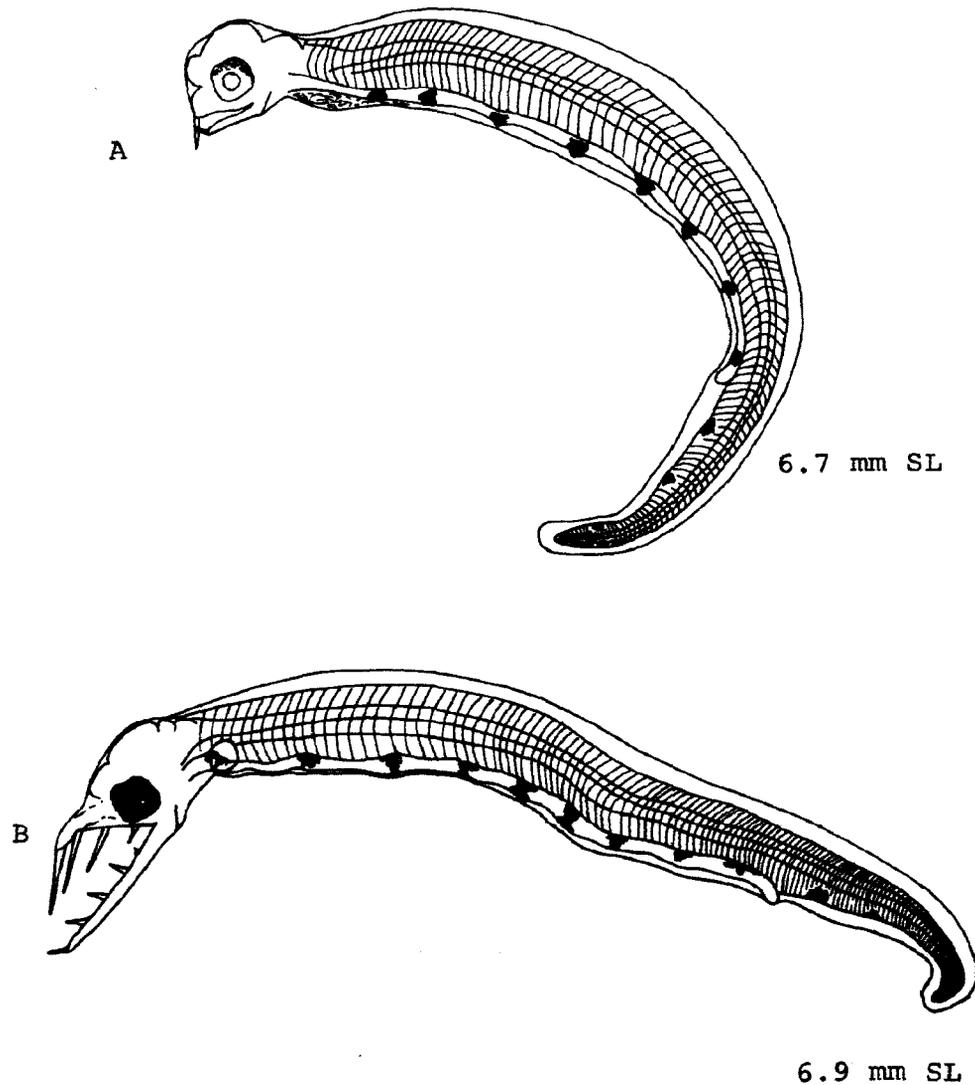


Fig. 26. *Pisoodonophis cruentifer*, Snake eel. A. Leptocephalus, 6.7 mm SL. B. Leptocephalus, 6.9 mm SL. (A, B, Richardson, S. L., 1974: fig. 2.)

Pigment also described as follows (size range 13.0 to 83.5 mm TL): pigment along dorsal edge of body; myosepta sporadically pigmented with few dashes ventral to midline; flank pigment present on upper angle of a few myosepta between midline and dorsal edge of body and on lower angle of a few postanal myosepta between midline and ventral edge of body; extent of flank pigment increases in specimens from ca. 50 mm TL to ca. 79 mm TL when the flank pigment becomes faint; prominent pigment spots along dorsal edge of body; gut pigmented on and between swellings, on dorsal as well as ventral

aspects; anal base pigment in short, linear clusters separated by unpigmented gaps; 5 to 7 subcutaneous spots ventral to midline, posterior to vent; spots on head, snout, lower jaw, and gular area all increase in extent and intensity with growth.¹²

JUVENILES

Minimum size described (although stage uncertain): 65 mm.

Pigmentation: At 65 mm pale with dark speckles.⁵

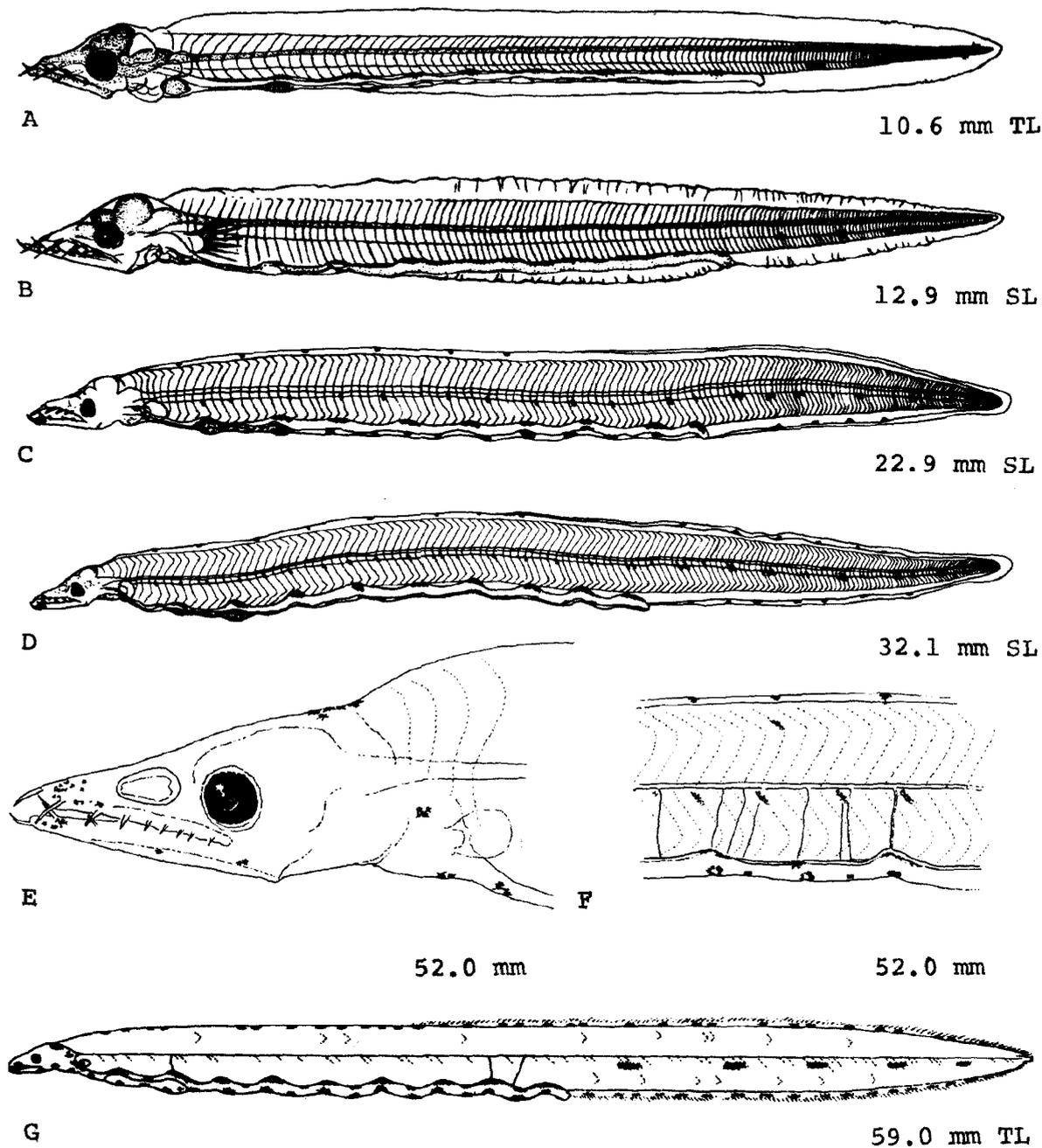


Fig. 27. *Pisonodonophis cruentifer*, Snake eel. A. Leptocephalus, 10.6 mm TL. B. Leptocephalus, 12.9 mm SL. C. Leptocephalus, 22.9 mm SL. D. Leptocephalus, 32.1 mm SL. E. Detail of head of a specimen 52.0 mm TL. F. Detail of mid-body region of a 52.0 mm specimen. G. Leptocephalus, 59.0 mm TL. (A, Original drawing, A. J. Lipson. B-D, Richardson, S. L., 1974: fig. 3. E-G, Fahay, M. P., and C. L. de Gorgue, MS.)

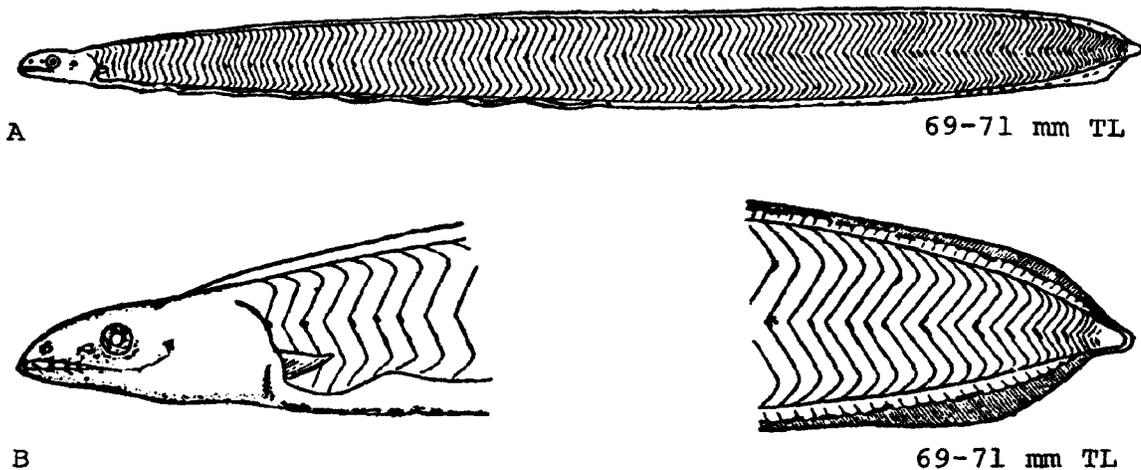


Fig. 28. *Pseudonophis cruentifer*, Snake eel. A. Leptocephalus, 69-71 mm TL. B. Head and caudal region of A. (A, B, Eigenmann, C. H., and C. H. Kennedy, 1901: fig. 11.)

AGE AND SIZE AT MATURITY

No information.

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Scomberesox saurus

sauries

Scomberesocidae

FAMILY SCOMBERESOCIDAE

The family Scomberesocidae contains two genera and four species, one of which is undescribed. These fishes occur primarily in subtropical and temperate marine waters in both the northern and southern hemispheres, but are essentially lacking in tropical waters. *Scomberesox saurus*, the only regional representative of the group, occasionally reaches subarctic waters in the Barents Sea. Two of the four scomberesocid fishes (*Cololabis adocetus* and *Somberesox sp.*) are dwarf species. Unlike the remaining species, these two apparently have limited swimming ability and drift freely with the current.

Scomberesox sp., currently being described by Carl Hubbs and Robert L. Wisner, occurs in part of the North Atlantic, the South Atlantic, and the Indian Ocean. It is, unfortunately, almost certain that some of the information given in the present account refers to the new species. Hartman's 62+ mm female "*Scomberesox saurus*" with well-developed (2.0 mm) eggs (Hartmann, 1970) is clearly *Scomberesox sp.*

Fishes of the family Scomberesocidae are distinguished by the following characteristics: a long, slender, and compressed body; prolonged jaws, forming a slender beak; feeble teeth; long, numerous, and slender gill rakers; small, thin, and deciduous scales; dorsal, anal, and pelvic fins far back on the body; and dorsal and anal fins followed by 4-7 detached finlets.

Scomberesocid fishes produce somewhat oval, moderately large eggs that lack oil globules and may be equipped with either tufts of long attachment filaments (as in *Cololabis saira*) or numerous short chorionic bristles (as in *Scomberesox saurus*).

In larvae of the regional species (*S. saurus*) the anus is at a point approximately three-fifths to seven-tenths the distance to the tail tip. A long preanal finfold, pectoral fin rays, and bright blue pigment are evident at the time of hatching.

Scomberesox saurus (Walbaum), Atlantic saury**ADULTS**

D. 9–12 + 5–6 finlets; ^{12,49} A. 12–13 ¹⁶ + 5 ⁵³–7 finlets; ¹⁰ C. 3 + 14–15 + 4, ⁵³ 12–13 branched rays; ²² P. 11 ⁵³–14; V. 6; ^{8,12} lateral scale rows 110 ¹³–ca. 132, ⁵⁷ predorsal scales 73–81; ^{26,70} total vertebrae 64 ⁶–68; ⁶⁸ preanal vertebrae 39–42; ⁶ gill rakers on first arch 5–6 ⁵⁷ + 39–51; ⁶⁸ branchiostegals 13. ⁵³

Proportions expressed as times in TL: Head 3.33–3.5, depth 9–13. ^{12,52,53}

Body elongate, compressed; ⁸ head long, broad above, narrow below, and tapering gradually to narrow beak; ^{33,53,60} lower jaw slightly longer than upper ⁸ (much longer in juveniles ⁴²); upper jaw thin, narrow. ⁵³ Teeth minute, ²⁸ in bands in jaw; ³⁰ lacking on vomer, palatines, and tongue. ¹² Scales small, deciduous. ⁸ Lateral line present, low on side. ¹⁰ Pelvics at mid-body; ²³ dorsal and anal fin origins at about latter third of body (RLW), dorsal origin usually over fifth ray of anal.

Pigmentation: Various described (and possibly varying with age and locality) as bright ultramarine blue, ⁵³ dark blue, ^{9,12} greenish, ³³ olive green, ¹⁰ olive brown, ^{13,60} or brownish above; ⁸ silvery white ⁹ or silvery with golden tinge below; a silvery lateral band as broad or nearly as broad as eye and almost at same level as eye; ^{8,60} lateral band with darker lower edge; ¹² tip of jaw sometimes red, sometimes black; ¹⁸ a dark green or blue spot at pectoral base; ^{10,23} iris silvery ⁵³ or silvery white. ⁵⁷ Fins variously described: All fins dark brown, ⁴¹ "light" ⁴⁹ or "pale"; ⁹ also upper fins dark, lower fins, including pectorals, yellowish, ¹² dorsal greenish, ^{10,23} caudal and upper finlets grayish blue. ⁵³

Maximum length: Ca. 762 mm. ^{11,15}

DISTRIBUTION AND ECOLOGY

Range: *Scomberesox saurus* occurs in two widely separated disjunct populations: one in the North Atlantic (and possibly divided into two discrete populations) and the other in a circumglobal band in the southern seas (in both of these major areas, waters nearest the equator are used for reproduction and those nearest the poles are used for foraging). In the North Atlantic from the Canary Islands in the east to Norway and Denmark (and rarely the White and Barents Sea as far as Novaya Zemlya), then to Iceland and Nova Scotia, south along the North American coast to latitudes of Bermuda; also in the Mediterranean, Adriatic, and Aegean seas. In the southwestern Atlantic north to Uruguay or Brazil (or to latitudes of 32° or 33° S) and in the eastern Atlantic north to 15° S latitude on the coast of Africa; also ap-

parently north to at least 10° S in the central Atlantic. In the Indian Ocean from southeastern Africa (ca. 30° S) to northwestern part of Australia, also western and southern Australia, Tasmania, Victoria, and New South Wales. In the Central Pacific northward to 25° S latitude; in the eastern Pacific north to ca. 6° S on coast of Peru. Southern limit in all oceans between 45° and 50° S latitude, or roughly at the 10–12 C summer isotherm. ^{4,38,39,55,67,68,69,71}

Area distribution: New Jersey; ⁵⁰ off Maryland; ³² mouth of Chesapeake Bay. ^{31,37,51}

Habitat and movements: Adults—a schooling, pelagic, or nektonic, migratory species ^{2,7,19,62,66} normally found in offshore waters at surface ^{8,15,54,56,58} but also recorded from bays, harbors, and the mouths of rivers. May ascend rivers to freshwater. ^{12,22,59} Frequently strand on beaches, ² sometimes by thousands (as in Massachusetts); ^{8,25} stranding also reported in England, ^{5,27} Scotland, ²⁴ Ireland, ²¹ and Norway. ¹⁷ Maximum depth, 30 m. ⁶⁷ Salinity range, fresh ¹² to full strength seawater. ⁷ Temperature range, 12 to 24 C (mostly at 15–19 C). ⁶⁶

Although Meek ³⁵ suggested a general inshore-offshore movement in this species, with spawning taking place in mid-ocean, recent evidence suggests a typical north-south migratory pattern. ^{2,36,66,67} Sauskan and Semenov ⁶⁷ state that, in the northwest Atlantic, *Scomberesox* moves northward in spring, arriving in New England from mid-June to October. Storer ²⁹ and Bean, ⁶¹ however, report that it generally arrives in Massachusetts in fall, primarily in October. Nichols and Breder ¹⁵ found it "inshore" in New York and southern New England from August to December, although Leim and Scott ¹⁰ report it occurring in Canada only when the water is warmest. Off Maryland in August and September. ³² Zilanov and Bogdanov ⁶⁶ comment that the northeast Atlantic population is generally restricted to the area below the 40th parallel during the winter, but moves northward to feed in spring and summer, reaching the 60th parallel in August and September. Saemundsson ³⁶ found that populations in northern Europe retire in winter to warm waters around the Azores, Madeira, the west coast of the Iberian Peninsula, or "further south"; and in spring move in large shoals to the North Sea, Denmark, Norway, Sweden, the Faroes, and Iceland. (Individuals moving south through the North Sea in early autumn frequently strand, possibly as a result of low temperatures.) ² Sauskan and Semenov ⁶⁷ noted that in September and November, at the start of cooling, there is a northern movement from the Azores to Madeira and the Canary Islands. This movement is associated with spawning, during which time feeding apparently ceases. The species is essentially absent from the Azores from December

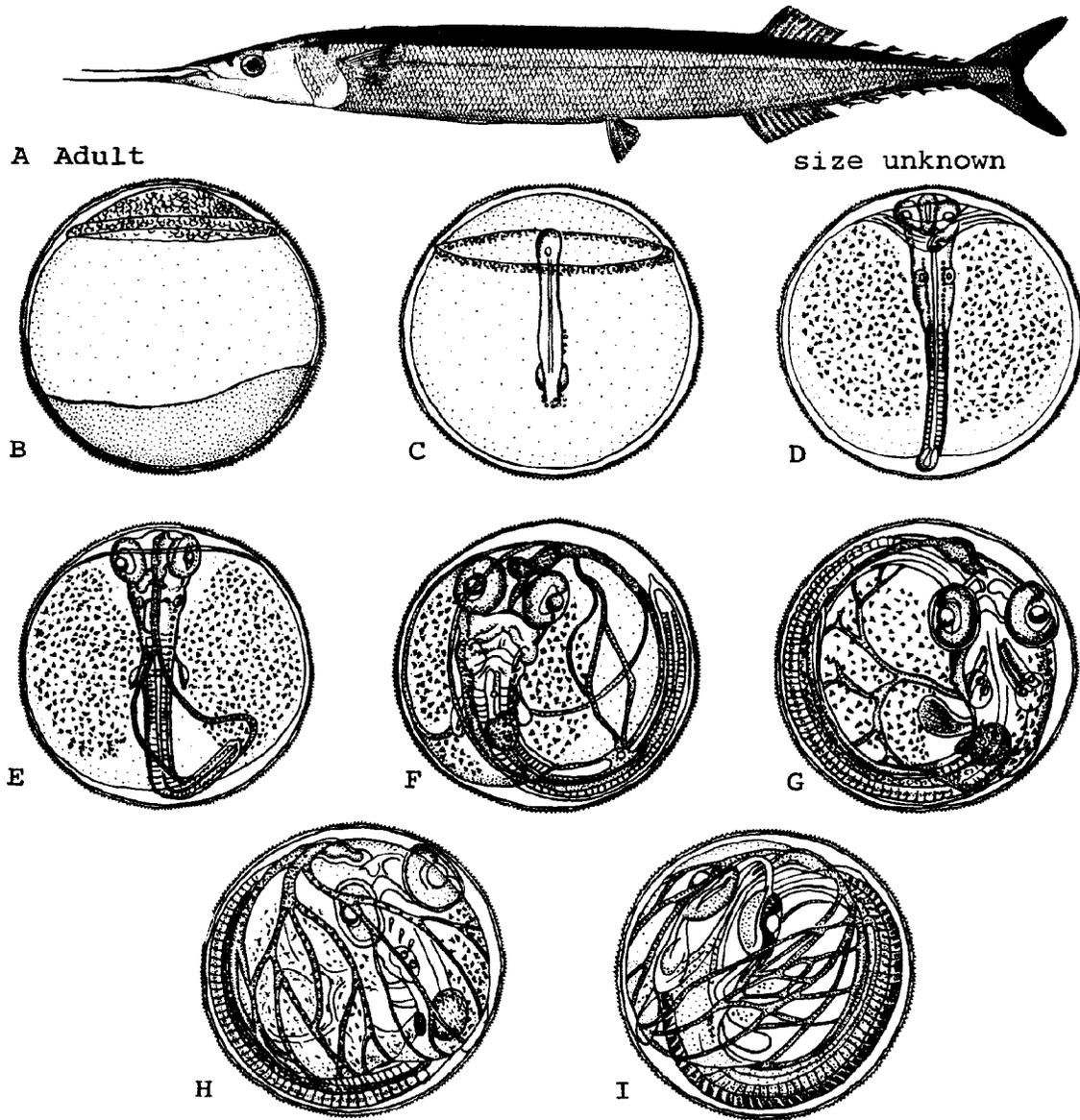


Fig. 29. *Scomberesox saurus*, Atlantic saury. A. Adult, size unknown. B. Blastoderm extending over yolk. C. Embryo formed, optic vesicles evident. D. Auditory vesicles, somites formed, pigment on yolk and in discrete rows on body. E. Vitelline vessels, otoliths evident. F. Tail free, pectoral fins evident. G, H. Vitelline circulation established. I. Advanced embryo, pigment in eye and greatly increased on body. (A, Coode, G. B., 1884: pl. 181. B-I, Sanzo, L., 1940: figs. 1-8, Deborah C. Kennedy, delineator.)

to April. In April, when temperatures rise, some individuals return northward in search of food while others apparently die after spawning.

There are both seasonal and diurnal changes in depth. In summer at or near the surface, during autumn deeper down,¹² specimens larger than 20 mm (thus including juvenile stages) in the pleustral zone (defined as the upper 150 mm) only at night.^{1,64}

Larvae—recorded both from oceanic waters⁶⁴ and in bays (as at Naples).⁴⁴ In the southeastern Pacific, larvae occur over a wide expanse of sea: thus over a north-south distance of at least 3447 km off South America.⁶⁵ Specimens 6 to 29 mm long remain within the first 100 mm of the surface, and do not make diurnal vertical migrations.⁶⁴ In the northeast Atlantic, larvae (and young) produced during early part of season drift in

northeasterly direction carried by waters flowing just within the eastern limits of the North Atlantic Current. Later produced larvae drift east and then southeast where anticyclonic current delivers them to the Azores.⁶⁶ Recorded salinity range 35.58–36.18 ppt, recorded temperature range 16.8–25.7 C.⁷⁰

Juveniles—pelagic,²⁰ found in schools⁷⁰ at or near surface.^{15,16,20} Lütken outlined the following areas of greatest abundance of juveniles: Atlantic Ocean, 11° 30' to 48° 0' N latitude (and between 9° and 40° W longitude) and 12° 0' to 40° 32' latitude (and between 52° W and 16° 30' E longitude); in the Indian Ocean 27° S to 38° 20' S latitude (and between 24° 30' E and 101° 40' E longitude).¹² Juveniles 50–80 mm long preferred temperatures of 14–16 C, while larger juveniles preferred 10–16 C.⁶⁹

In the western Atlantic float with Gulf Stream, sometimes toward Europe. In eastern Atlantic transported mainly by Canary Current.^{17,67} Specimens larger than 29 mm make vertical migrations (maximum depth unknown) and are in the pleustal zone (defined as the upper 150 mm) only at night.⁶⁴

SPAWNING

Location: A number of authors have stated that spawning takes place in open ocean or at "mid-ocean,"^{15,22,33,35,54} but actual spawning areas are probably more restricted (JDH), and spawning has been noted in coastal waters only 32 to 64 km offshore¹⁴ as well as in straits (as at Messina).⁴⁶ Breder, writing presumably of the western Atlantic population, noted spawning between 11° and 40° N latitude.¹¹ In the eastern Atlantic Zilanov and Bogdanov found that spawning occurred between 34° 0' and 46° 30' N latitude but was primarily restricted to south of 40° N latitude.⁶⁶ In the same area Sauskan and Semenov reported that the principal spawning area was in the vicinity of the Canary Islands between 28° and 35° N latitude and 13° and 25° W longitude.⁶⁷ Spawning probably takes place at the surface.^{22,54}

Season: Generally eggs, larvae and spawning adults observed in all months but July, and may actually spawn throughout year.⁷¹ In eastern Atlantic specimens with developed gonads observed September through December and March through June;⁶⁰ smallest Atlantic larvae (6.0 mm) collected in April, June or July.⁶⁴ Eggs in straits of Messina, Italy, in November and December;⁴⁶ also, eggs and ripe adults from October to December at Naples, Italy;⁴⁷ in South Africa eggs collected in June, July and September.¹⁴

Temperature: Ripe adults encountered at 17 to 19 C,⁶⁶ eggs and larvae at 11.93⁶⁵ to 23.7 C.⁷¹

Fecundity: Unknown. Zilanov and Bogdanov point out that ovarian eggs develop asynchronously.⁶⁶

EGGS

Location: Planktonic,⁵¹ pelagic,^{6,14} float at surface;⁴⁴ sometimes far from land,³³ as in Sargasso Sea.^{35,44}

Ovarian eggs: Capsule transparent; surface smooth, unmodified; no sculpturing or filaments^{2,6} (Kolliker⁴⁸ described apparently ripe eggs as having "small nipples or cones on the capsule," but his material was probably misidentified); yolk yellowish,⁶ granulated,⁷¹ and with numerous tiny oil globules at surface;⁶ micropyle single;⁴⁷ diameter variously described as 1.75^{2,6}–3.2 mm,⁷¹ and 2.7–3.1 mm.⁶⁶

Fertilized eggs: Eggs not truly spherical, greatest diameter 2.15⁶⁵–2.76 mm⁶ (range of average diameters 2.32–2.52 mm).⁶⁵ Chorion somewhat opaque and with distinct short rigid hair-like darkly pigmented bristles^{6,13,40,43,48} which may be distributed uniformly⁴⁷ or in discrete groups;^{40,43} also described as having very large pore canals.⁴⁷ Yolk clear, nonvesicular and without oil globules.¹⁴

EGG DEVELOPMENT

Development at unspecified temperature (Sanzo series):⁴⁶

- At time of collection—Blastoderm 1/6 around yolk.
- Ca. 24 hours after collection—Blastoderm 3/4 around yolk, optic lobes, Kupffer's vesicle formed.
- Ca. 48 hours after collection—Blastopore closed, black pigment in definite rows on body.
- Ca. 72 hours after collection—Tail-tip free; lenses forming; 31–32 somites; pigment generally increased; 2 rows of pigment on body beginning a little in front of auditory vesicle.
- Ca. 120 hours after collection—Vitelline vessels, pectoral buds evident; otoliths formed.
- Ca. 168 hours after collection—Circulation and movement established, liver formed, branchial arches forming, pectorals much larger, ca. 24 caudal somites.
- Ca. 264 hours after collection—Tail extended to head region; mouth open; branchial arches well-formed; pectorals large, movable; gas bladder formed.
- Ca. 288 hours after collection—Pigment on yolk reduced to small dots; pigment concentrated on tail, dorsally and dorsolaterally in two lines; pigment less developed, irregular below lateral line.⁴⁶

Development at unspecified temperature (Gilchrist series):

- At time of collection—Tail free, equal to 1/2 circumference of egg; a few dark spots scattered sparsely over body and a few stellate chromatophores on yolk immediately adjacent to body of embryo; circulation estab-

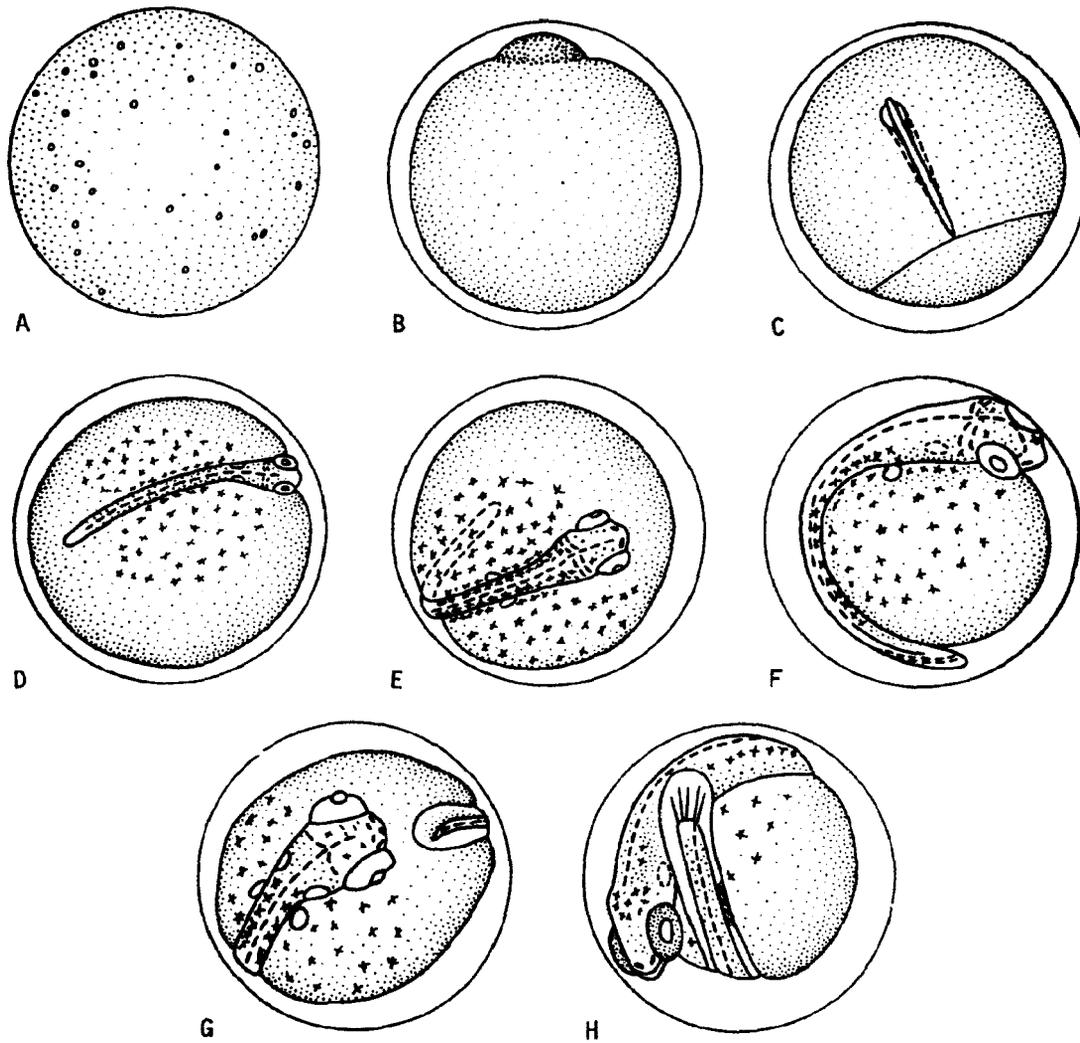


Fig. 30. *Scomberesox saurus*, Atlantic saury. A. Unfertilized egg. B. Blastodisc formed. C. Early embryo. D. Eyes, otocysts forming, pigment on yolk. E. Pigment formed on body. F. Tail free. G. Embryo nearly around yolk. H. Embryo completely around yolk, eyes pigmented. (A-H, Nesterov, A. A., and T. A. Shiganova, 1976: fig. 2.)

lished.

24 hours after collection—Pectoral fins distinct.

72 hours after collection—Entire surface of yolk with network of vessels.

384 hours after collection—Remain more or less as in previous stage.

2 days before hatching—Pectoral fins constantly in motion; orbits dark blue; dark blue pigment on body near pectoral fin, and small blue flecks along length of body.⁷¹

Development at unspecified temperature (Nesterov and Shiganova series):⁷¹

Embryo over 1/4 yolk surface—Optic vesicles

formed, no pigment on yolk or body.

Embryo over 1/3 yolk surface—Lenses formed in optic vesicles, auditory capsules and cerebral vesicles forming. Pigment developed on occiput, most of body except posterior-most area, and on yolk along body.

Embryo over 1/2 yolk surface—Pectoral buds formed; pigment intensified; two rows of melanophores along body, but these not reaching caudal region.

Embryo over 2/3 yolk surface—Eyes ellipsoidal, pectoral fins larger, tail free from yolk, pigment essentially as in previous stage.

Embryo around most of circumference of yolk—In

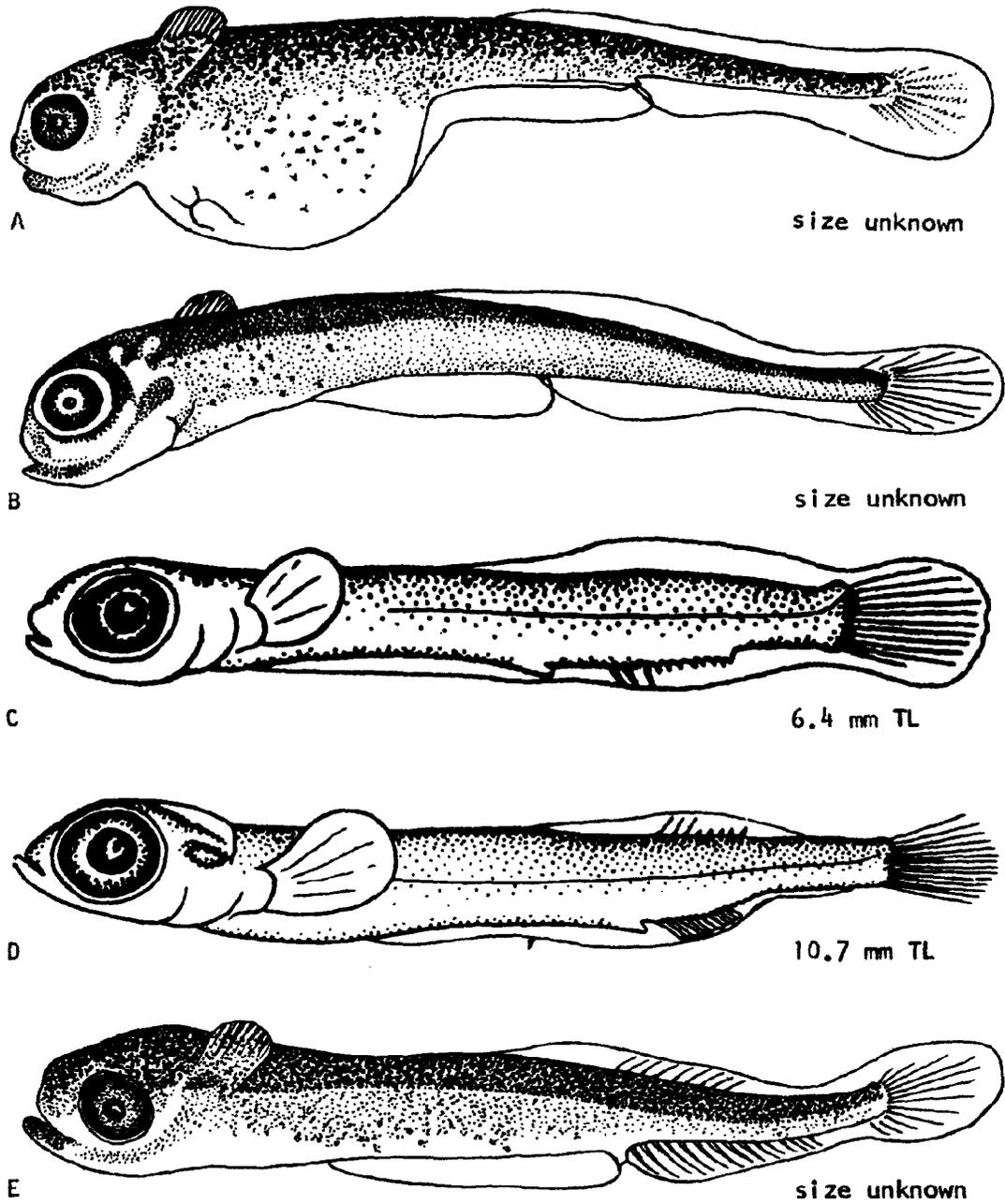


Fig. 31. *Scomberesox saurus*, Atlantic saury. A. Yolk-sac larva, size unknown. B. Larva, size unknown. C. Larva, 6.4 mm TL, anal fin forming. D. Larva, 10.7 mm TL, dorsal fin forming. E. Larva, size unknown. (A, B, E, Gilchrist, J. D. F., 1904: pl. 10, A. J. Lippson, delineator. C, D, Nesterov, A. A., and T. A. Shiganova, 1976: fig. 4.)

region of caudal fin a thickening of mesenchyme developed, rows of body pigment extended to end of body.

Tail overlapping head, prehatching embryo—Mouth opening noticeable, caudal rays forming, thickened mesenchyme developed in area of future anal, yolk mass noticeably decreased, eye pigmented.

Note: There is apparently some geographic variation in pigment development. In saury from the North Atlantic pigment is evident on the head, body, and yolk when the embryo encompasses 1/3 of the yolk; in the same stage in Pacific saury pigment is not developed.⁷¹

Incubation period: Ca. 2 weeks from time embryo extends 1/6 around yolk at unspecified temperature;⁴⁶ but apparently much longer in other rearing experiment (at least 18 days accounted for from time tail equals 1/2 circumference of egg).¹⁵

YOLK-SAC LARVAE

Known hatchlings with yolk sacs, 8.5 mm,¹⁵ but specimens of unknown age and lacking yolk as small as 6.0 mm. Maximum length reported 8.0–9.5 mm⁴⁶ (although the figure of the largest of these specimens appears to lack yolk and is regarded as a larva in the present study, JDH).

At hatching yolk sac (if present) oval;¹⁵ head blunt;⁴⁶ mouth well-developed, but lower jaw apparently not extended beyond upper; pectoral and caudal fins with incipient rays; dorsal finfold extended forward ca. 1/3 distance from anus to tip of snout.¹⁵

Pigmentation: At hatching deep blue except fins and yolk, with pigment much denser dorsally.¹⁵

LARVAE

Size range described, 6.0⁶⁴–26.0 mm.⁴⁷

At 9.5 mm eye diameter equal to twice preorbital space, anus 3/5 along TL.⁴⁷ Proportions as percent body length, preanal distance 67.0–71.0, head 24.6–27.5.⁷¹

Body slender, elongate, almost cylindrical at 9.5 mm;⁴⁷ fusiform at 10.7 mm⁷¹ increased in depth and appearing flattened at ca. 17 mm. Head large depressed at 9.5 mm.⁴⁷ Lower jaw initially variable, beyond upper jaw in some hatchlings lacking yolk,¹⁴ shorter than upper jaw in other individuals up to 9.5 mm long.⁴⁶ Jaws barely elongate 15–17 mm;⁵⁴ lower jaw considerably longer than upper at 20.5–21.6 mm.⁷¹ During larval stage gape to or near to anterior margin of eye; by ca. 20 mm not reaching eye. At 6.4 mm eyes ellipsoidal; round at 20.5–21.6 mm.⁷¹ Teeth forming at 9.5 mm.⁴⁶ At 23–24 mm

bottom of nasal fossa with fleshy stripe which ultimately divides nasal opening.⁴⁷ Dorsal finfold lost at 11.5 mm, preanal finfold at 14⁴⁵–ca. 25 mm.^{46,47} Median fin ray formation variable: In one specimen, anal rays developing at 6.4 mm.⁷¹ In 9.5 mm specimen, long incipient rays in dorsal, anal and caudal,^{46,47} and in other individuals no median fin rays at 15–17 mm.⁵⁴ Caudal rounded, symmetrical at 9.5 mm, straight or slightly concave at 11.5–12.0 mm, definitely bilobed at ca. 20 mm.^{45,47} Finlets first evident behind dorsal and anal at 15.0⁴²–18.0 mm.⁵⁶ Pectorals oblong or rounded at 9.5 mm,^{46,47} at 11.5 mm relatively larger, more pointed than in earlier stages,⁴⁵ with definite rays at 11.5 mm.⁴⁷ Pectorals with upper rays noticeably longer than lower at 20.5–21.6 mm.⁷¹ Pelvics first evident at 14⁴⁵–ca. 17 mm, rays forming at ca. 20 mm.⁴⁷

Pigmentation: Larvae generally described as having a broad dark blue band along back; remainder of body, below the band, silvery tinged with blue.¹⁴ At 6.4 mm, brown pigment over entire body, upper part of body and head strongly colored, isolated melanophores scattered along sides of head and on jaws; large pigment cells on occiput and base of caudal.⁷¹ At 9.5 mm eye with silvery reflections, body with numerous black spots.⁴⁶ At 10.7 mm a distinct accumulation of pigment at pectoral base.⁷¹ At ca. 17.0 mm sides and belly with definite silver tones. At 20.5–21.6 mm intensity of pigment on occipital division of brain decreased. At ca. 25.0 mm a prominent spot at base of pectoral. In preserved specimens whole body with scattered small chromatophores which are denser dorsally.⁴⁷

JUVENILES

Minimum length described, 24.8 mm.⁷¹

At 140–150 mm head (from apex of mandible) 4/5 times in TL. Tip of mandible to anterior margin of eye, 1/2 length of head.⁴⁷

Proportions as percent body length in specimens 65–84 mm long: Head 23.2–25.0, preanal distance 66.3–76.0, prepelvic distance 48.5–64.3, greatest depth 12.3–13.8, least depth 2.6–3.1, eye diameter 3.8–4.9.⁷⁰

Both jaws begin to develop noticeably at 38¹⁵–ca. 40 mm^{23,28} or 50 mm;⁴² at 50–60 mm lower jaw longer than upper by eye diameter, upper jaw short, pointed; maximum difference in jaw lengths occurs at 90–100 mm;⁵⁴ at 100–150 mm resemble jaws of halfbeaks;²⁸ beak adult-like at ca. 160 mm¹⁷ (although one author states that jaws reach full development when fish are ca. 100–150 mm long¹⁰).

Caudal forked at 24.8 mm;⁷¹ lower lobe of caudal longer than upper at 48 mm;⁴⁵ in some specimens pelvic “forming” at 30 mm;⁵⁴ finlets still fused to each other at 40–50 mm.^{44,45,56} At 47 mm body covered with scales.⁷¹ Sexes

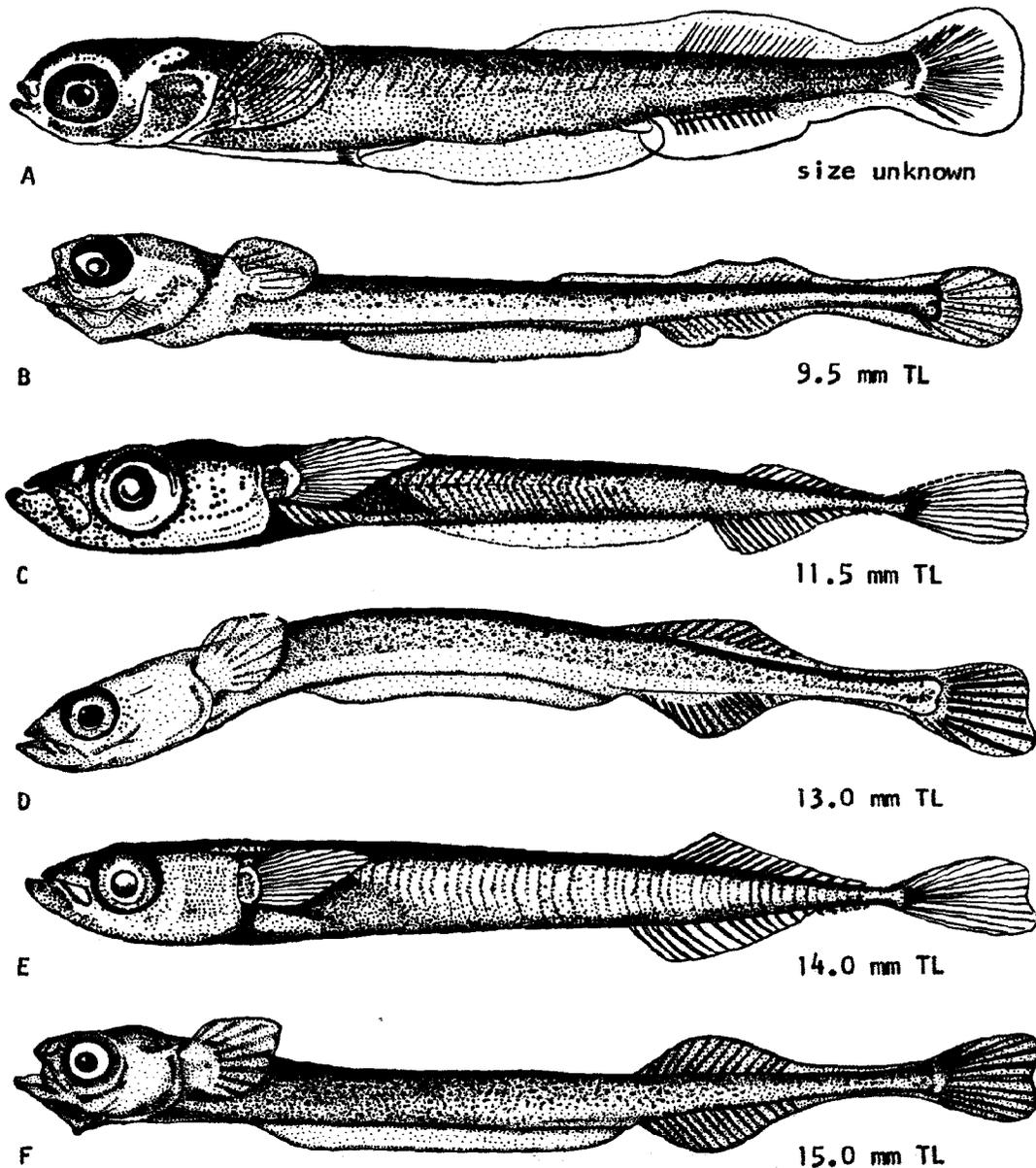


Fig. 32. *Scomberesox saurus*, Atlantic saury. A. Larva, size unknown, pigment increased on body and invading finfold. B. Larva, 9.5 mm TL, body conspicuously more slender. (Note that specimen is smaller but more advanced morphologically than last specimen for which length is known.) C. Larva, 11.5 mm TL, finfold essentially obliterated except preanally, pectoral fin pointed, tail slightly emarginate. D. Larva, 13.0 mm TL, dorsal and anal finlets barely evident, caudal fin definitely forked. E. Larva, 14.0 mm TL, lacking both preanal finfold and ventral buds. F. Larva, 15.0 mm TL, preanal finfold reduced. (A, Sanzo, L., 1940: fig. 9, Deborah C. Kennedy, delineator. B, D, F, D'Ancona, U., 1931: pls. 8, 9, Deborah C. Kennedy, delineator. C, E, Roule, L., and F. Angel, 1930: figs. 101, 102, Deborah C. Kennedy, delineator.)

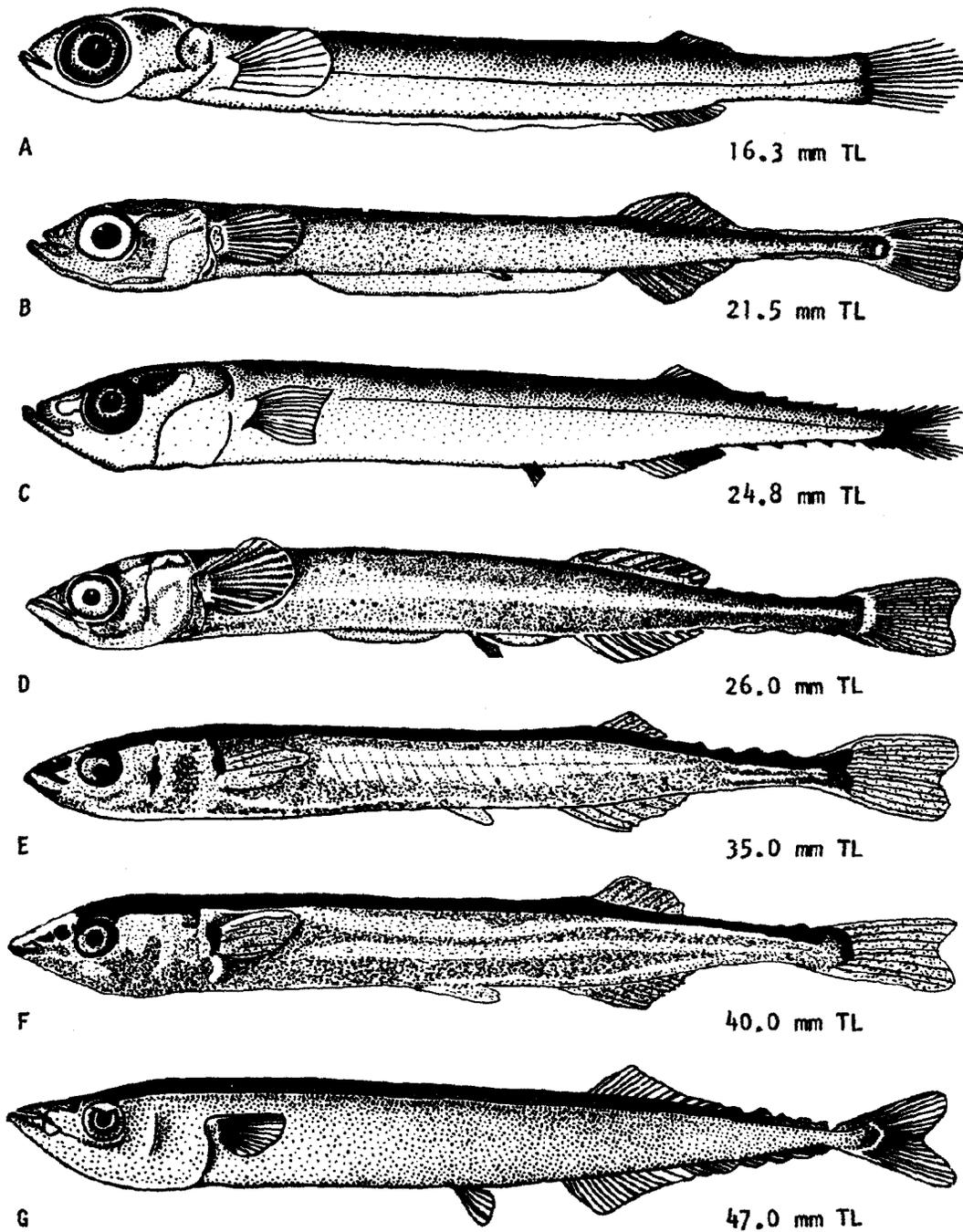


Fig. 33. *Scomberesox saurus*, Atlantic saury. A. Larva, 16.3 mm TL. B. Larva, 21.5 mm TL, ventral buds evident. C. Larva, 24.8 mm TL. D. Larva, 26.0 mm TL, preanal finfold greatly reduced and divided into anterior and posterior sections. E. Juvenile, 35.0 mm TL, dorsal surface bright blue, otherwise silvery white, a row of bluish dots ventrally between throat and ventral fins. F. Juvenile, 40.0 mm TL, mouth beginning to elongate. G. Juvenile, 47.0 mm TL. (A, C, G, Nesterov, A. A., and T. A. Shiganova, 1976: fig. 4. B, D, D'Ancona, U., 1931: pls. 8, 9, Deborah C. Kennedy, delineator. E, F, D'Ancona, U., 1931: pls. 8, 9, Tamiko Karr, delineator.)

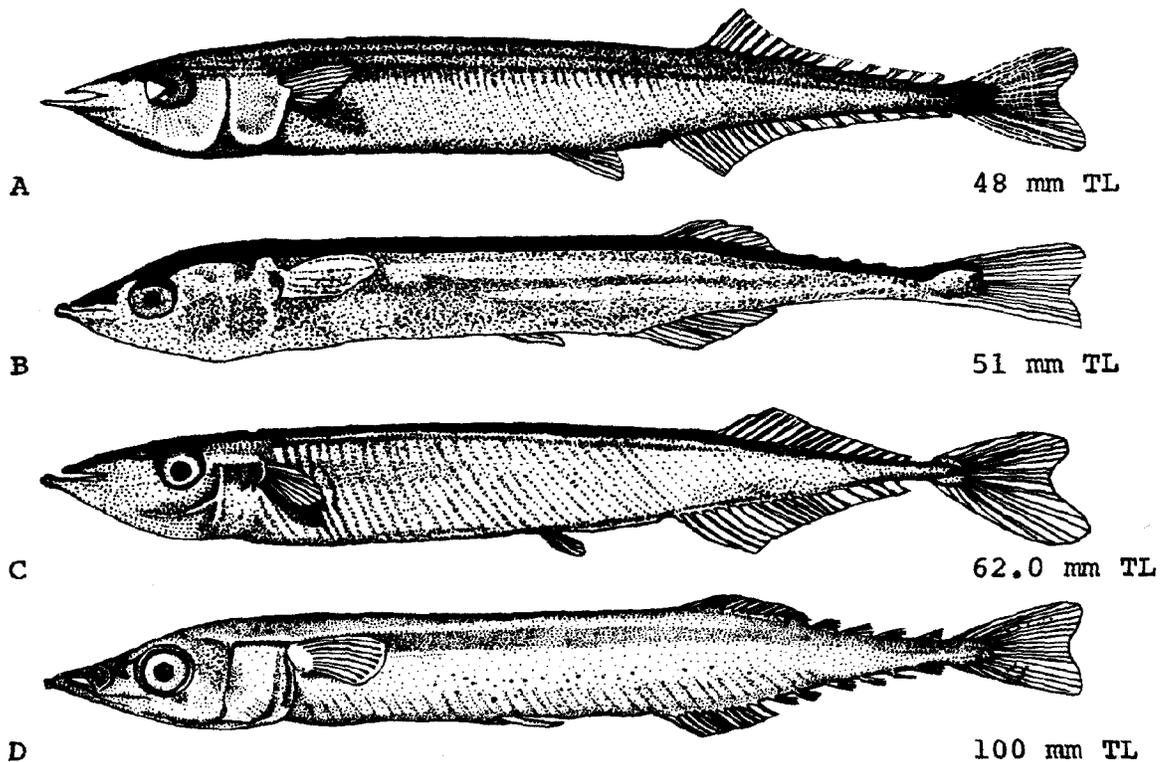


Fig. 34. *Scomberesox saurus*, Atlantic saury. A. Juvenile, 48 mm TL, mandible elongate, remnant of preanal finfold evident behind pelvics. B. Juvenile, 51 mm TL. C. Juvenile, 62.0 mm TL. D. Juveniles, 100 mm TL, punctations evident on ventral part of body and caudal fin, finlets well-developed. (A, Roule, L., and F. Angel, 1930: fig. 103, Deborah C. Kennedy, delineator. B, D'Ancona, U., 1931: pl. 9, Tamiko Karr, delineator. C, Murray, J., and J. Hjort, 1912: fig. 541, Deborah C. Kennedy, delineator. D, D'Ancona, U., 1931: pl. 8, Deborah C. Kennedy, delineator.)

distinguishable microscopically at 80–100 mm.⁶⁸

Pigmentation: "Young" generally described as having dark blue backs and silvery sides;²³ lateral pigment mirror-like.³⁴ At 24.8 mm dorsal, anal, pectorals, and pelvics transparent. At 47.0 mm upper part of head and dorsum black with a blue hue; sides of body and abdomen light cinnamon-brown; dorsal and caudal fins pigmented.⁷¹

AGE AND SIZE AT MATURITY

Mature at 2 years;⁶⁷ some males mature at 230 mm, all mature 320 mm; some females at 230 mm, all at 340 mm.⁶⁶

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Ablennes hians
Strongylura marina
Tylosurus acus
Tylosurus crocodilus

needlefishes
Belonidae

FAMILY BELONIDAE

The family Belonidae occurs in tropical and temperate waters throughout the world. Members of the family are found in marine, estuarine, and freshwater, but are primarily surface-dwelling, schooling, marine and estuarine fishes. Needlefishes have slender, elongate bodies; fairly large, essentially opposite, posteriorly placed dorsal and anal fins; and relatively small pectoral and pelvic fins. Both jaws are conspicuously produced (except in two South American species in which the upper jaw is short), and are equipped with numerous sharp teeth. Most species are green or blue above with silvery lateral and ventral surfaces. Nine genera are currently recognized, and recent estimates of the numbers of species vary from 26 to approximately 60.

Needlefishes deposit large demersal eggs with well-developed chorionic filaments by which they are attached to plants or other objects in the water. Oil globules are absent in most species, but may be present as very tiny yolk inclusions in others. According to Breder (1959) eggs of *Strongylura notata* may be stranded and become semidesiccated. This may result in delayed hatching similar to that which occurs in the eggs of certain cyprinodontid fishes.

Ryder (1882) described the chorionic filaments of *Strongylura marina* eggs as being "looped and twisted together in all directions" and his illustration shows single filaments randomly distributed over the egg. Breder (1948) stated that the eggs "are provided with tufts of long threads." Foster (1974) described the chorion as having two discrete bunches of filaments at opposite poles of the egg. He concluded that the eggs described and figured by Ryder (1882) were those of *Tylosurus acus*, not *Strongylura marina*. In *Tylosurus acus*, however, the filaments are not single (as indicated in Ryder's figure) but are in discrete groups of two or three. Needlefish eggs reared at Chesapeake Biological Laboratory produced typical *Strongylura marina* larvae. These eggs, unfortunately, were not well described; however, unpublished sketches suggest that the filaments were single and randomly distributed as in Ryder's figure. Either some of the eggs used in the various descriptions were, in fact, misidentified, or the distribution of filaments on the egg of *Strongylura marina* is remarkably variable.

In larvae of the regional needlefishes the body is elongate and slightly tapered; the mouth is terminal; the anus is located roughly two-thirds the distance to the tip of the tail; there is a long preanal finfold; the dorsal and anal fins develop far back on the body; the urostyle is oblique at or near the time of hatching; and pigment is developed over the entire body even in the earliest stages, and not limited to discrete rows as in larval hemiramphids.

A conspicuous but transitory melanistic lobe develops in the posterior half of the dorsal fin in juveniles of *Tylosurus* and *Ablennes*. This structure never occurs in *Strongylura*. In *Tylosurus*, lappets appear on the lower jaw of developing juveniles, but these are lost in later development.

Key to belonid eggs of the Mid-Atlantic Bight.

- 1A. Eggs described 2
- 1B. Eggs undescribed *Ablennes hians*
- 2A. No oil globules in yolk 3
- 2B. Minute oil globules in yolk; chorionic filaments single, about equal to egg diameter; diameter 4.0-4.1 mm *Tylosurus crocodilus*
- 3A. Chorionic filaments in clusters of 2 or 3, conspicuously longer than diameter of egg; egg diameter 3.2-4.0 mm *Tylosurus acus*
- 3B. Chorionic filaments single, randomly distributed, generally less than diameter of egg; egg diameter 3.5-3.6 mm *Strongylura marina*

Key to yolk-sac larvae of Mid-Atlantic Bight belonid fishes.

- 1A. Yolk-sac larvae described 2
- 1B. Yolk-sac larvae undescribed *Ablennes hians*
- 2A. Pigment on dorsal and anal fins at ca. 10.0 mm 3
- 2B. No pigment on dorsal and anal fins at sizes less than 14.4 mm, 69-77 vertebrae *Strongylura marina*
- 3A. Pigment on body diffuse, melanophores widely separated; pigment developed only on dorsal and anal bases; in western Atlantic population, vertebrae 79-86 *Tylosurus crocodilus*
- 3B. Pigment on body dense, melanophores tending to be confluent; pigment extended almost to edge of dorsal fin; in western Atlantic population, vertebrae 90-95 *Tylosurus acus*

Key to larvae of belonid fishes of the Mid-Atlantic Bight.

- 1A. Lateral pigment in two distinct bands above and below lateral line 2
- 1B. Lateral pigment more or less evenly distributed 3
- 2A. Lateral pigment concentrated below mid-lateral line, dorsal fin with 14-17 rays, anal with 16-20 rays, 69-77 vertebrae *Strongylura marina*
- 2B. Large stellate melanophores below mid-lateral line, punctate melanophores above; dorsal with 23-26 rays, anal with 24-28 rays (in western Atlantic populations); 93-97 vertebrae; dorsal fin with melanistic lobe (but note early larvae not described) *Ablennes hians*
- 3A. Vertebrae 90-95; pigment diffuse, melanophores widely spaced; dorsal fin darkly pigmented only in advanced larvae *Tylosurus crocodilus*
- 3B. Vertebrae 79-86; pigment dense, melanophores crowded; dorsal darkly pigmented throughout stage *Tylosurus acus*

Ablennes hians (Valenciennes), Flat needlefish**ADULTS**

D. 22⁵¹–27⁹ (in western Atlantic 23–26); A. 24–29 (in western Atlantic 24–28); P. 13–15⁵¹ (a report of 12²⁹ is questioned, JDH); V. 6;^{4,40} vertebrae 82–97 (in western Atlantic 93–97);⁵¹ scales along side to caudal base 410¹⁹–ca. 520;⁵ predorsal scales 360⁴¹–430;¹⁰ scales above lateral line 25.¹⁰

Proportions expressed as times in TL: Head 3.0–3.8, depth 15.9–16.5.¹⁴ Proportions as percent of SL: Head width 2.6–3.5.⁴

Body very elongate, strongly compressed,^{4,46} ribbon-like; sides flattened,²⁹ nearly straight and vertical;¹⁴ head compressed,⁴ flattened on top, narrowly constricted below,²⁶ naked except on occiput and cheeks; top of head with broad, shallow, longitudinal groove;^{30,42} preopercular

bone porous.⁵¹ Maxilla arched strongly upward;¹⁵ jaws incapable of closing basally;^{36,52} teeth in jaws rather small, in narrow bands, the inner ones enlarged, round, and sharply pointed.^{14,43} Gill rakers and pseudobranchiae absent.^{6,29} Scales minute,^{11,35} narrowly imbricated.³⁶ Lateral line ventrad,²⁹ on edge of abdomen. Dorsal fin high, acutely falcate,⁵² the anterior lobe notably elevated;⁴⁵ dorsal fin origin opposite anal fin origin;⁴⁸ caudal fin deeply forked; pectoral fin falcate;¹⁶ base of pelvic fin nearer head than caudal fin.⁴⁸

Pigmentation: Back brownish,^{36,46} bluish,⁴⁶ or greenish^{8,43} with bluish green reflections;^{7,46} lower sides and abdomen bright silvery,^{7,8} white,⁴⁶ or pearly,¹⁹ with ventral pigment beginning abruptly.⁵² Snout green^{7,37} or tipped with red;¹⁸ inside of mouth scarlet (Australian population);⁵¹ iris silvery white.¹² A narrow dark green verte-

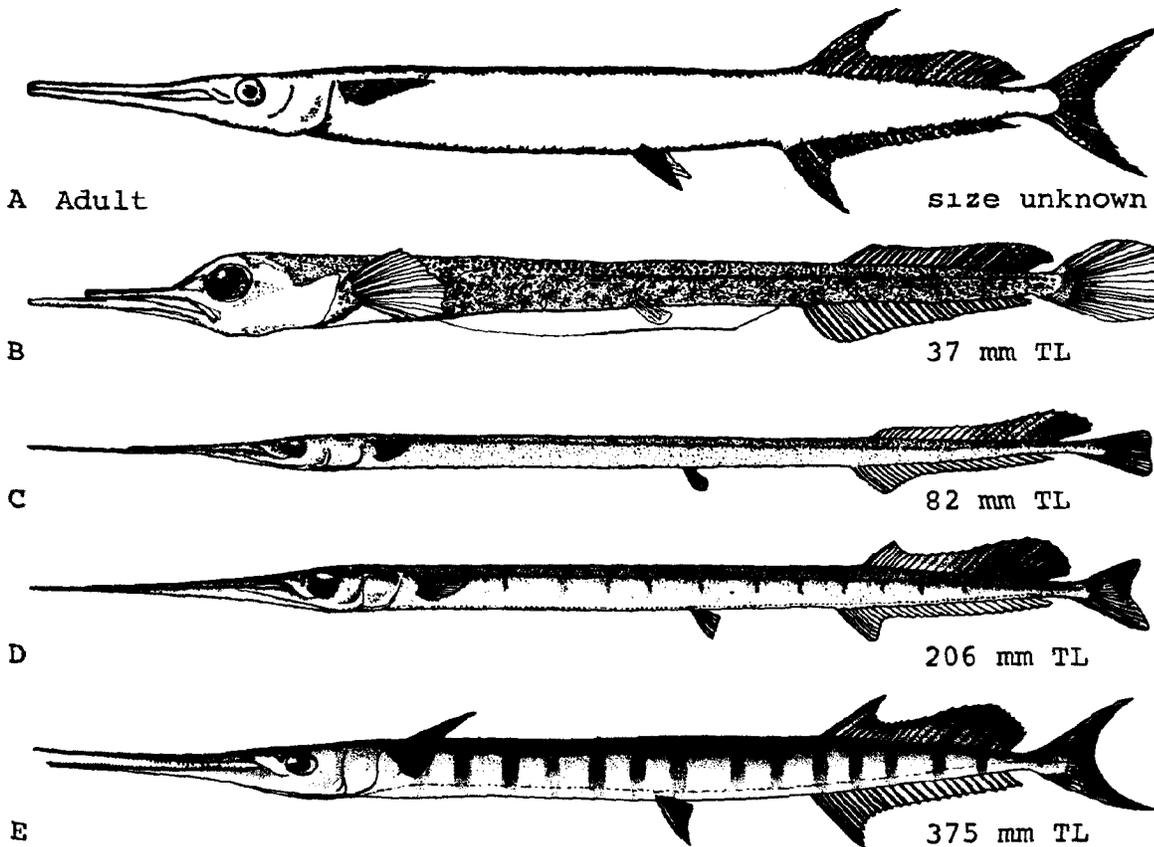


Fig. 35. *Ablennes hians*, Flat needlefish. A. Adult, size unknown. B. Larva, 37 mm TL. C. Juvenile, 82 mm TL. D. Juvenile, 206 mm TL. E. Juvenile, 375 mm TL. (A, Bigelow, H. B., and W. C. Schroeder, 1953: fig. 80. B, Original drawing, Nancy S. Smith. C, D, Parin, N. V., 1963: fig. 17. E, Poll, M., 1953: fig. 68.)

bral stripe from occiput to dorsal fin, below this a dark sea green band extending to tail.⁴⁶ Sometimes plain silvery,¹⁴ otherwise marked with 3¹⁹–15 black or blue-black quadrate bars of various sizes on sides, confined, at least in some specimens, to caudad section of body,^{19,33,52} or with a pale bluish band along edge of dark color and on it 12 or more dark or dusky blotches;⁴¹ sometimes with indistinct sooty or blue crossbars on back.⁷ Dorsal fin described as greenish with rusty anterior edge,⁴⁶ with rays black-tipped,⁷ or wholly black;⁴³ posterior lobe of dorsal fin melanistic throughout life;⁵¹ anal fin yellowish¹⁹ or dark greenish with rusty anterior edge;⁴⁶ caudal fin grayish⁷ with upper and lower edges rusty red, or with tips nearly black;⁴³ pelvic fins yellowish,¹⁹ or greenish black with rusty red anterior edge.⁴⁶ Also described as having all fins pale to dark brown.^{36,37}

Maximum length: 1800 mm.³⁸

DISTRIBUTION AND ECOLOGY

Range: Circumtropical;^{32,49} both sides of the Atlantic Ocean,⁹ throughout the Pacific Ocean^{24,28} as far north as Japan, the Indian Ocean, and the Red Sea;⁹ in the eastern Atlantic from Cape Verde Islands and Dakar through the Gulf of Guinea to the Congo and Moçamedes, southern Angola;⁵¹ in the western Atlantic from Massachusetts^{14,17} and Bermuda to San Salvador, Bahia, Brazil; widespread in the Gulf of Mexico.^{3,20,45,53}

Area distribution: Coastal waters of New Jersey,^{24,26,50} Delaware,²¹ and Virginia;⁸ north in Chesapeake Bay to vicinity of Potomac River.¹³

Habitat and movements: Adults—a pelagic species³⁸ found in water up to 3770 m deep;⁴² also recorded inshore,^{25,27,32} particularly at night;³⁴ maximum depth 17 m.³¹ Apparently move northward or shoreward during

summer in western North Atlantic, recorded from coastal waters of New Jersey in June and July.²⁶

Larvae—no information.

Juveniles—a “quite young” specimen from Beaufort Harbor, North Carolina.¹⁷

SPAWNING

Location: Probably offshore.⁴

Season: Probably in spring (a specimen from North Carolina had ripe roe in May).¹⁴

Fecundity: No information.

EGGS

Ripe ovarian eggs. Diameter ca. 3.0 m.¹⁴

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

JUVENILES

Minimum size described: 37.0 mm TL (NSS).

At 43.0 mm SL first gill arch with minute tubercles.⁴ At 50.0 mm or slightly larger, tubercles of first gill no longer evident.²² At 116–131 mm upper jaw short, lower jaw elongate.³⁹

At ca. 56.5 mm SL upper jaw ca. 48 percent of lower jaw;

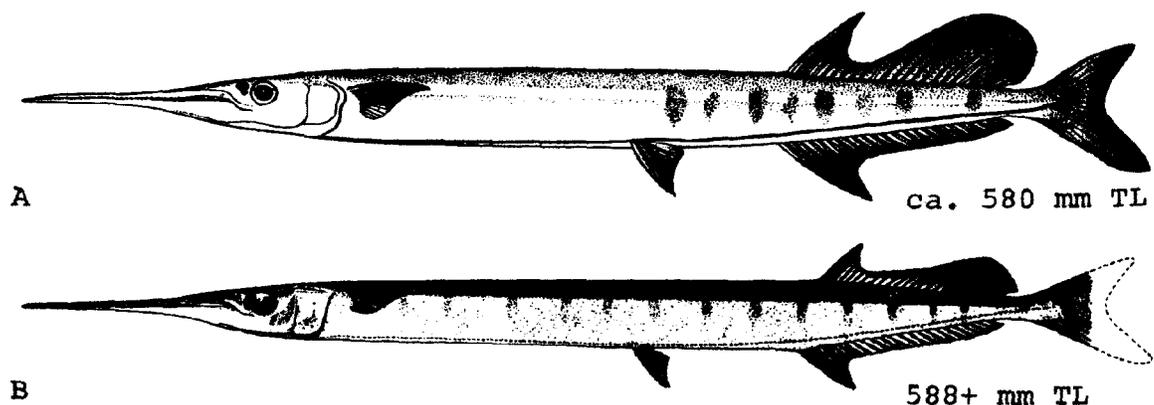


Fig. 36. *Ablennes hians*, Flat needlefish. A. Juvenile or young adult, ca. 580 mm TL, dorsal lobe still expanded. B. Juvenile or adult, 588+ mm TL, dorsal lobe still expanded, pigment blotches still evident anteriorly. (A, Fowler, H. W., 1944: 104. B, Parin, N. V., 1963: fig. 17.)

at 141–165 mm upper jaw 81–91 percent of lower jaw.²² At ca. 123 mm depth in length to caudal ca. 24.¹⁴ At 37.0 mm TL preanal finfold prominent (NSS). Posterior rays of dorsal longer than median ones²⁸ and forming a melanistic lobe which sloughs off with development² (the extended lobe still evident at 600 mm).¹⁰ First pelvic ray usually branched at ca. 200–300 mm SL.⁴

Pigmentation: At 37 mm TL dorsum with numerous punctate melanophores, lower sides with widely spaced stellate melanophores, posterior part of dorsal fin dark (NSS). In young 12¹²–15 dark, dusky, vertical or round blotches on sides;^{18,30,35} posterior lobe of dorsal dark.² At 375 mm silver with iridescent specks, back slate gray, sides with 14–15 transverse vertical bars, especially visible toward back, fins grayish, ends of pectorals and posterior region of dorsal blackish.³⁶

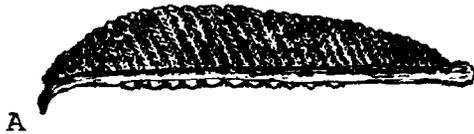


Fig. 37. *Ablennes hians*, Flat needlefish. A. First gill arch of a 52 mm SL specimen showing vestigial gill rakers. These are subsequently lost. (A, Nichols, J. T., and C. M. Breder, Jr., 1928: fig. 169.)

AGE AND SIZE AT MATURITY

No information.

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Strongylura marina (Walbaum), Atlantic needlefish**ADULTS**

D. 14-17; A. 16-20;⁷² C. 3+19+3;¹⁹ P. 10¹⁰⁻¹³; ⁵³ V. 6; ⁷⁻¹⁰ scales along lateral line ca. 300⁴ to ca. 325;²⁴ predorsal scales 213-304, mean 255; ^{28,37} total vertebrae 69-77, precaudal vertebrae 41-50; caudal vertebrae 23-29.⁷²

Proportions expressed as times in TL: Head 2.45-3.25, depth 14.3-20.0.²⁴ As times in SL: Head ca. 2.9. As times in head length: Depth ca. 5.5.⁴

Body rather slender, cylindrical, not compressed; ^{17,24,52,68} a distinct caudal ridge or low keel on side of caudal peduncle; ^{4,20} jaws about twice as long as rest of head. Teeth in bands in jaws, sharply pointed, the innermost ones enlarged and canine-like.²⁴ Pelvics closer to anal than to pectorals; ⁴ caudal square or slightly concave.^{23,24}

Pigmentation: Green above, silvery on sides, pale⁴ or white³⁰ below; a silvery⁷ or bluish silvery band on side becoming broader and less distinct toward tail; ¹³ snout dark green; cheeks and opercles silvery; a blackish vertical bar on upper part of opercle; scales and bones green; ^{20,24} pupil black.²¹ Fins olivaceous; ³⁰ dorsal somewhat dusky, longest rays yellowish at tips; caudal bluish at base, lobes yellowish; anal sometimes dusky.²⁴

Maximum length: 1220 mm.^{20,64}

DISTRIBUTION AND ECOLOGY

Range: Maine to mid-peninsular Florida; Gulf coast of United States and Mexico and southward, in coastal waters, at least to Rio de Janeiro, Brazil.² Records from

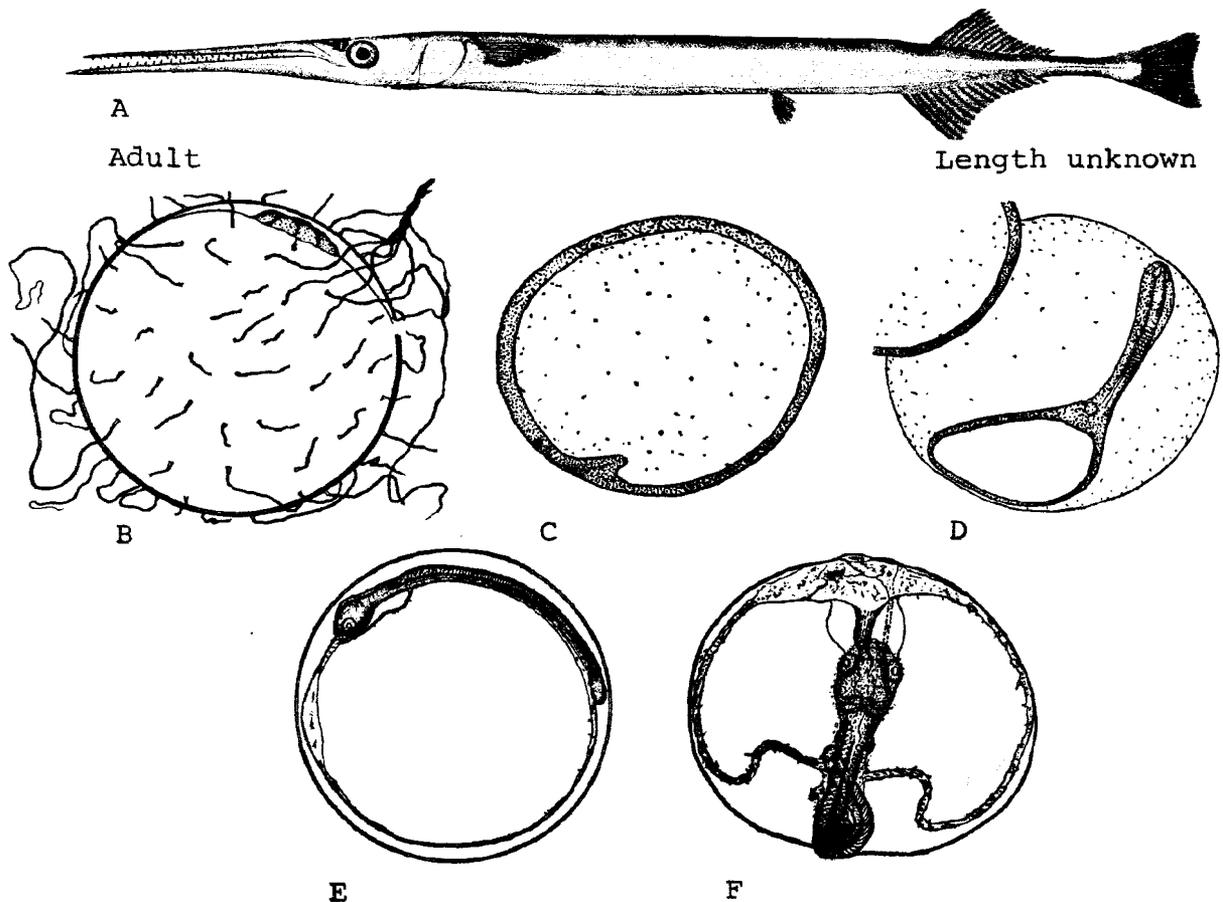


Fig. 38. *Strongylura marina*, Atlantic needlefish. A. Adult, length unknown. B. Egg with attachment filaments, 4-cell stage, 3 hours and 23 minutes after fertilization. C. Blastoderm, 31 hours and 20 minutes. D. Early embryo, 43 hours and 40 minutes, eyes, somites, Kupffer's vesicle formed. E. Early embryo, 70 hours, tail bud forming, heart tubular, 80+ somites. F. Embryo, 94 1/2 hours, notochord conspicuous, yolk vessels established. (A, Goode, C. B., et al., 1884: pl. 181. B-F, Ryder, J. A., 1882: pls. 19-21.)

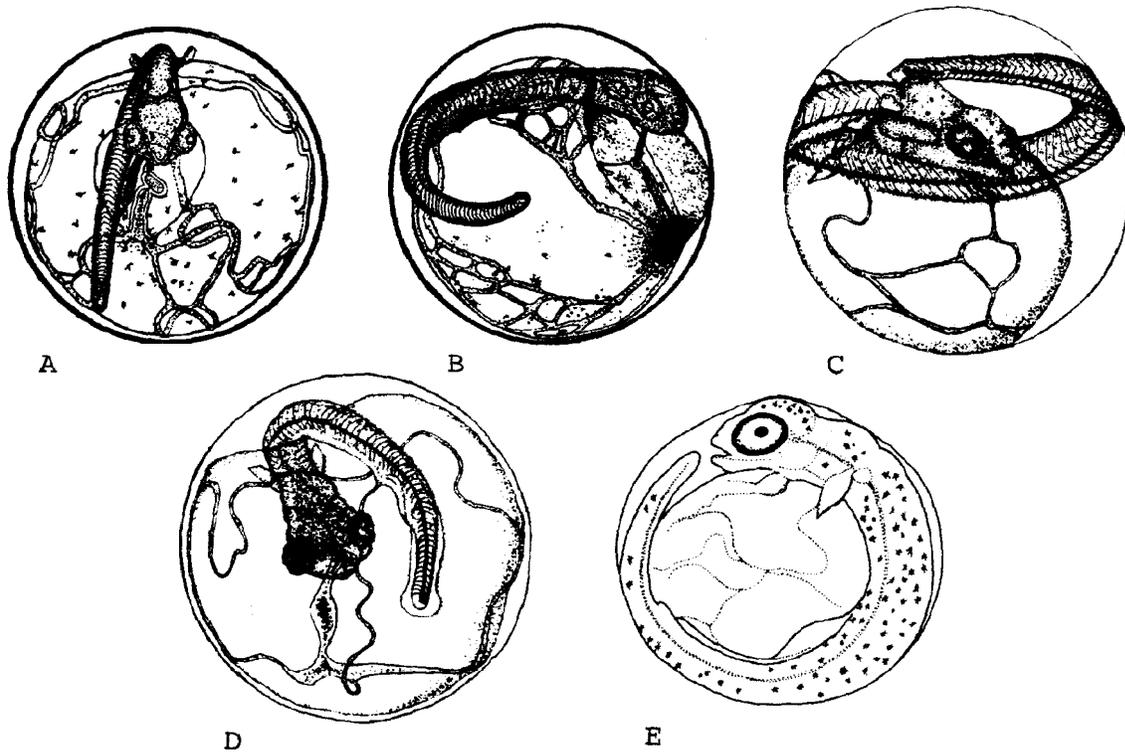


Fig. 39. *Strongylura marina*, Atlantic needlefish. A. Embryo, 116 hours and 40 minutes, pigment on yolk and heart, intestine and urinary bladder well-developed. B. Embryo, 165 1/2 hours, pericardial cavity enormously developed. C. Advanced embryo, age unknown, pigment developing on head. D. Advanced embryo, age unknown, finfold and pectoral fins developing. E. Embryo just before hatching, pigment well-developed on body. (A-B, Ryder, J. A., 1882: pls. 19-21. C-E, Original drawings, Peni G. Lang.)

the West Indies and Africa^{8,15,39,41,63,66,69} refer to *S. timucu* and *S. senegalensis* (BBC).

Area distribution: Coastal waters of New Jersey,⁵ Delaware,⁵⁵ Maryland,^{1,24} and Virginia;⁷⁰ north in Chesapeake Bay to Havre de Grace, Maryland²⁴ and ascending regional rivers for considerable distances, i.e., to the vicinity of Washington, D.C., in the Potomac,^{3,38} to Lancaster County, Pennsylvania in the Susquehanna,⁵⁷ and 64 km upstream in the Pamunky River, Virginia.³¹

Habitat and movements: Adults—primarily an inshore, shallow water species¹⁰ usually found at the surface and ascending fresh water rivers at least 607 km to points up to 69.2 m above sea level;^{14,25,40,56} also reported from lakes,⁴ coastal ponds,⁶² large springs,^{32,58} and canals.⁵⁰ Landlocked populations may exist wholly within fresh water lakes in Florida.⁴⁸ Maximum salinity, 36.9 ppt.¹⁸ Maximum temperature 32.9 C. Apparently make definite inshore-offshore movements according to the following observations: Inshore in Gulf coast bays in May and June;⁶⁵ in St. Johns River, Florida, April to October;¹⁶ reported to run up the Potomac River “with the branch herring” and remain all summer;³ arrives in upper Chesapeake Bay in April;⁴⁴ inshore in bays at Ocean City, Maryland from August to September 15;⁴⁶ May to mid-November in Long Island;⁹ and in Hudson River and its tributaries in autumn.⁷

Larvae—yolk-sac larvae reported from freshwater feeders of the Delaware-Raritan Canal.⁴⁹

Juveniles—specimens down to 22 mm along beaches in Long Island,⁶⁷ and specimens 25–50 mm long reported to form “solid green masses” in Long Island in October.⁴⁵

“Young” also in small creeks,⁶ and a 23 mm specimen reported from Pamunky River, Virginia.³¹ Specimens 125–245 mm long in lakes (connected to the sea),⁴⁶ rivers,¹⁰ bays and harbors,^{33,46} along beaches,⁵⁴ and in small groups around wharves.⁴³

SPAWNING

Location: Inshore in bays and estuaries^{10,22,24,29,30} (specifically recorded 12 to 27 m from shore in Florida bays);⁶⁰ possibly also in river mouths.¹³ Freshwater spawning has been suggested in Florida;³⁶ yolk-sac larvae have been collected in fresh water feeders of the

Delaware-Raritan Canal;²⁷ and a running ripe female was collected 16 km above the tide in Chickohominy River, Virginia.³¹ Maximum recorded salinity, 18.0 ppt.⁵¹

Season: Probably May and June in Rhode Island and New York, although large "immature" ovarian eggs have been observed in Rhode Island in August;^{7,26} ripe adults from May 9³¹ to August in Virginia;¹² gravid females as early as June 9 at head of Chesapeake Bay,⁴⁴ and with ovarian eggs of ca. 1.0 mm diameter on May 21 in bay;²⁴ near ripe females in mid-February in Texas,⁴² and spawning from April 25 through June in Florida and the Gulf of Mexico^{38,60} (records from the Gulf

coast may be based in part or in whole on *Strongylura timucu*²).

Fecundity: Unknown.

EGGS

Description: Demersal,¹² attached to weeds and other objects and remaining in compact masses.^{11,61}

Ovarian eggs: Egg membrane with tightly coiled filaments even in ovarian follicles.^{12,61}

Fertilized eggs: Diameter ca. 3.5–3.6 mm;^{12,61} entire egg,

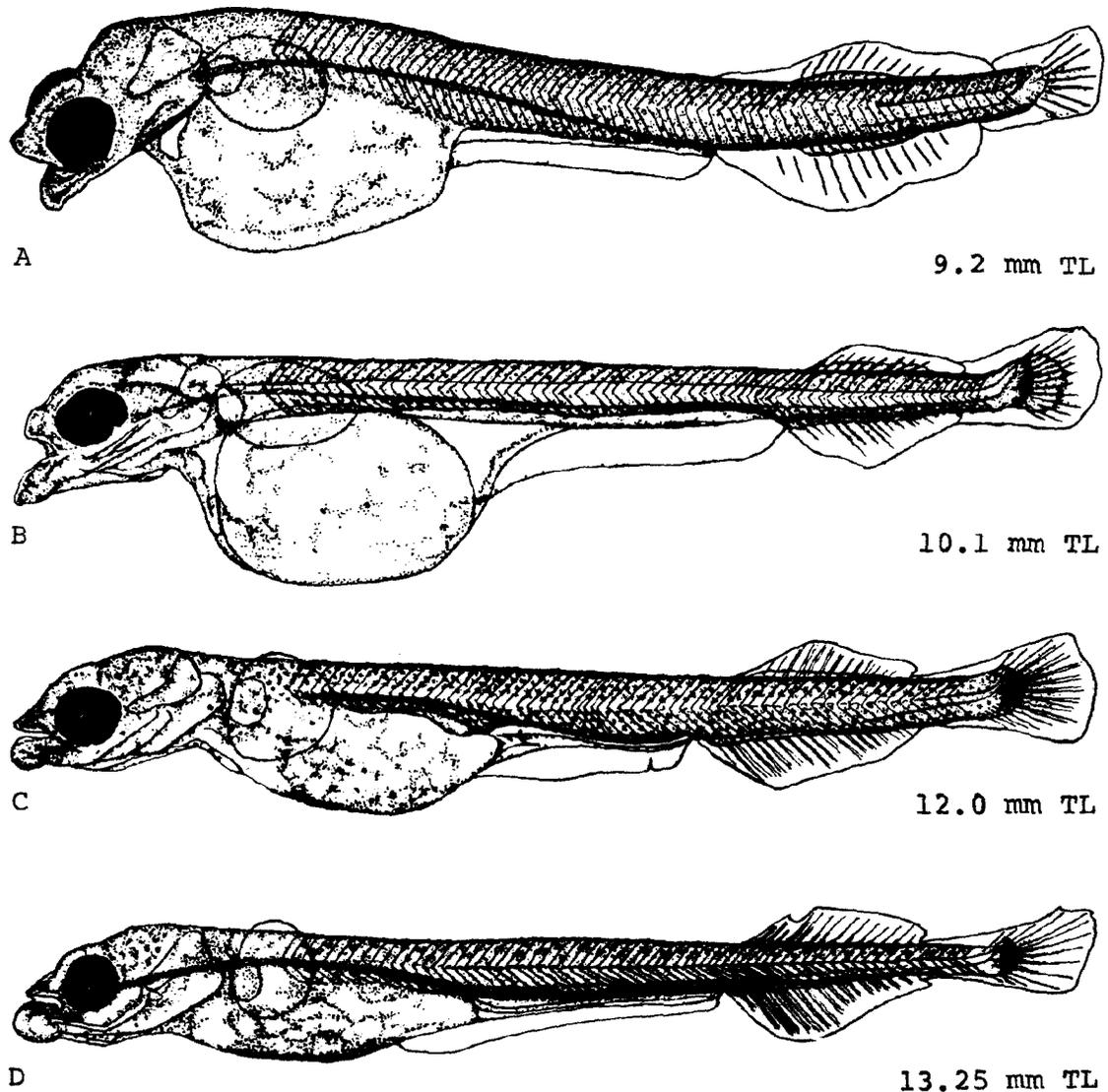


Fig. 40. *Strongylura marina*, Atlantic needlefish. A. Yolk-sac larva, 9.2 mm TL. B. Yolk-sac larva, 10.1 mm TL. C. Yolk-sac larva, 12.0 mm TL. D. Yolk-sac larva, 13.25 mm TL. (A-D, Original drawings, Peni G. Lang.)

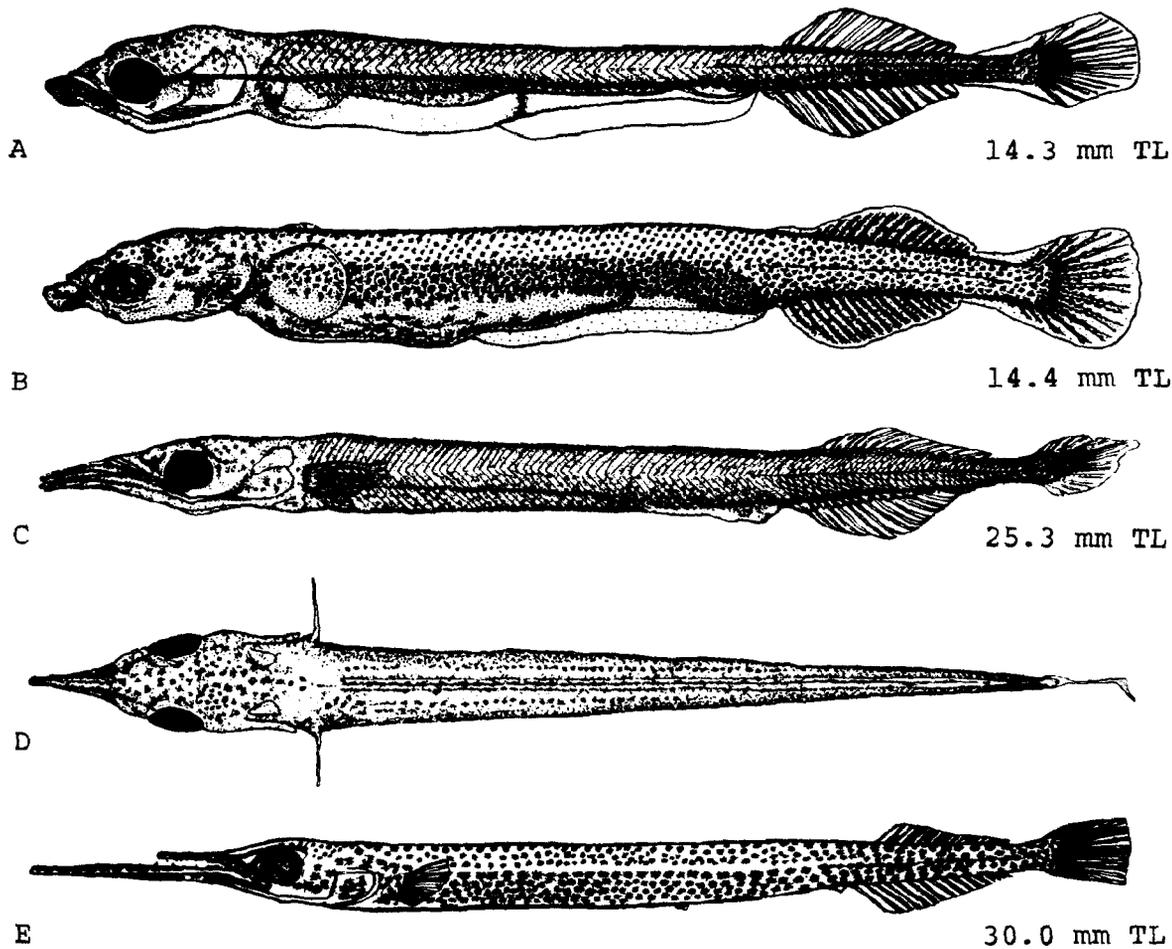


Fig. 41. *Strongylura marina*, Atlantic needlefish. A. Yolk-sac larva or larva, 14.3 mm TL. B. Yolk-sac larva, newly-hatched, 14.4 mm TL, showing distinctive lateral pigment pattern and lack of rays in pectoral fin. C. Larva, 25.3 mm TL, rays formed in pectorals. D. Dorsal view of C. E. Larva, 30.0 mm TL, pelvic fins forming. (A-D, Original illustrations, Peni G. Lang. E, Original illustration, Nancy S. Smith.)

including developing yolk, completely transparent; egg membrane with attachment filaments; ^{11,59} filaments variable, but generally less than diameter of egg, cylindrical, tapering distally, and attached at swollen truncated cone; perivitelline space very narrow, the yolk almost in contact with egg membrane; oil globules absent.¹²

EGG DEVELOPMENT

Development at unspecified temperature:^{12,26}

- 3 hours, 23 minutes—8-cell stage.
- 4 hours, 45 minutes—16-cell stage.
- 10 hours—early blastula.
- 24 hours—embryo forming.
- 31 hours—embryo developed beyond blastodermic rim.

43 hours, 40 minutes—eyes, somites, Kupffer's vesicle formed.

70 hours—80+ somites, pectoral buds, auditory vesicles evident; heart tubular; vitelline vessels formed.

94 hours, 30 minutes—notochord conspicuous.

116 hours, 40 minutes—otoliths evident; chromatophores on body, yolk and heart.

165 hours, 30 minutes—finfold developing.^{12,26}

Incubation period: Unknown.

YOLK-SAC LARVAE

Hatching length 9.2 (PGL)—14.4 mm.⁷³ At hatching yolk mass large, oval; head not flexed over yolk; mouth open. Lower jaw apparently becoming bulbous by end of stage.

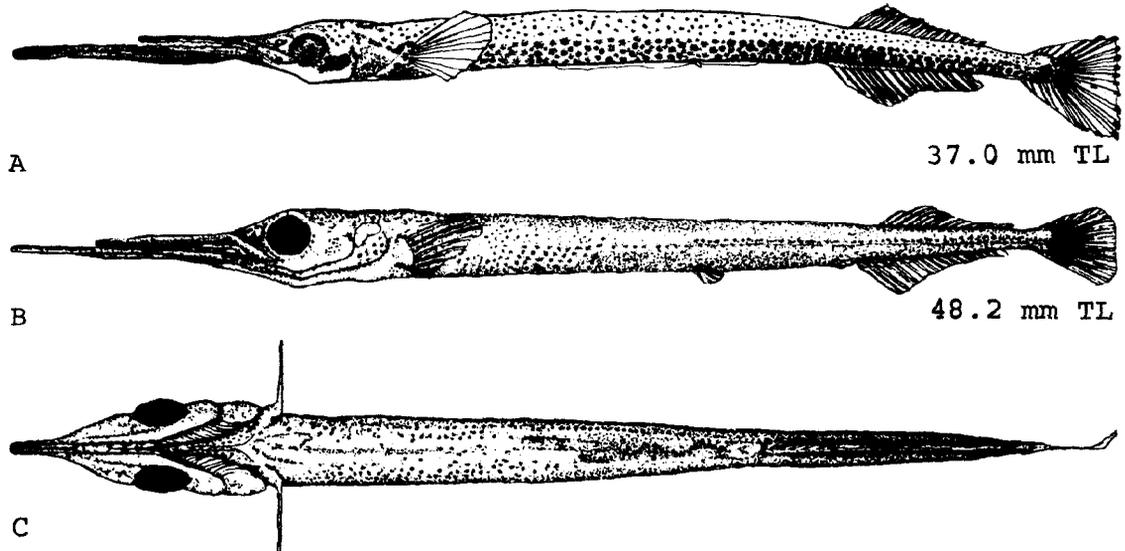


Fig. 42. *Strongylura marina*, Atlantic needlefish. A. Larva, 37.0 mm TL. B. Larva, 48.2 mm TL. C. Ventral view of B. (A, Original illustration, Nancy S. Smith. B, C, Original illustrations, Peni G. Lang.)

Finfold small except preanally, continuous between dorsal and caudal and anal and caudal, but not developed in front of dorsal. Incipient rays in dorsal, caudal, and anal throughout stage. Urostyle flexed at hatching (PGL).

Pigmentation: Pigment developed dorsally above lateral line, on yolk sac, and in eye throughout stage (PGL). In a 14.4 mm TL specimen, a distinct broad band of pigment on lateral aspect of body between head and anus.⁷³

LARVAE

Size range described 25.3–48.2 mm TL.

Jaws equal in length at beginning of stage, lower jaw much longer than upper by end of stage. Preanal finfold evident to 37.0 mm. Pelvic buds developed at 30.0 mm (PGL).

Pigmentation: At 25.3 mm melanophores scattered over head and body, large melanophores concentrated on lower sides anterior to anus, and a distinct row of melanophores on each side of mid-dorsal line. At 30.0–37.0 mm body and head covered with large melanophores, these concentrated on body below lateral line. At 48.2 mm melanophores more numerous, punctate (PGL).

JUVENILES

Minimum length described, ca. 45.0 mm.⁴⁷

At ca. 45.0 mm caudal peduncle relatively deeper than in adult, eye relatively larger.⁴⁷ At 44.5 mm SL upper jaw ca. 60 percent of lower jaw, at 114–129 mm SL, ca. 85–89 percent of lower jaw.³⁴ At 170 mm SL jaws approxi-

mately equal.⁹ At 200–300 mm SL (thus possibly including adults) first ray of pelvic fin branched.¹⁰ Caudal fin somewhat forked at ca. 45 mm.²²

Pigmentation: At ca. 45 mm, dark above, light below; a definite dark mid-lateral band of pigment from eye to base of caudal becoming progressively lighter and more narrow posteriorly.²²

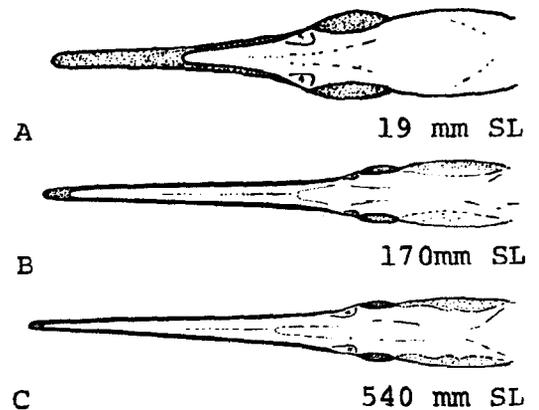


Fig. 43. *Strongylura marina*, Atlantic needlefish. A-C. Development of head and beak. A. 19 mm SL. B. 170 mm SL. C. 540 mm SL. (A-C, Breder, C. M., Jr., 1934: pl. 1.)

AGE AND SIZE AT MATURITY

Age at maturity, possibly during 2nd season; minimum size at maturity, ripe ovaries in a specimen not much greater than ca. 205 mm.²²

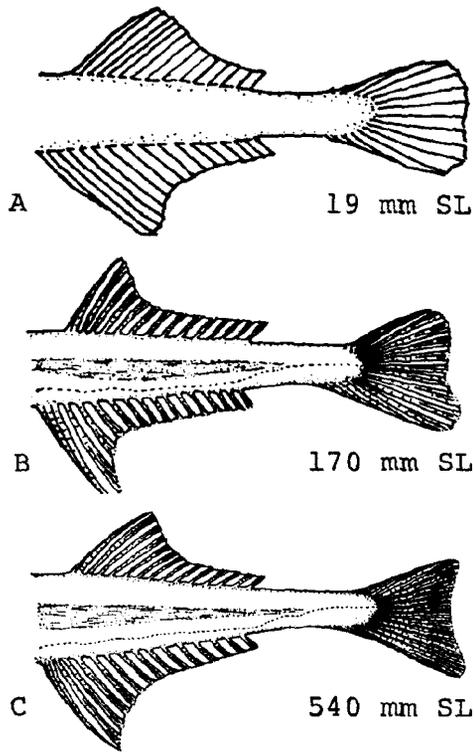


Fig. 44. *Strongylura marina*, Atlantic needlefish. A-C. Development of median fins. A. 19 mm SL. B. 170 mm SL. C. 540 mm SL. (A-C, Breder, C. M., Jr., 1934: pl. 3.)

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Tylosurus acus (Lacépède), Agujon**ADULTS**

D. 20–27 (in western Atlantic 22–26); A. 18⁴¹–25²² (in western Atlantic 20–24⁴¹); C. 14²²–16; P. 12²⁴–14; ⁷ V. 6; ^{7,24} vertebrae 74–96 (in western Atlantic 90–95), vertebral count also given as 55 + 28 (based on specimen from Java Sea); ³² scales in lateral series ca. 350⁵–400,^{11,12} predorsal scales 267–430 (325–389 in western Atlantic); ⁴¹ branchiostegals 14.^{22,25}

Proportions expressed as times in TL: Head 2.6, depth 18.5¹¹–22.0,^{25,30} Proportions as percent SL: Lower jaw 22.4–23.8 (in specimens larger than ca. 170 mm), lower jaw extension 1.6–3.7, length of anal lobe 5.5–6.2.⁷

Body elongate, slightly compressed, a little deeper than broad; caudal peduncle depressed, broader than deep, and with lateral keel; head somewhat depressed above; cheek and opercle straight, nearly vertical; ^{4,11} preopercle scaled, opercle naked; ¹¹ eye ellipsoid.²⁸ Teeth in bands in jaws, the inner ones enlarged, pointed; longest teeth near center of length of snout.^{11,25} Scales small, cycloid; lateral line complete, upturned on caudal peduncle.¹¹ Dorsal and anal fins opposite, but last anal ray considerably anterior to last ray of dorsal; dorsal and anal fins both with enlarged anterior lobes.^{14,25}

Pigmentation: Dark green,^{4,28} dark blue with greenish flashes,²⁵ brilliant ocean blue, or brownish above; ¹² silvery²⁵ or silvery white below; ⁴ no lateral band; ¹¹ keel on caudal peduncle black; ^{18,26} iris silvery or silvery white; dorsal greenish dusky²⁸ with anterior rays blackish; ⁴ anal whitish; caudal greenish dusky or transparent with blackish tints on ray bases; pectorals greenish dusky^{25,28} with blackish anterior rays; ⁴ pelvics white.²⁵

Maximum length: 1525 mm.²⁸

DISTRIBUTION AND ECOLOGY

Range: Circumtropical¹ but divided into 5 subspecies in western Atlantic, Mediterranean, Gulf of Guinea, Indo-west Pacific and eastern Pacific (BBC); in the western Atlantic, Buzzards Bay, Woods Hole, and Nantucket^{22,29,33} to Brazil; ⁸ also Bermuda, and the West Indies; ¹⁶ the Mediterranean and tropical eastern Atlantic; ³⁹ South and East Africa, through Indian Ocean, the Malay Archipelago and the Philippines to Japan and, in the south Pacific, to the Bismarck Archipelago and Australia; ^{9,35,36,37,40} also in eastern Pacific (BBC).

Area distribution: Atlantic coastal waters of New Jersey^{2,19,29} and Maryland,¹⁰ and north in Chesapeake Bay to Cecil County and lower Susquehanna River basin.²³

Habitat and movements: Adults—probably an offshore

species, although frequently recorded inshore,^{7,16} particularly in inlets,⁶ harbors,²¹ and shallow bays,³¹ also at breakwaters.³⁸ Minimum salinity, 28.7 ppt. May move inshore during late summer and fall; thus recorded from Beaufort Harbor, North Carolina in June,³ early July,²¹ September, October and November.³

Larvae—no information.

Juveniles—specimens 114 mm long recorded from harbors; ¹⁴ “young” may follow floating offshore weeds.¹⁸

SPAWNING

Location: Probably offshore waters.⁷

Season: Spring in the Bahamas and West Indies;¹⁷ March to May in Haiti; June through July at Dry Tortugas, Florida.^{5,12}

Fecundity: No information.

EGGS

Location: Demersal, presumably entangled together and attached to objects in the water.³⁴

Fertilized eggs: Diameter 3.22³⁴–4.0; egg membrane with long attachment filaments; ³² filaments apparently longer than diameter of egg and in evenly spaced groups of 2–3 filaments each.³⁴

EGG DEVELOPMENT

Development at 25.0–30.4 C: ³⁴

2 hours—first cleavage.

2 hours, 30 minutes—4-cell stage.

18 hours—blastula.

28 hours—blastoderm over 2/3 yolk, 3 myomeres.

39 hours—eye spots formed, blastopore closed, 20 myomeres.

50 hours—choroid fissure, otoliths evident; tail rounded, attached; 36 myomeres.

55–61 hours—yellow pigment on body, black pigment on yolk, blood vessels developed.

86 hours—pectoral fins evident, 76 myomeres.

110 hours—urostyle oblique, black pigment on body, network of pigment on yolk.

159 hours—caudal fin developing.

168 hours—mouth open, incipient dorsal and anal fins developing.

182 hours—heavy pigment developed over eye, body, and yolk sac.

244 hours (ca. 10 days)—hatching.³⁴

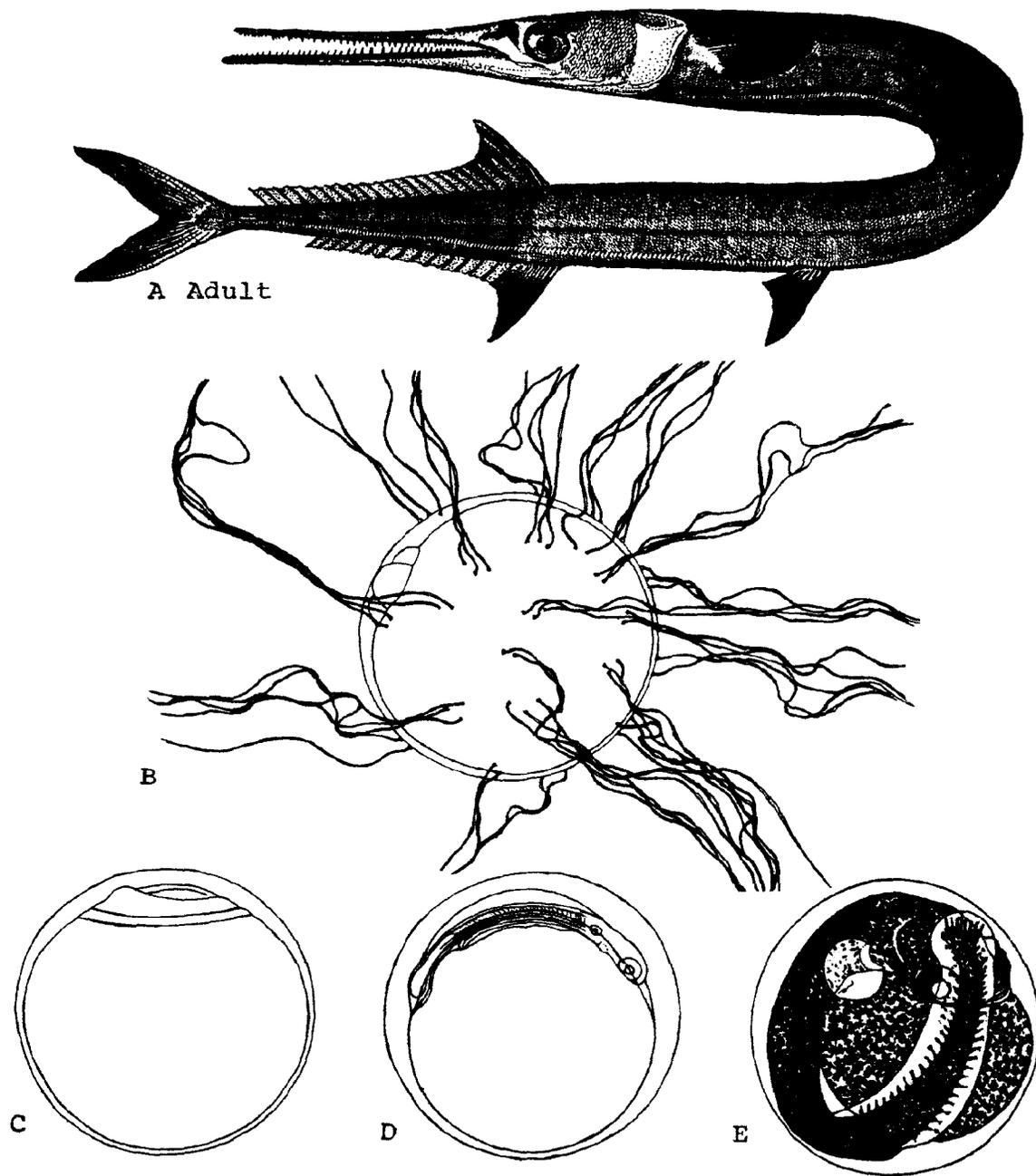


Fig. 45. *Tylosurus acus*, Agujon. A. Adult, length unknown. B. Egg, 4-cell stage, 2 hours and 30 minutes after fertilization. C. Egg, 18 hours, blastula stage. D. Egg, 50 hours, 36 myomere stage. E. Advanced embryo, 182 hours. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 309. B-E, Mito, S., 1958: pl. 23, figs. 1-4.)

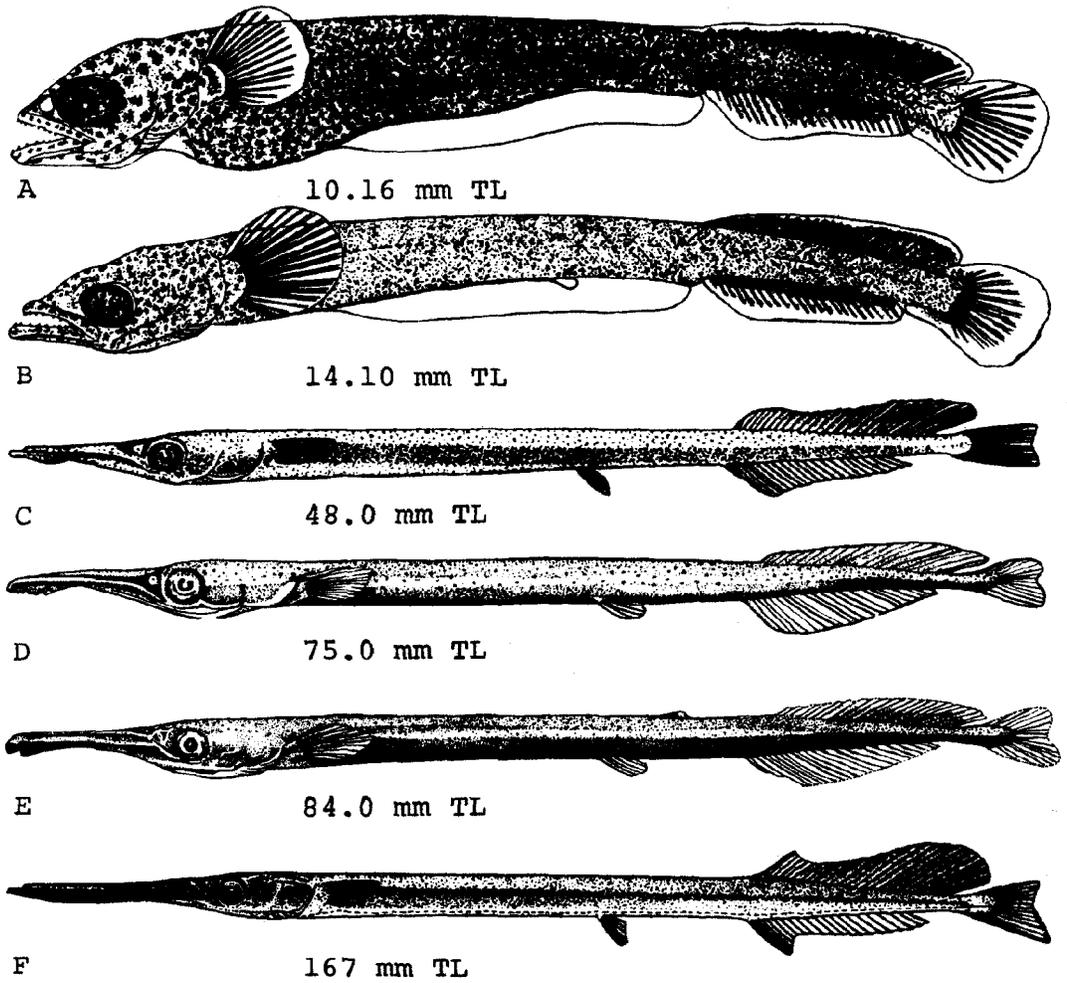


Fig. 46. *Tylosurus acus*, Agujon. A. Yolk-sac larva, newly-hatched, 10.16 mm TL. B. Larva, 2 days old, 14.10 mm TL. C. Juvenile, 48.0 mm TL. D. Juvenile, 75.0 mm TL. E. Juvenile, 84.0 mm TL. F. Juvenile, 167 mm TL. (A, B, Mito, S., 1958: pl. 23, figs. 5-6. C, F, Parin, N. V., 1967: fig. 20. D, E, D'Ancona, U., 1931: pl. 9, Deborah C. Kennedy, delineator.)

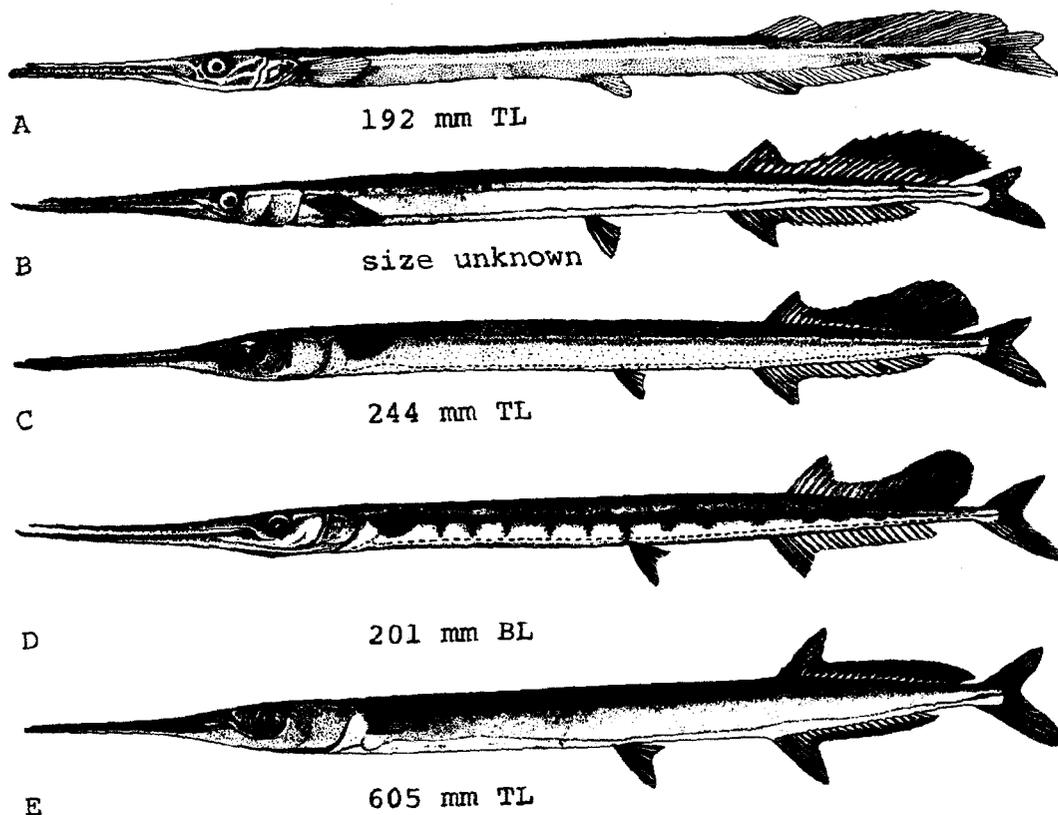


Fig. 47. *Tylosurus acus*, Agujon. A. Juvenile, 192 mm TL. B. Juvenile, size unknown, showing well-developed dorsal fin lobe. C. Juvenile, 244 mm TL. D. Juvenile, 201 mm TL. E. Juvenile or young adult, 605 mm TL, posterior portion of dorsal fin still darkened. (A, D'Ancona, U., 1931: pl. 9, Deborah C. Kennedy, delineator. B, Lozano Rey, L., 1947: fig. 172, after Bonaparte, C. L., 1832-1841: color plate, unnumbered. C, E, Parin, N. V., 1967: fig. 20. D, Collette, B. B., and N. V. Parin, 1970: fig. 12.)

Incubation period: Ca. 10-12 days in same batch of eggs at 25.0-30.4 C; peak hatching on 11th and 12th days, with hatching occurring mostly at night.³⁴

YOLK-SAC LARVAE

Specimen described, 10.16 mm, newly-hatched.

Body relatively deep, short; yolk sac greatly reduced, oval anteriorly, tubular posteriorly; teeth developed; nasal fossa not divided. Preanal finfold long, broad. Dorsal and anal fins in contact with caudal; incipient rays in pectoral; urostyle oblique.³⁴

Pigmentation: Body and yolk sac completely covered with chromatophores; chromatophores less numerous, more stellate on head and jaws; pigment developed in dorsal and anal fins and near base of caudal.³⁴

LARVAE

Specimen described, 14.10 mm TL.

At 14.10 mm TL body relatively much deeper than in following (juvenile) stages, lower jaw distinctly longer than upper jaw, pelvic fin buds formed, preanal finfold still evident.

Pigmentation: At 14.10 mm TL pigment essentially as in yolk-sac larvae.³⁴

JUVENILES

Size range described 23-300 mm SL.

Snout projected at 23 mm SL, the upper jaw about one half length of lower jaw. At 79 mm snout greatly projected, upper jaw ca. two-thirds lower. At 205 mm jaw with broad, fleshy, dark mandibular lappets; lappets reduced at 205 (or 215) mm, greatly reduced at 242 mm.¹² Teeth in "young" vertical and straight.⁹ Dorsal fin with greatly produced melanistic 2nd lobe which is first evident at 23 mm SL, at maximum development from 169-244 mm, and apparently still evident in one specimen of 605 mm.^{5,12} First ray of pelvic branched at 200-300 mm SL.⁷

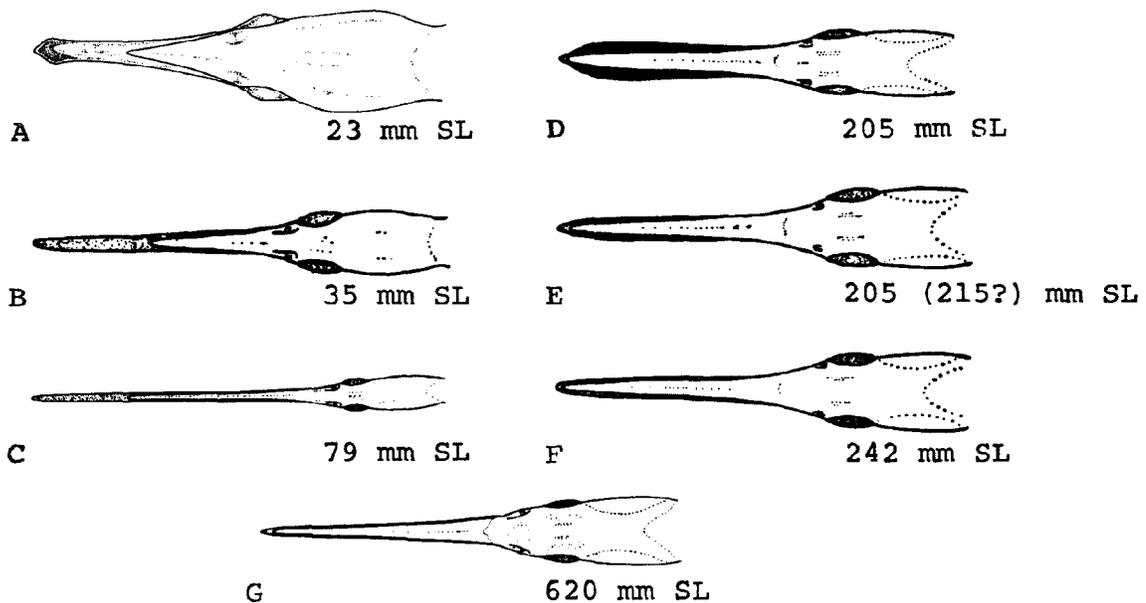


Fig. 48. *Tylosurus acus*, Agujon. Development of head and beak. A. 23 mm SL. B. 35 mm SL. C. 79 mm SL. D. 205 mm SL. E. 205 (or 215) mm SL. F. 242 mm SL. G. 620 mm SL. (A, Breder, C. M., Jr., 1934: pl. 2, Elizabeth Ray Peters, delineator. B, C, G, Breder, C. M., Jr., 1934: pl. 2. D, E, F, Breder, C. M., Jr., and P. Rasquin, 1954: fig. 1, fig. E reported as 215 mm in fig. 7 of source.)

Pigmentation: Young up to ca. 30 mm sometimes light green with four broad bands of bright silver, the first through the eye, the second just in advance of the pelves, the third at dorsal origin, and the fourth at caudal peduncle. In young pectorals usually hyaline or dusky.¹² In a specimen ca. 115 mm long posterior lobe of dorsal black^{5,12} and black pigment also on caudal fin.¹⁴ At ca. 150 mm bright silvery, translucent, somewhat darker above, and with indistinct dark bars on side.¹⁸ A juvenile of unknown size, but with dorsal lobe black, was dark blue above, pale grayish tinged with red on sides, grayish below, and with fins yellowish and dusky.²⁷

AGE AND SIZE AT MATURITY

First mature in 2nd or 3rd year;¹² or at ca. 600–700 mm SL.^{5,12,15}

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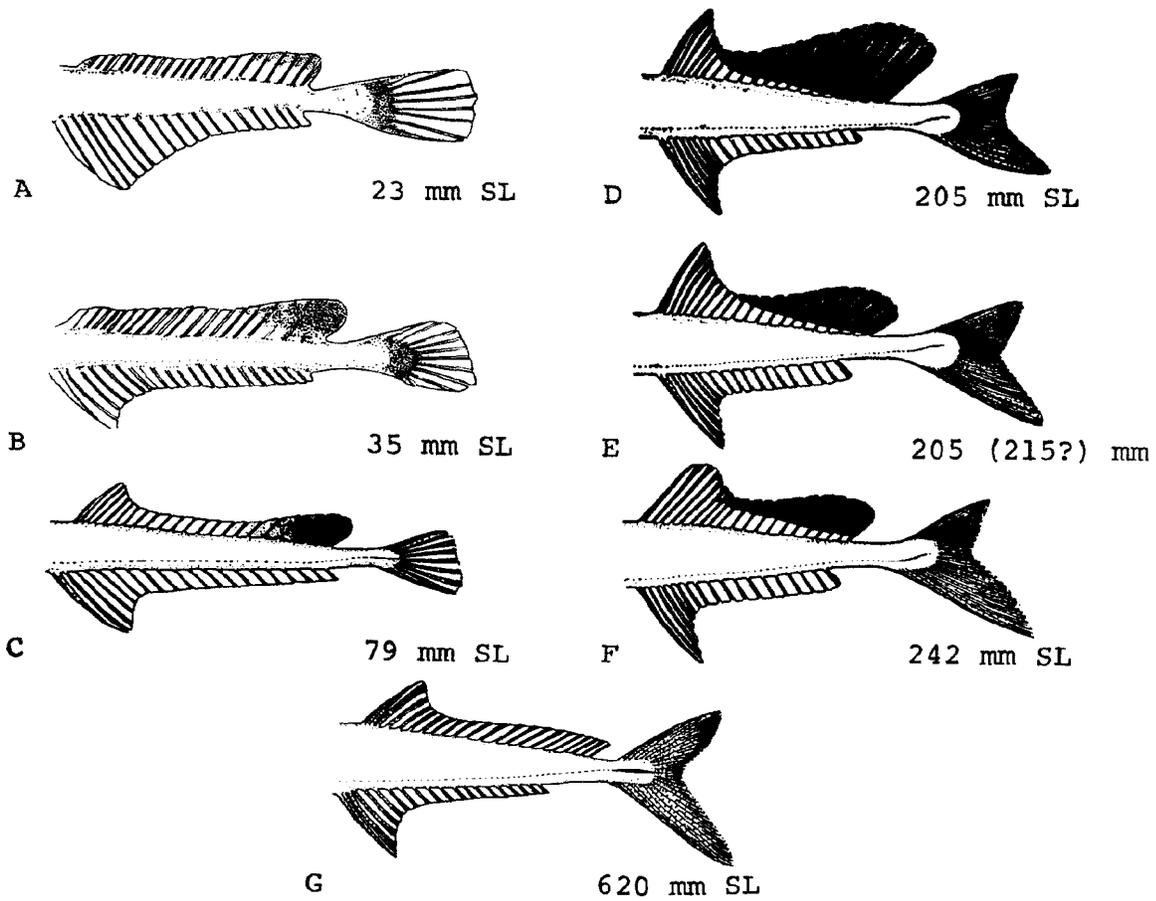


Fig. 49. *Tylosurus acus*, Agujon. Development of median fins. A. 23 mm SL. B. 35 mm SL. C. 79 mm SL. D. 205 mm SL. E. 205 (or 215) mm SL. F. 242 mm SL. G. 620 mm SL. (A, B, Breder, C. M., Jr., 1934: pl. 5, Elizabeth Ray Peters, delineator. C, G, Breder, C. M., Jr., 1934: pl. 5. D-F, Breder, C. M., Jr., and P. Rasquin, 1954: fig. 2.)

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Tylosurus crocodilus (Peron and Lesueur), Houndfish**ADULTS**

D. 18–25 (in western Atlantic 21–23); A. 17–22 (in western Atlantic 18–22);⁶⁵ C. 28;¹⁴ P. 14–15; V. 6;^{37,56} vertebrae 67–86 (in western Atlantic 79–86),⁶⁵ preanal vertebrae 55²⁷–57, caudal vertebrae 27²⁹–28;²⁷ scales in lateral series 195⁴⁶–388,⁵⁴ scales between occiput and dorsal fin 138–142;⁴⁶ teeth on each side of upper jaw ca. 25, on each side of lower jaw 23.²

Proportions expressed as percent SL (includes juvenile): Head width 5.0–6.0 in specimens longer than 100 mm SL; head depth 5.5–6.8 in specimens longer than 60 mm SL; lower jaw length 18.8–21.8 in specimens larger than ca. 170 mm; anal length 7.2–9.5.⁷ Beak ca. 1 1/2–1 5/6 times in rest of head;¹⁸ greatest width of body 1.1–1.3 times in greatest depth.⁵⁶

Body robust, elongate, slightly compressed;^{2,26,58} caudal peduncle cylindrical, about as wide as deep;⁵⁴ caudal keel rather strong;¹⁵ head flat above, somewhat quadrate, a little deeper than wide, middle of upper surface with very shallow groove.⁴⁸ Scales minute;¹⁰ opercle naked^{43,52} or with scales on anterior margin.⁵⁵ Lateral line with short branch to pectoral base.⁵⁴ A broad band of small outer teeth and an inner row of large, strong, canine-like teeth in both jaws; vomerine teeth lacking;^{22,54,58,63} gill rakers absent.²³ Dorsal fin exactly or nearly opposite anal;^{8,10} caudal fin deeply forked,²² the lower lobe much longer than the upper.⁴⁸

Pigmentation: Green,^{18,33} dark green,^{2,48} blue-green,⁵² or bluish black⁴⁵ above; white³¹ or silvery below;^{2,48,52} middle of back with dark band outlined with narrow black lines; sides with indistinct silvery band; caudal keel black;^{17,22,48} slight dusky shade on upper cheek; yellow bar on anterior edge of opercle;² jaws with blue shades;³³ iris pale;³⁴ fins variable, either mostly yellow¹⁶ or dusky,¹⁷ or with dorsal and pectorals black or blackish, anal yellowish and with slightly soiled lobe, caudal and pelvics dusky;^{2,15,48} dorsal, caudal and pectorals sometimes brownish, olive green at base, grayish distally.⁴⁷

Maximum length: Ca. 1524 mm.^{2,4,57}

DISTRIBUTION AND ECOLOGY

Range: Circumtropical¹ (2 subspecies, with *T. c. fodiator* present in the eastern Pacific, BBC); in western Atlantic from New York and Bermuda to Bahia, Brazil, including Gulf of Mexico^{28,36,60} and West Indies;^{39,42} in eastern Atlantic, west coast of Africa^{45,51,54} and Ascension Island;⁶⁵ Indian Ocean, including Malay Archipelago,^{43,53,62} east coast of Africa, and Australia;^{53,59} in western Pacific, Samoa and Tahiti north to Formosa and

Japan;^{44,50} in eastern Pacific, Cape San Lucas and Mazatlán, Mexico, to Galapagos Island.²⁰

Area distribution: Coastal waters of Maryland²⁰ and New Jersey;³⁵ also off Lewes, Delaware.²¹¹

Habitat and movements: Adults—a pelagic⁴⁵ schooling species³⁷ (although largest fish may, at least at times, travel singly or in pairs⁴) found both offshore in open sea (where possibly more abundant^{7,9}) and to within 9 m of shore;³² recorded from shallow bays,³⁸ lagoons,^{30,56} harbors,³² and coral reefs^{37,41,59} in both open water along rocky shores and over beds of turtle grass,³² also from mangrove channels (FDM); typically at surface at night,⁴⁵ with larger fish sometimes in large schools. Move inshore at night,⁴ and apparently tend to remain inshore during spawning season.⁷⁶

Larvae—yolk-sac larvae initially move on substrate by lateral flickering of tail, subsequently swim upward; remain motionless at surface.⁶⁴

Juveniles—specimens 21 mm long remain at surface;⁶⁴ at 30–50 mm at surface up to 1.6 km or more offshore;¹⁷ at ca. 50–150 mm associated with drifting flotsam such as broken eelgrass and weeds,^{4,11,21,29} and reported to float head down in these circumstances³¹ (association with flotsam is abandoned before loss of early juvenile traits, i.e., expanded dorsal lobe and mandibular lap-pets¹⁹); at 200–250 mm form small schools along shore during day;⁴ recorded from harbors³¹ and straits between islands.⁴⁰ Minimum salinity 33.7 ppt.³¹ Sometimes drift northward with current along east coast of North America, abundantly to capes off Carolinas, rarely to New Jersey.²⁹

SPAWNING

Location: Inshore, among seaweed;^{25,64} possibly also offshore.⁷

Season: Probably May and June in Haiti;¹⁷ September and October in India;^{25,64} ripe specimens June and July at Dry Tortugas, Florida,^{4,18} early February, late March, and late October in West Africa.⁴⁵

Fecundity: More than 25,000 ripe eggs in a 1321 mm specimen.⁴⁹

EGGS

Description: In tangled masses held together by filaments; sometimes washed ashore.⁶⁴

Ripe ovarian eggs: Diameter 4.0⁶⁴–4.6 mm,⁴⁹ although average stated as 3.7 mm;¹⁵ yolk vacuolated, transparent.

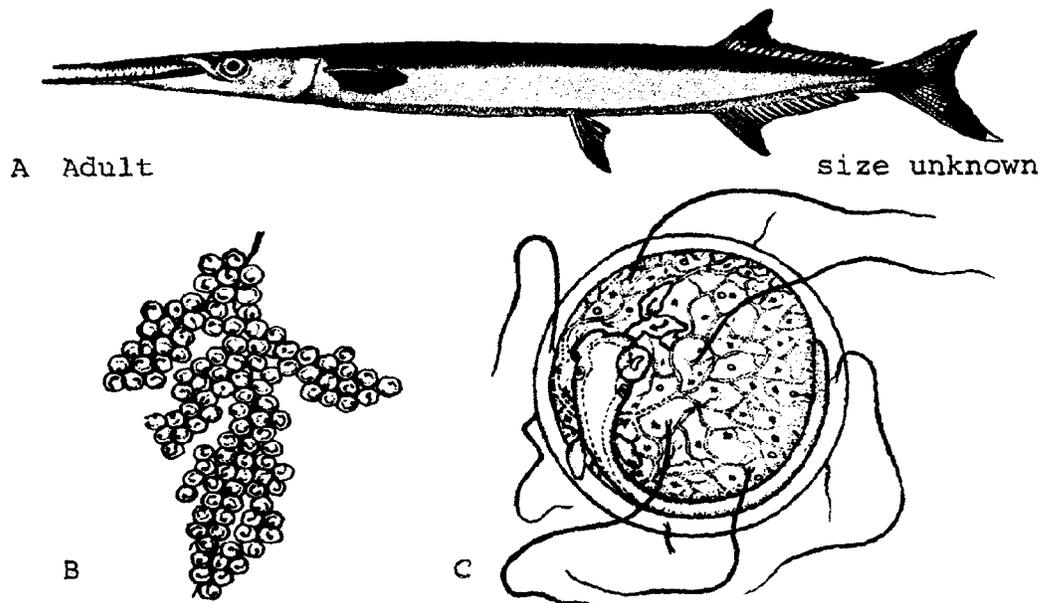


Fig. 50. *Tylosurus crocodilus*, Houndfish. A. Adult, size unknown. B. Portion of egg mass. C. Egg ca. 66-90 hours old, egg diameter 4.0 mm. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 308. B, C, Masarekar, V. B., 1967: figs. 1-2.)

and with minute scattered oil globules⁶⁴ (oil globules were not observed in specimens from Puerto Rico, JDH); egg membrane with numerous tiny threads.⁴⁹

Fertilized eggs: Spherical; diameter 4.0-4.1 mm (note smaller than largest reported ovarian eggs, JDH); egg membrane very tough, equipped with a number of long, fine, transparent, thread-like filaments; yolk transparent; oil globules minute, scattered.⁶⁴

EGG DEVELOPMENT

Development at unspecified temperature:

- 18 hours after collection (estimated age 66-90 hours)
—embryo around more than one-half yolk; yolk mass transparent, spherical, and still with minute oil globules; auditory vesicles, optic cups, lenses formed; mouth developed as slit-like opening; circulation established, prominent over yolk; dorsal and ventral finfolds barely evident; pectorals movable, lacking rays; stellate chromatophores evenly distributed over yolk surface.
- 42 hours after collection (estimated age 90-114 hours)—embryo slightly more elongated, yolk sac somewhat reduced; finfolds distinct; operculum evident.
- 66 hours after collection (estimated age 114-138 hours)—oil globules coalesced into single large

globule; lenses prominent; eyes protuberant and with black pigment around lens; tail free; movements established throughout body and in opercles and lower jaw.

72 hours after collection (estimated age 120-149 hours)—head large, broad; posterior half of body free from yolk; yolk sac reduced; gas bladder evident; otoliths formed.

96 hours after collection (estimated age 144-168 hours)—embryo completely around yolk; caudal with ca. 8-10 incipient rays; gape extended to anterior edge of eye; lower jaw constantly in motion; brain and nerve cord distinct; body covered with yellowish brown and black melanophores; eye black.

120 hours after collection (estimated age 168-192 hours)—incipient dorsal and anal rays; head still free of pigment; body covered with small stellate melanophores which spread on to dorsal third of yolk (in addition to original melanophores in this region); numerous brownish or reddish brown spots between black melanophores.

At time of hatching (estimated age 184-280 hours)—egg membrane soft, flaccid; hatching is head first; larva remains with head out of egg for ca. 15 minutes; sideways movements of head begin; eye constantly in motion.⁶⁴

Incubation period: Probably 8-10 days.⁶⁴

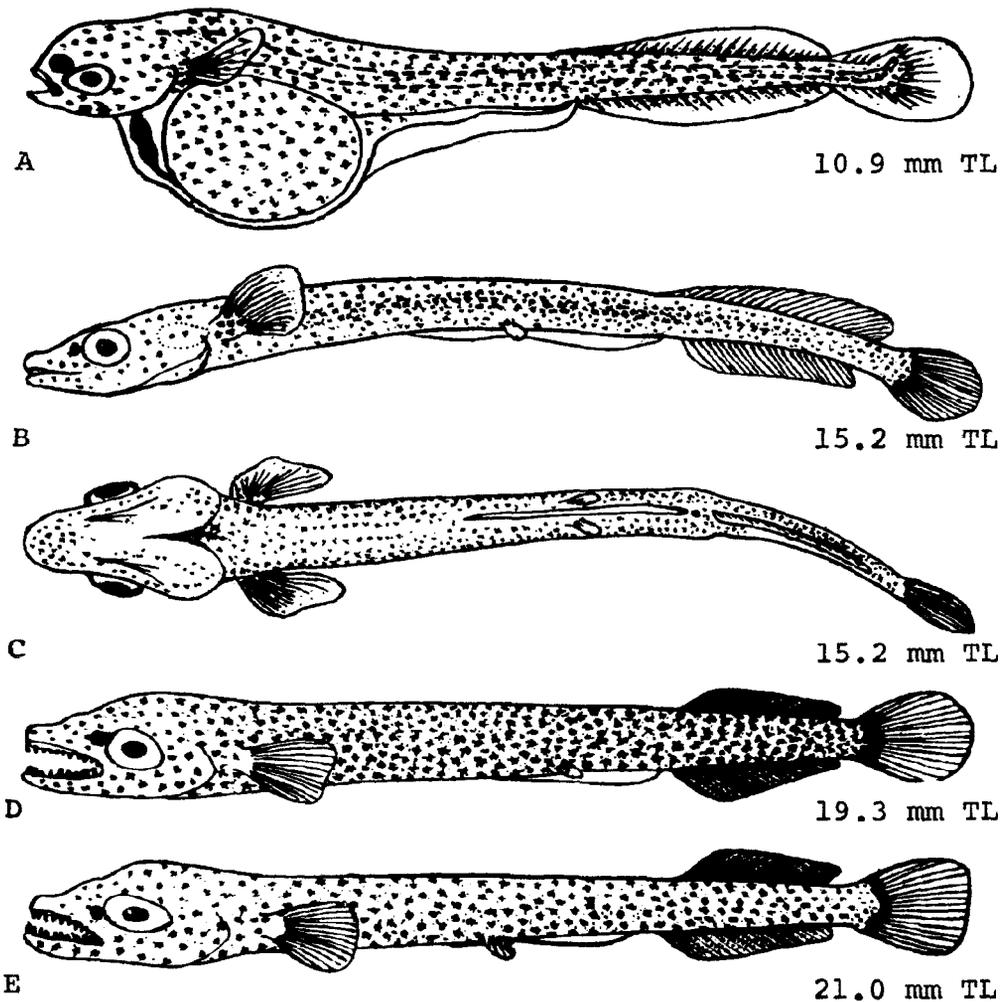


Fig. 51. *Tylosurus crocodilus*, Houndfish. A. Yolk-sac larva, 10.9 mm TL, newly hatched. B. Larva, 15.2 mm TL. C. Ventral view of B. D. Larva, 19.3 mm TL. E. Juvenile, 21.0 mm TL. (A-E, Masurekar, V. B., 1967: figs. 3-7.)

Optimum rearing temperature: 28-29 C.⁶⁴

Optimum pH: 7.9-8.1 (high mortality was observed at pH 7.5).⁶⁴

YOLK-SAC LARVAE

Hatching length, 10.7-12.0 mm. Specimen described, 10.9 mm.⁶⁴

Duration of stage, ca. 24 hours (yolk sac more or less completely absorbed).⁶⁴

At 10.9 mm, head free from yolk; yolk sac broadly oval; upper jaw oblique; lower jaw slightly longer than upper; dorsal finfold to slightly beyond level of anus; preanal finfold wide; urostyle oblique; incipient rays in dorsal

(ca. 20), anal (ca. 19), caudal (ca. 15), and pectorals.⁶⁴

Pigmentation: At 10.9 mm head and body more or less uniformly covered with brownish black melanophores and orange chromatophores; body gray in appearance when viewed from a distance; basal portions of median fins uniformly scattered with black melanophores; dorsal and caudal tinged with orange.⁶⁴

LARVAE

Size range of specimens described, 12.9-19.3 mm. Duration of stage 24 hours to 6 days (2 specimens are described without known size: one 36 hours old and one 44 hours old.⁶⁴ These are probably between 12.9 and 15.2 mm long, JDH).

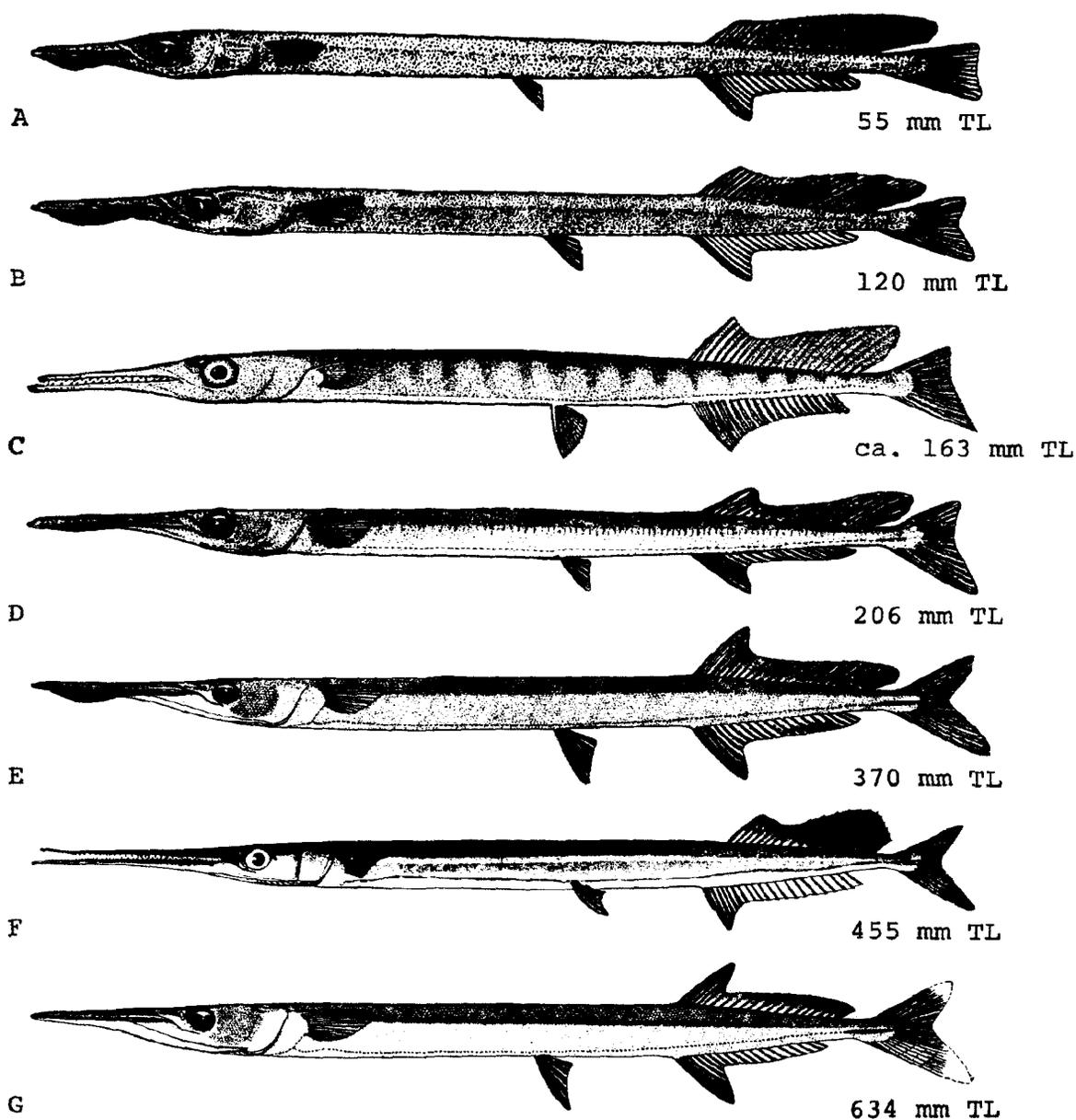


Fig. 52. *Tylosurus crocodilus*, Houndfish. A. Juvenile, 55 mm TL. B. Juvenile, 120 mm TL. C. Juvenile, ca. 163 mm TL. D. Juvenile, 206 mm TL. E. Juvenile, 370 mm TL. F. Juvenile, 455 mm TL. G. Possible juvenile, 634 mm TL. (A, B, D, E, G, Parin, N. V., 1967: fig. 22. C, Bean, T. H., 1903: fig. 15. F, Poll, M., 1953: fig. 38.)

At 15.2 mm body elongate, cylindrical; at 19.3 mm head and anterior half of body comparatively deeper.⁶⁴ At 11 mm SL scarcely any beak at all, lower jaw decidedly prognathous; ⁴ at 44 hours jaws slightly elongate. Minute teeth at 44 hours; teeth conspicuous at 19.3 mm. Eye noticeably oval at 19.3 mm; nostrils distinct at 12.9 mm. Pelvic buds evident at 36 hours, all other fins with full ray complements at 12.9 mm; caudal truncate at 19.0 mm.⁶⁴

Pigmentation: At 12.9 mm tip of snout to region of pectorals greenish yellow; dorsal and dorsolateral region behind pectorals with small stellate black melanophores giving gray appearance to region; melanophores along ventral and ventrolateral surfaces larger, more conspicuous; top of head, behind eyes, crowded with black stellate melanophores. At 36 hours whole body greenish yellow or brown; head with mixture of black stellate

melanophores and orange spots; dorsal finfold completely black; belly less pigmented than rest of body. At 15.2 mm pigment heavily concentrated along sides; chromatophores at base of pectorals more conspicuous; 3-4 large chromatophores in row along isthmus; pelvics unpigmented. At 19.3 mm ventrolateral region with pitch black melanophores; melanophores of rest of body faint brownish; interspinous membrane of dorsal and anal deeply pigmented; caudal fin deeply pigmented at base, otherwise colorless; pelvics and distal parts of pectorals colorless.⁶⁴

JUVENILES

Minimum size described, 21.0 mm.⁶⁴

Head measured from tip of upper jaw 3 times in TL in young; depth 7.2 times in distance from occiput to dorsal.⁵⁴

At 24-50 mm jaws short, strong;³⁴ no pronounced half-beak condition at any time, jaws nearly co-terminal at all sizes.^{4,18} Beak of "young" more slender and proportionately longer than in adult.¹³ At 21 mm 11 teeth on each side of upper jaw, 9 on each side of lower, the upper series the strongest; teeth well-developed, raptorial at 30 mm,^{4,17} distinctly curved forward in specimens less than 500-600 mm long.^{12,65} A thin, flexible, membranous flap capable of muscular movements developed on each

side of lower jaw, beginning at 19.5 mm and retained to sizes of less than ca. 150 mm SL⁴ to extreme of 300 mm SL;¹⁹ at 165 mm flap folded under lower jaw, meeting its fellow from the opposite side.^{2,3} Second lobe of dorsal fin greatly extended and darkly pigmented; time of formation of lobe variable, just beginning to elongate in some specimens at 11 mm SL, and not evident, or well-developed, in others at 59 mm;^{4,19} at maximum development (ca. 150¹⁸-165 mm) lobe heavily pigmented and capable of moving in water like flag;^{4,19} longest dorsal ray equal to distance from middle of pupil to end of head;² elevated lobe retained in some specimens to 300 mm SL;¹⁹ lost through disintegration or sloughing rather than resorption,¹⁸ the loss accompanied by elevation of anterior dorsal rays which soon exceed length of posterior rays. Last anal rays not elevated⁴ (a report of last anal rays much elevated⁵⁵ is questioned, JDH). First pelvic ray branched at 200-300 mm SL.⁷ Caudal definitely forked in some specimens at 19.5 mm SL,⁴ apparently rounded in others at 30-50 mm.¹⁷ Preanal finfold still evident at 21 mm.⁶⁴ Lower jaw extension 0.5-1.6 percent of SL in specimens smaller than ca. 170 mm SL.⁷

Pigmentation: At 21 mm faint brownish stellate chromatophores on upper body, ventral and ventrolateral surfaces dark.⁶⁴ At 25-50 mm posterior rays of dorsal blackish, other fins whitish.³⁴ Specimens up to about 50 mm capable of extensive and rapid color changes, apparently matching environment in shade and, to some

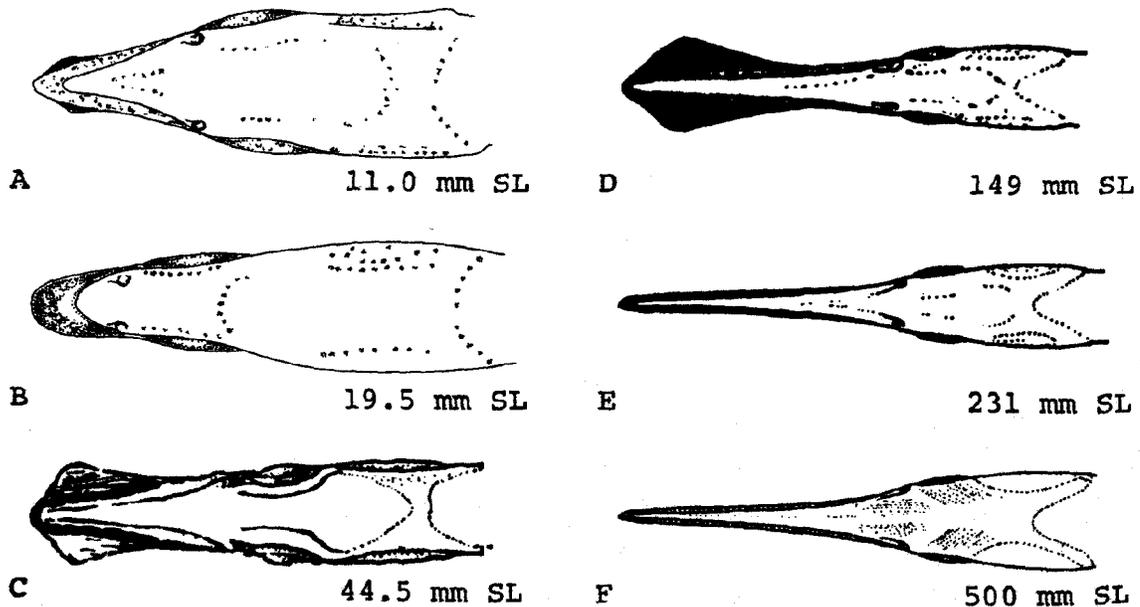


Fig. 53. *Tylosurus crocodilus*, Houndfish. Development of head and beak. A. 11.0 mm SL. B. 19.5 mm SL. C. 44.5 mm SL, lappets developing. D. 149 mm SL, lappets fully developed, pigmented. E. 231 mm SL. F. 500 mm SL. (A, B, Breder, C. M., Jr., 1934: pl. 2, Elizabeth Ray Peters, delineator. C-F, Breder, C. M., Jr., 1934: pl. 2.)

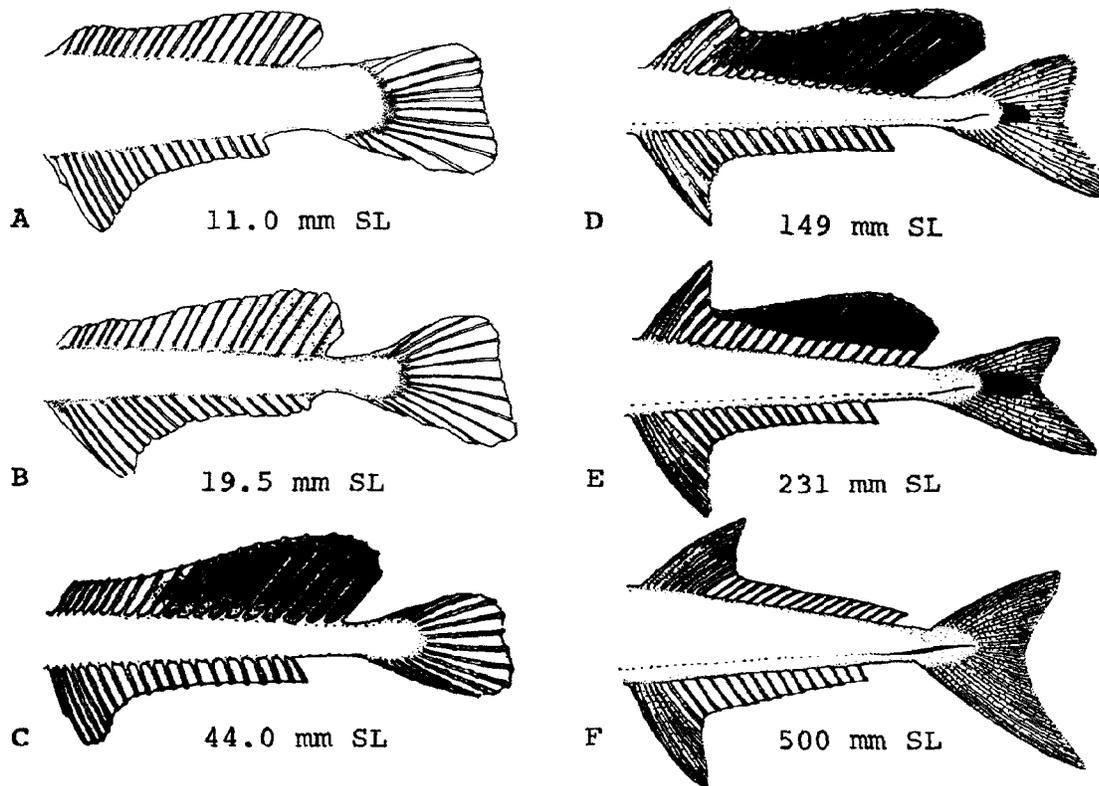


Fig. 54. *Tylosurus crocodilus*, Houndfish. Development of dorsal fin. A. 11.0 mm SL. B. 19.5 mm SL, pigment developing on posterior lobe of dorsal. C. 44.0 mm SL. D. 149 mm SL, posterior lobe of dorsal at maximum development. E. 231 mm SL, dorsal lobe diminishing. F. 500 mm SL, definitive form of dorsal fin established. (A, B, Breder, C. M., Jr., 1934: pl. 4, Elizabeth Ray Peters, delineator. C-F, Breder, C. M., Jr., 1934: pl. 4.)

extent, pattern, commonly pale cream to tan; some individuals of these sizes with dark band and resembling *Sphyræna barracuda*.^{4,24} At 50 mm light brown above, brownish below, lappets jet black.¹⁷ At 59 mm back olive-green, prominently sprinkled with melanophores; color of back bounded by black lateral stripe from snout to top of central caudal rays; silvery below, except for dark band running from isthmus to vent; lower jaw black below; lateral band about 3/4 diameter of eye; ventral band 1/2 eye diameter; iris golden centrally, silvery below, brownish above; fins hyaline.^{4,5} A specimen ca. 114 mm long from Bermuda was apparently patternless, but was covered throughout with stellate chromatophores.⁶ At ca. 152 mm straw-colored, possibly to match flotsam in environment;²¹ adult pattern may develop at this size. At ca. 165 mm greenish above; silvery below; 14 black blotches on side not extending to caudal, the largest 2/3 as wide as length of eye; mandibular lappets dark; dorsal black except for first 6 rays which are pale; pelvics, pectorals, anal, and most of caudal pale; anterior half of upper caudal lobe with black in membrane covering rays.^{2,2} Lappets initially white,⁴ partially pigmented at

30 mm, jet black at 50 mm.¹⁷ In "young" an overall reddish cast and conspicuous black bars while black dorsal lobe is evident;³¹ lateral pattern also described as a row of large, round, dusky spots;³³ final shape of dorsal fin foreshadowed by shape of melanin area before 2nd dorsal lobe is lost.¹⁹

AGE AND SIZE AT MATURITY

Mature at 1 1/2 years¹⁹ to possibly 3rd year,¹⁸ and 446¹⁰–800 mm.⁴

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Cheilopogon heterurus

flyingfishes
Exocoetidae

FAMILY EXOCOETIDAE

Flyingfishes are closely related to the halfbeaks (Hemiramphidae) and the flying halfbeaks (Oxyporhamphidae). Although Greenwood, *et al.* (1966), combined these three groups into a single family, Exocoetidae, some researchers have continued to recognize them as distinct (but closely similar) families. Flyingfishes may be distinguished from halfbeaks by their more compact bodies, lack of a prolonged lower jaw, and by the noticeably elongate pelvic and/or pectoral fins. Parin (1961) found minor but apparently consistent differences between the Exocoetidae and Oxyporhamphidae and suggested that the genus *Oxyporhamphus* (the only genus which he attributed to Oxyporhamphidae) was more closely related to the hemiramphids than to the exocoetids. There are two major groups of flyingfishes: the four-winged flyingfishes in which both the pectoral and pelvic fins are greatly elongated, and the two-winged flyingfishes in which only the pectoral fins are noticeably enlarged.

The exocoetids, represented by seven genera and 46 species, are primarily surface-dwelling, offshore, oceanic fishes and are found in tropical and temperate waters throughout the world. They are best known for their remarkable aerial flights, the most spectacular of which are made by the four-winged species. According to Stephens (1965) glides of up to 1000 feet or more are possible, but the average gliding distance is probably between 100 and 300 feet. Flyingfishes usually glide 4 or 5 feet above the surface, but flights are reported to reach extreme altitudes of 25 to 36 feet.

Although a number of flying fishes have been reported off Virginia, Maryland, Delaware, and New Jersey, or northward of this area,* there are definite records for only one species, *Cheilopogon heterurus*, within the Mid-Atlantic Bight as defined here. Several subspecies of *heterurus* are recognized, one of which, *Cheilopogon h. doderleini*, occurs in the Sea of Japan.

The eggs of flyingfishes are highly variable. Those of the two-winged species are buoyant and lack attachment filaments, while those of the four-winged species are demersal and have well-developed chorionic filaments. The filaments may be of equal length and evenly distributed over the chorion; may be evenly distributed, but with one filament noticeably longer than the others; may be of equal length and arranged in clusters at opposite poles of the egg; may be in opposing clusters with one filament noticeably longer than the others; or may be in a cluster at one pole with a single, large filament at the opposite pole. All flyingfish eggs lack oil globules.

There are apparently minor differences in eggs of *Cheilopogon heterurus* from the West Indies and Japan (length and possibly number of filaments); but in both of these populations the filaments are distributed evenly over the chorion. In eggs from the Mediterranean attributed to *Cheilopogon heterurus* by D'Ancona (1933) there are 9 to 16 filaments in a cluster at one pole and a single somewhat longer filament at the opposite pole. Larvae described with these eggs do not agree in details of pigment development with larvae from Japan, and it is unlikely that the Mediterranean eggs and larvae are, in fact, conspecific with *Cheilopogon heterurus*.

In yolk-sac larvae of the regional species (*C. heterurus*) the anus lies about three-fifths of the distance of the tail tip, the body is heavily pigmented throughout, and there are well-developed pectoral buds in the smallest specimens de-

**Cheilopogon cyanopterus*, *exsiliens*, and *frucatus*; *Cypselurus comatus*; *Exocoetus obtusirostris* and *volitans*; *Hirundichthys affinis* and *ronletii*; *Parexocoetus brachypterus*; and *Progonichthys gibbifrons*.

scribed. In larvae the pectoral and anal fins are relatively large, the dorsal fin is noticeably longer than the anal fin, the jaws are not extended, and the body is deep anteriorly, tapering to a narrow caudal peduncle. Developing juveniles are characterized by the presence of a pair of fringed barbels and a series of broad vertical lateral bars. The barbels are retained to a maximum length of about 110 mm SL, and the barred pattern to at least 80 mm SL. Parin (1961) has described a "*Parexocoetus* stage" in the juveniles of some members of the genus *Cheilopogon* and several other genera. This stage is characterized by a melanistic expanded lobe in the middle portion of the dorsal fin. It does not occur in *Cheilopogon heterurus*.

Cheilopogon heterurus (Rafinesque), Atlantic flyingfish

ADULTS

D. 10–15; A. 8–12¹ (a minimum count of 6²³ is questioned, JDH); C. 5–6+7+8+6–8;³² P. 13–17;¹ V. 6³ (D., A., and C. counts include juveniles as small as 15 mm SL); predorsal scales 22–38;^{1,15} predorsal scales in lateral series 16–24 (count includes some juveniles); lateral line scales 56–60;¹⁴ scales above lateral line 6–9 (count includes some juveniles);¹ gill rakers 5¹³–8²³+15¹³–18;⁶ vertebrae 42–49 (30–34+14–16).^{1,3,5,13,15}

Proportions expressed as percent SL (including some juveniles): Preanal length 74.7–81.6, predorsal length 65.3–71.7, pelvic length 51.8–58.2, prepectoral length 20.4–25.4, head length 20.0–27.1, snout length 3.2–8.7, interorbital width 6.9–8.8, pectoral length 39.3–77.8, dor-

sal height 7.8–23.8, anal height 6.2–13.4, dorsal base 18.0–23.0, anal base 10.7–13.5, greatest depth 14.5–20.3, depth of caudal peduncle 6.3–7.7, body width 11.8–16.2.¹

Body moderately robust,¹² quadrate; head blunt;⁸ mouth terminal, small; maxillary not reaching front of orbit.¹⁸ Teeth unicuspid; premaxillary teeth very small; palatine teeth lacking.^{1,11} Pectoral fins beyond anal when depressed, pelvics far forward and about half as long as pectorals, second pectoral ray branched.¹¹

Pigmentation: Grayish,²² dark blue-gray,¹¹ or brownish black above,²⁷ silvery on lower sides and belly. Cheeks, operculum, and iris silvery.²² Dorsal fin little pigmented, and frequently lacking pigment in specimens larger than 150 mm SL;¹ anal fin plain;^{12,13} caudal fin gray with

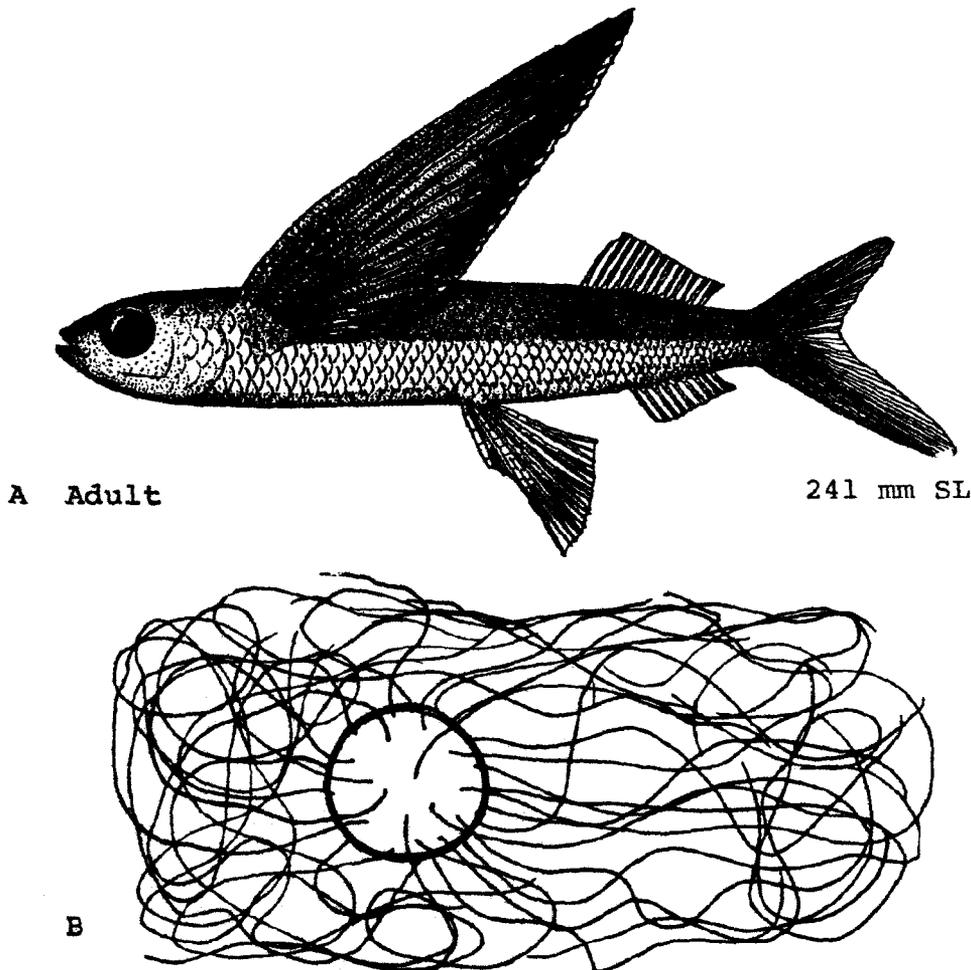


Fig. 55. *Cheilopogon heterurus*, Atlantic flyingfish. A. Adult, 241 mm SL. B. Egg of *Cypselurus heterurus dodderleini*, diameter 1.86 mm. (A, Breder, C. M., Jr., 1938: fig. 29. B, Tsukahara, H., et al., 1957: fig. 13.)

darker streaks;¹⁸ pelvic fins transparent⁹ or white,^{12,20} slightly dusky at axils,² described as lightly pigmented with vague pale crossbands, but nearly clear in many specimens longer than 180 mm SL; pectoral fins dark with pale crossbands and narrow pale posterior margin (at least at sizes greater than 150 mm), crossbands widest mesially and tapering toward anterior margin of fin, triangular in shape; first pectoral ray often lightly pigmented.¹

Maximum length: 435 mm.²⁷

DISTRIBUTION AND ECOLOGY

Range: Tropical and temperate waters of Atlantic; also the Mediterranean Sea,¹ the Red Sea,²⁸ and represented by a distinct subspecies, *Cypselurus heterurus doderleini*, in Japan.²⁶ In western Atlantic from the Newfoundland Banks and possibly Sable Island^{4,19} south to Rio de Janeiro,²⁹ including Bermuda.¹ In the eastern Atlantic from Oslo Fjord, Norway,⁷ southward, including the English Channel¹⁶ to 4° N.¹

Area distribution: North in Chesapeake Bay to mouth

of Potomac River;^{7,10} also coast of New Jersey,³⁰ and Atlantic coast of Maryland.³¹

Habitat and movements: Adults—a coastal, inshore species;^{1,21} sometimes entering bays.²⁹ Maximum recorded distance from land, 643 km.¹

Apparently follow currents seasonally in Japan;²⁵ more abundant in Puerto Rico in winter than summer suggesting inshore-offshore movements.²

Larvae—swim to surface after hatching, attach to seaweed several days later.²⁴

Juveniles—close inshore at surface;¹ begin making short, sporadic gliding flights about 1 month after hatching.²⁴

SPAWNING

Location: Coastal waters,¹ sometimes in major channels¹⁷ and near straits.⁶

Season: In Morocco, June and July,¹ also a “ripe specimen” October 5;¹³ in Puerto Rico, “developed eggs” April 1;² in the Bahamas, ripe eggs in March.¹⁷ A ripe

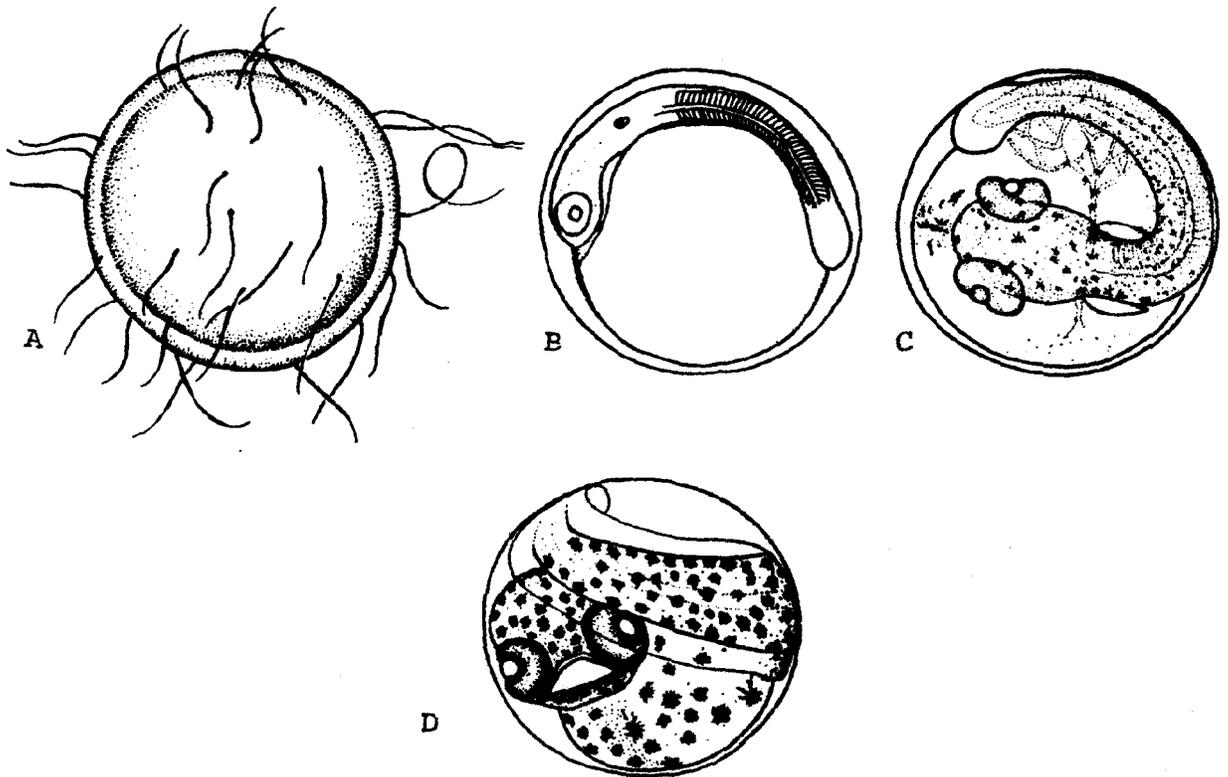


Fig. 56. *Cheilopogon heterurus*, Atlantic flyingfish. A. Ovarian egg, western Atlantic Ocean (note apparently short filaments compared to Japanese subspecies). B. Developing egg, 4 days old, myomeres evident. C. 10 days old, pigments developing. D. Advanced embryo, 14 days old. (A, Breder, C. M., Jr., 1927: 20. B-D, Tsukahara, H., et al., 1957: fig. 13.)

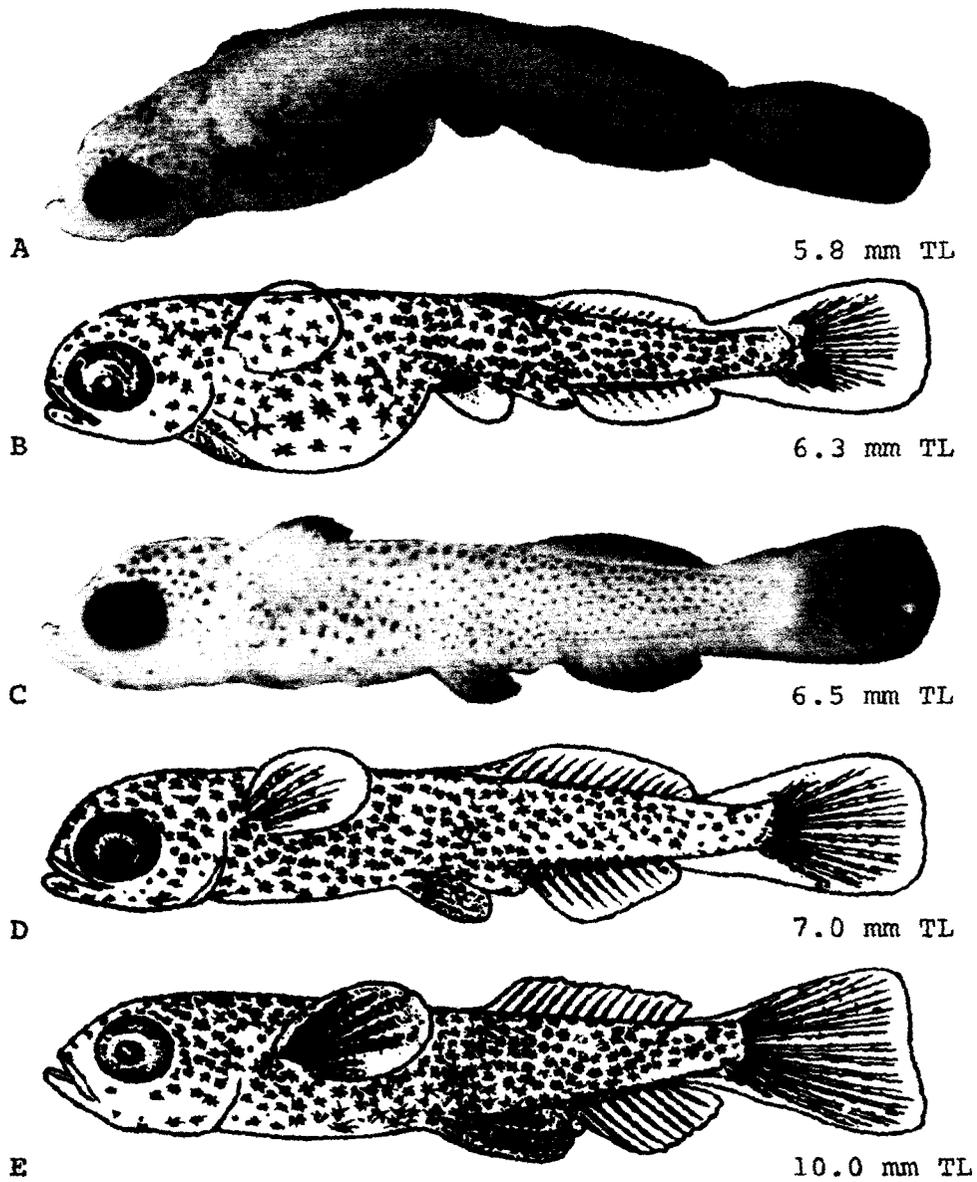


Fig. 57. *Cheilopogon heterurus*, Atlantic flyingfish. A-E. All specimens from Japan. A. Yolk-sac larva, 5.8 mm TL, pelvic fins developing. B. Yolk-sac larva, 6.3 mm TL. C. Larva, 6.5 mm TL. D. Larva, 7.0 mm TL. E. Larva, 10.0 mm TL. (A, C, Imai, S., 1958: pl. 37. B, D-E, Tsukahara, H., et al., 1957: fig. 13.)

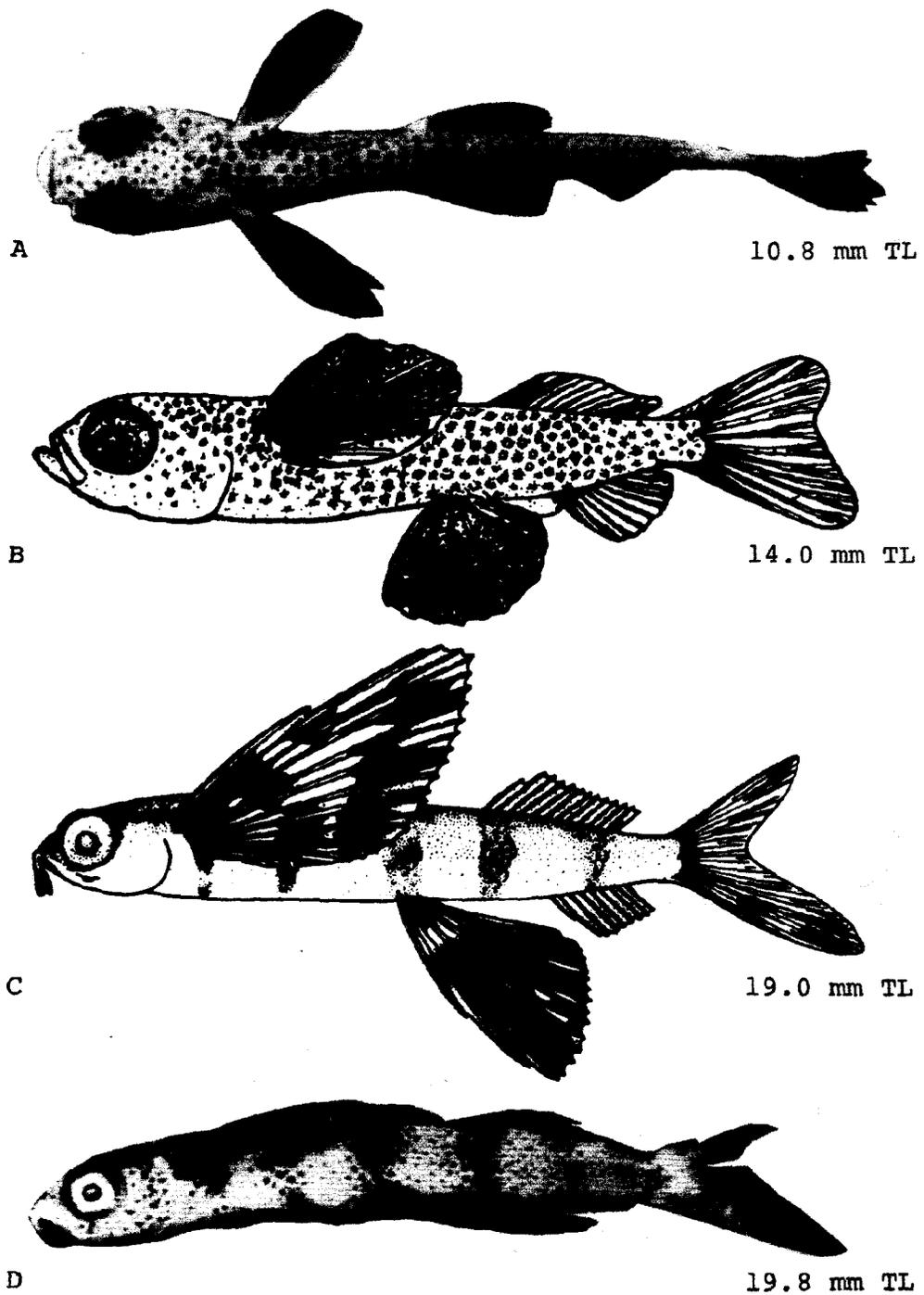


Fig. 58. *Cheilopogon heterurus*, Atlantic flyingfish. A-D. All from Japan. A. Larva, dorsal view, 10.8 mm TL. B. Larva (or early juvenile), 14.0 mm TL. C. Juvenile, 19.0 mm TL, barbels formed, banded pattern established. D. Juvenile, 19.8 mm TL. (A, D, Imai, S., 1958: pl. 37. B, C, Tsukahara, H., et al., 1957: fig. 13.)

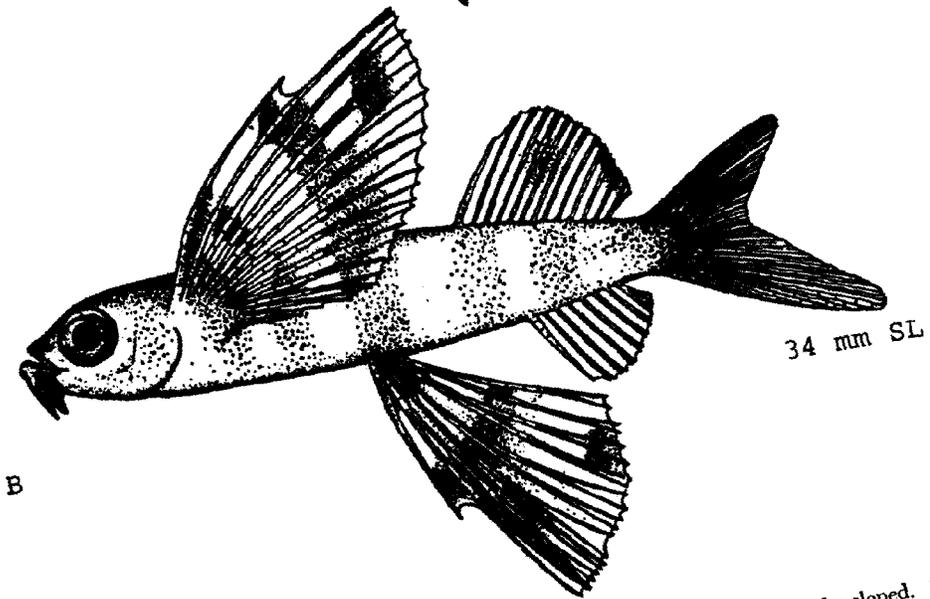
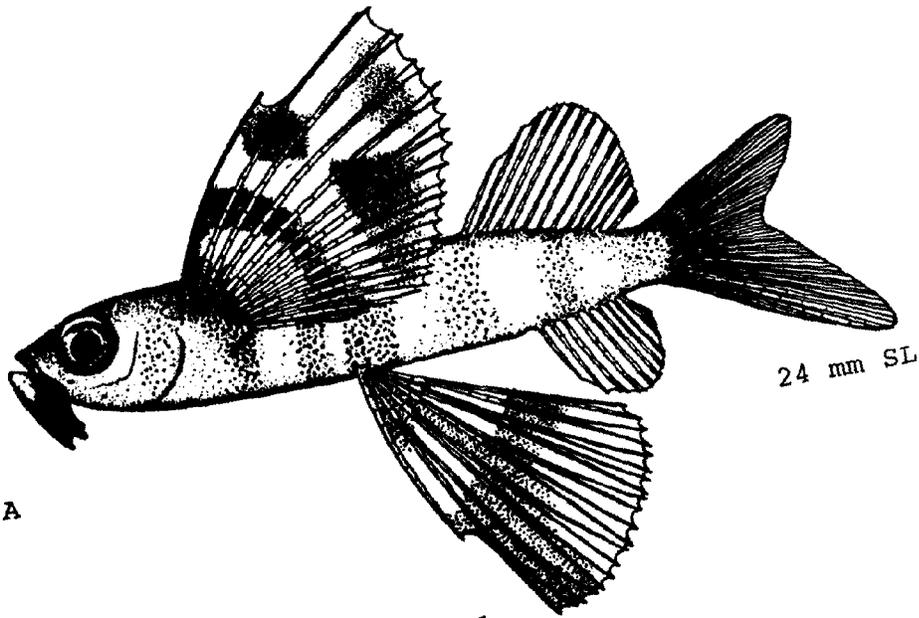


Fig. 59. *Cheilopogon heterurus*, Atlantic flyingfish. A. Juvenile, 24 mm SL, barbels well-developed. B. Juvenile, 34 mm SL. (A, B, Breder, C. M., Jr., 1938: fig. 31.)

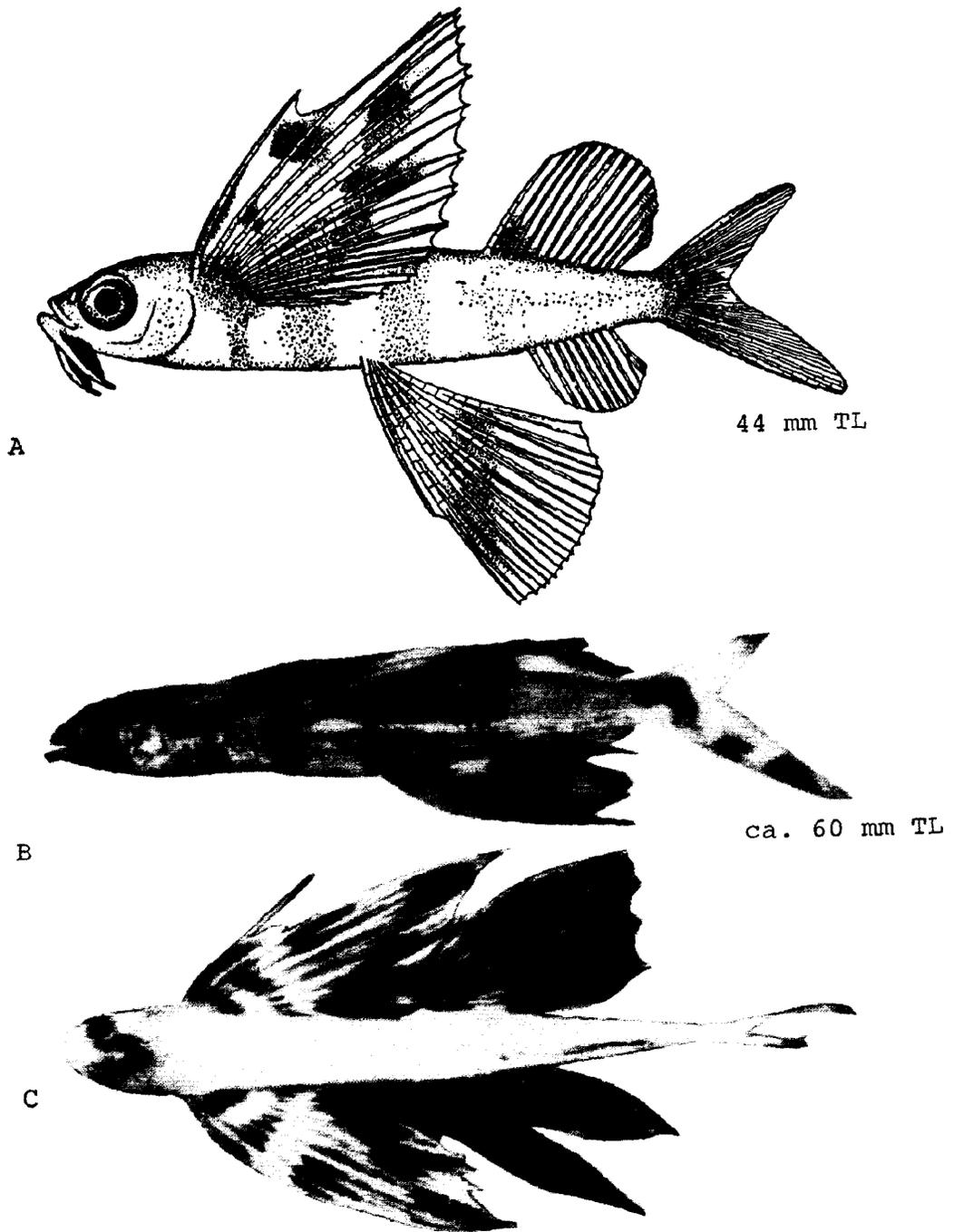


Fig. 60. *Cheilopogon heterurus*, Atlantic flyingfish. A. Juvenile, western Atlantic Ocean, 44 mm TL. B. Juvenile, Japan, ca. 60 mm TL. C. Dorsal view of B. (A, Breder, C. M., Jr., 1938: fig. 31. B, C, Tsukahara, H., 1957: fig. 16.)

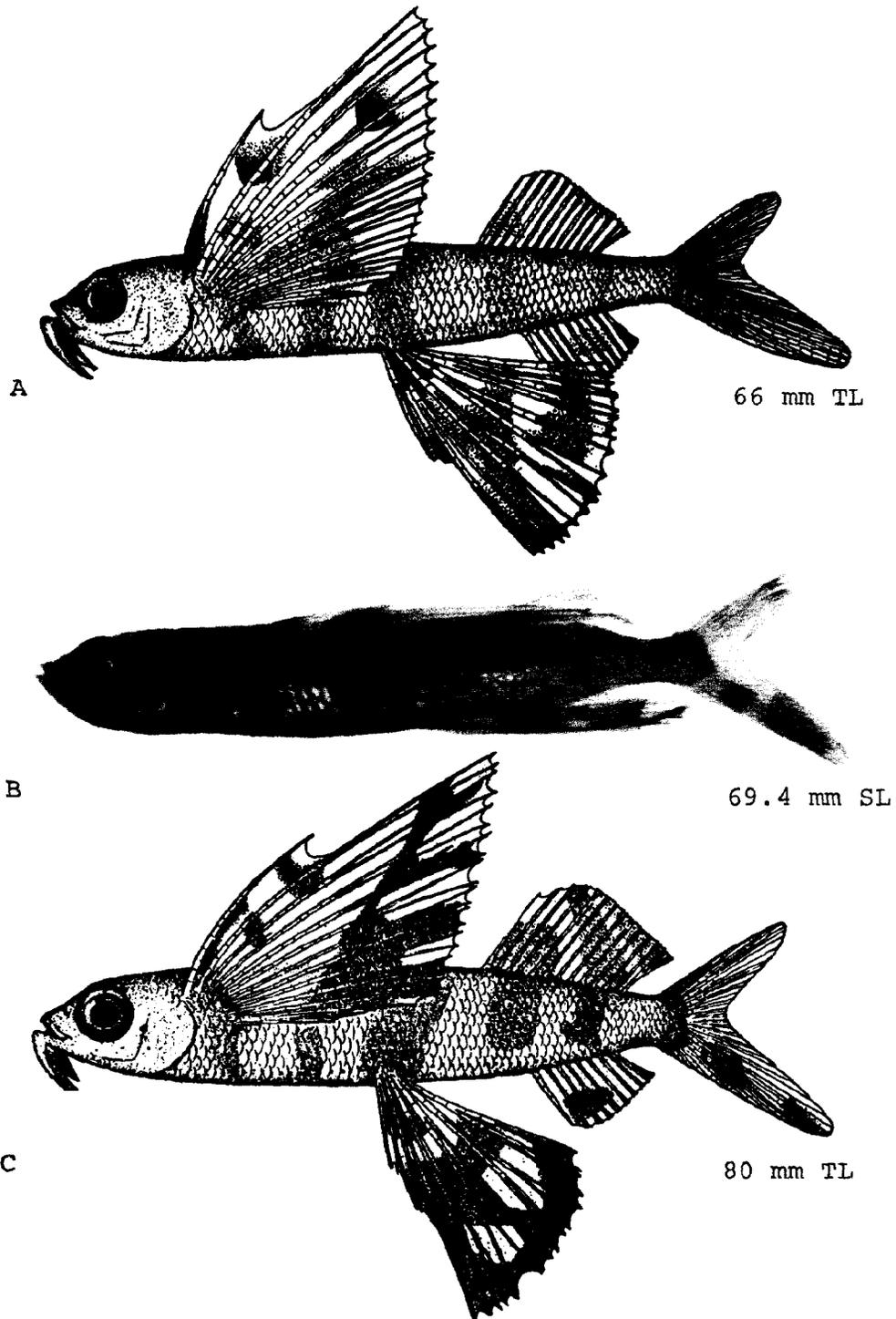


Fig. 61. *Cheilopogon heterurus*, Atlantic flyingfish. A. Juvenile, Atlantic Ocean, 66 mm TL. B. Juvenile, Atlantic Ocean, 69.4 mm SL. C. Juvenile, Atlantic Ocean, 80 mm TL. (A, C, Breder, C. M., Jr., fig. 30. B, Staiger, J. C., 1965: fig. 16.)

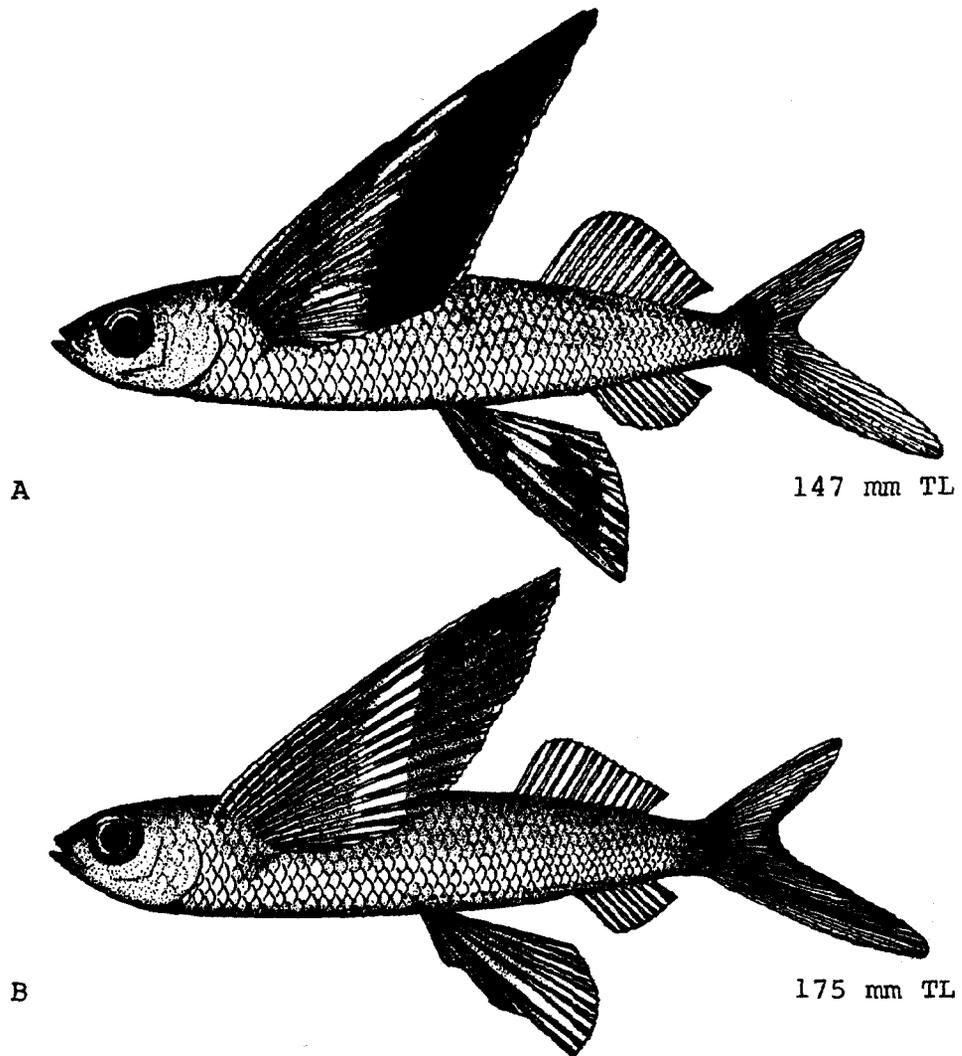


Fig. 62. *Cheilopogon heterurus*, Atlantic flyingfish. A. Juvenile, Atlantic Ocean, 147 mm TL (note lack of barbels and banded pattern). B. Juvenile, Atlantic Ocean, 175 mm TL. (A, B, Breder, C. M., Jr., 1938: figs. 29-30.)

male was reported in mid-August in Oslo Fjord (but this is almost certainly not a spawning area).⁶

Fecundity: About 8500-10,000.²⁴

EGGS

Location: Demersal.⁶

Ripe ovarian eggs: Diameter 1.6-1.8 mm (average ca. 1.7 mm);^{15,17} capsule with adhesive filaments.^{1,13}

Fertilized eggs: Average diameter, 1.86 mm; capsule with numerous, long, evenly distributed filaments;²³ oil globules absent.²⁴

EGG DEVELOPMENT

Development at unspecified temperature:

- | | |
|------------|--|
| At 4 days | Tail bud still apparently attached; eye, lens, and otoliths formed; somites developing. |
| At 10 days | Pectoral fins evident; scattered small chromatophores on head, body, and yolk. |
| At 14 days | Large, stellate chromatophores on head, body, yolk, and eyes; mouth apparently formed. ²³ |

Incubation period, at 20-22 C, ca. 14 days.²⁴

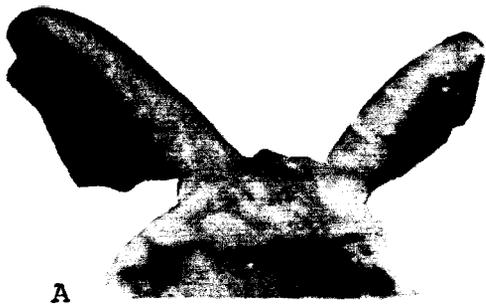


Fig. 63. *Cheilopogon heterurus*, Atlantic flyingfish. A. Barbels of juveniles. (A, Tsukahara, H., et al., 1957: fig. 17.)

YOLK-SAC LARVAE

Size range described, 5.8–6.3 mm TL.

Rays developed in vertical fins at 5.8 mm TL; pelvic buds well-developed, rayless throughout stage.^{23,26}

Pigmentation: Large chromatophores distributed more or less evenly over body and head, except in ventral part of yolk sac. At 6.3 mm chromatophores developed along caudal fin rays.^{23,26}

LARVAE

Size range described, 6.5–14.0 mm TL.

Rays developing in pectoral and caudal fins at 6.5 mm TL, well-developed (although pectoral apparently incomplete) at 14.0 mm TL.^{23,26}

Pigmentation: Chromatophores evenly distributed except, apparently, on abdomen. At 10.8 mm TL a definite row of closely spaced chromatophores along each side of mid-dorsal line, and chromatophores along rays of pectoral and pelvic fins.^{23,26}

JUVENILES

Minimum size described, 19.0 mm TL.

Barbels evident at 19.0 mm TL,²³ and reaching maximum relative length at ca. 25 mm SL; ¹ lost at ca. 89 mm TL ¹⁸ to 110 mm SL. ¹ In specimens less than 100 mm SL, first pectoral rays less than 38 percent SL, distance between first and second pectoral rays (measured at distal end of first) greater than 1.7 times distance between second and third. Height of dorsal fin ca. 17 percent (average) SL in specimens up to ca. 70 mm SL, decreasing to mean height of ca. 11 percent at 150 mm SL. Barbels never more than 15 percent SL. ¹ Sexes distinguishable at 175 mm SL.

Pigmentation: Initially with light background and ca. 6

broad vertical pigment bands on sides and belly; dorsal surface pale and lacking bands. Banded pattern retained to at least 80 mm SL. By ca. 125 mm SL back dark, belly silvery as in adult. ¹ At 175 mm TL dorsal fin uniform grayish, anal unpigmented. ¹³ Pectoral and pelvic fins highly variable with development (see figures 64 and 65); ¹ at 140 mm pectoral fin essentially dark with light median band. ¹⁵ In small juveniles lower lobe of caudal clear with a dark spot at base and another on distal half; upper lobe frequently devoid of pigment to length of ca. 55 mm SL, then 2 spots on upper lobe similar to those of lower lobe. Caudal pigment increases to 140 mm SL, and rest of fin darkly pigmented. ¹ Barbels apparently blackish in Atlantic specimens; ²² yellow with black outer edges in Japan. ²⁴

AGE AND SIZE AT MATURITY

One year; ²⁴ minimum size ca. 200 mm SL (sex not stated), ¹ ripe male at 342 mm TL. ⁶

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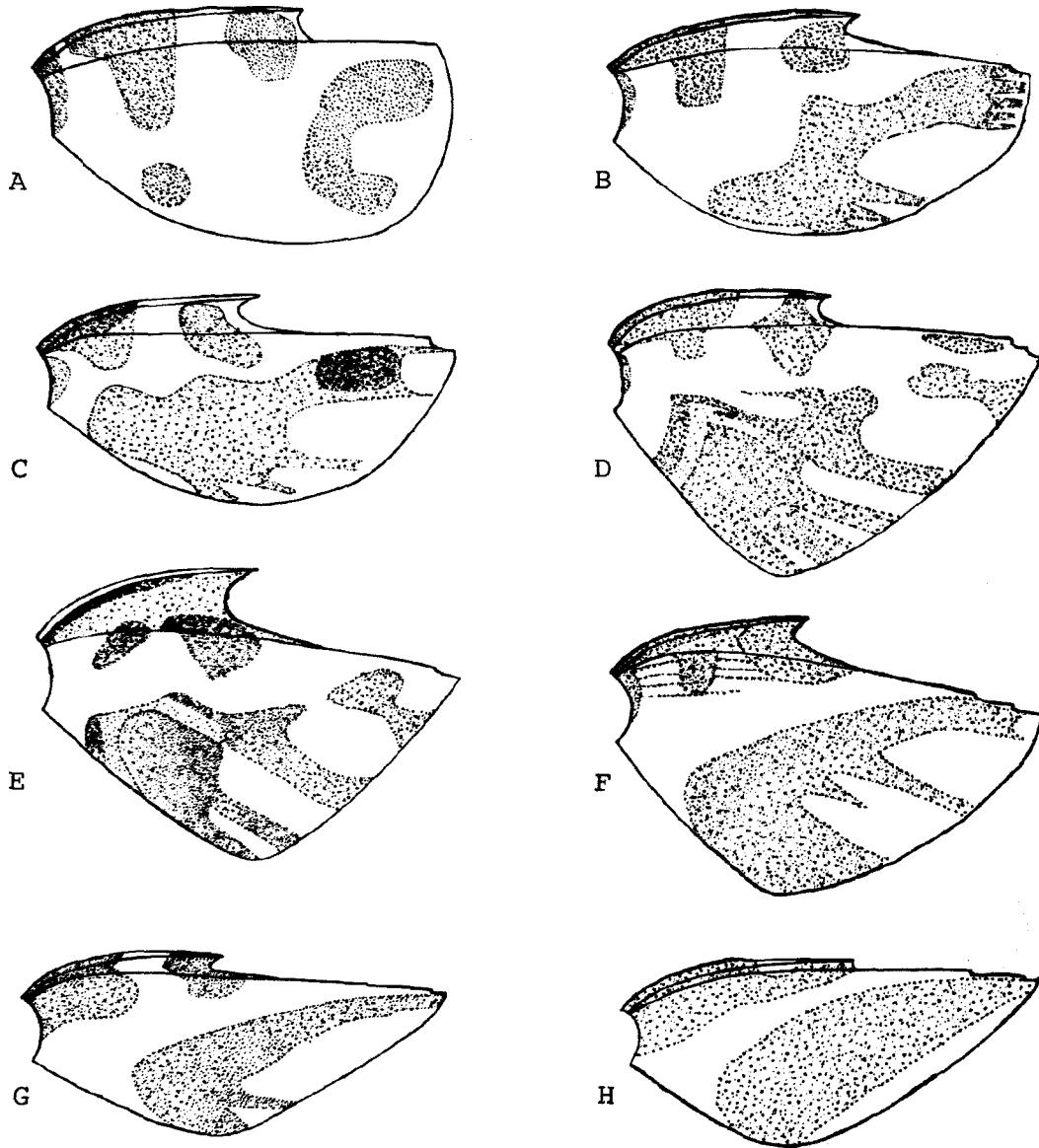


Fig. 64. *Cheilopogon heterurus*, Atlantic flyingfish. A-H. Development of pigment in pectoral fins. A. 21.5 mm SL. B. 20.3 mm SL. C. 40.0 mm SL. D. 77.9 mm SL. E. 86.3 mm SL. F. 99.9 mm SL. G. 111.4 mm SL. H. 125.2 mm SL. (A-H, Staiger, J. C., 1965: fig. 17.)

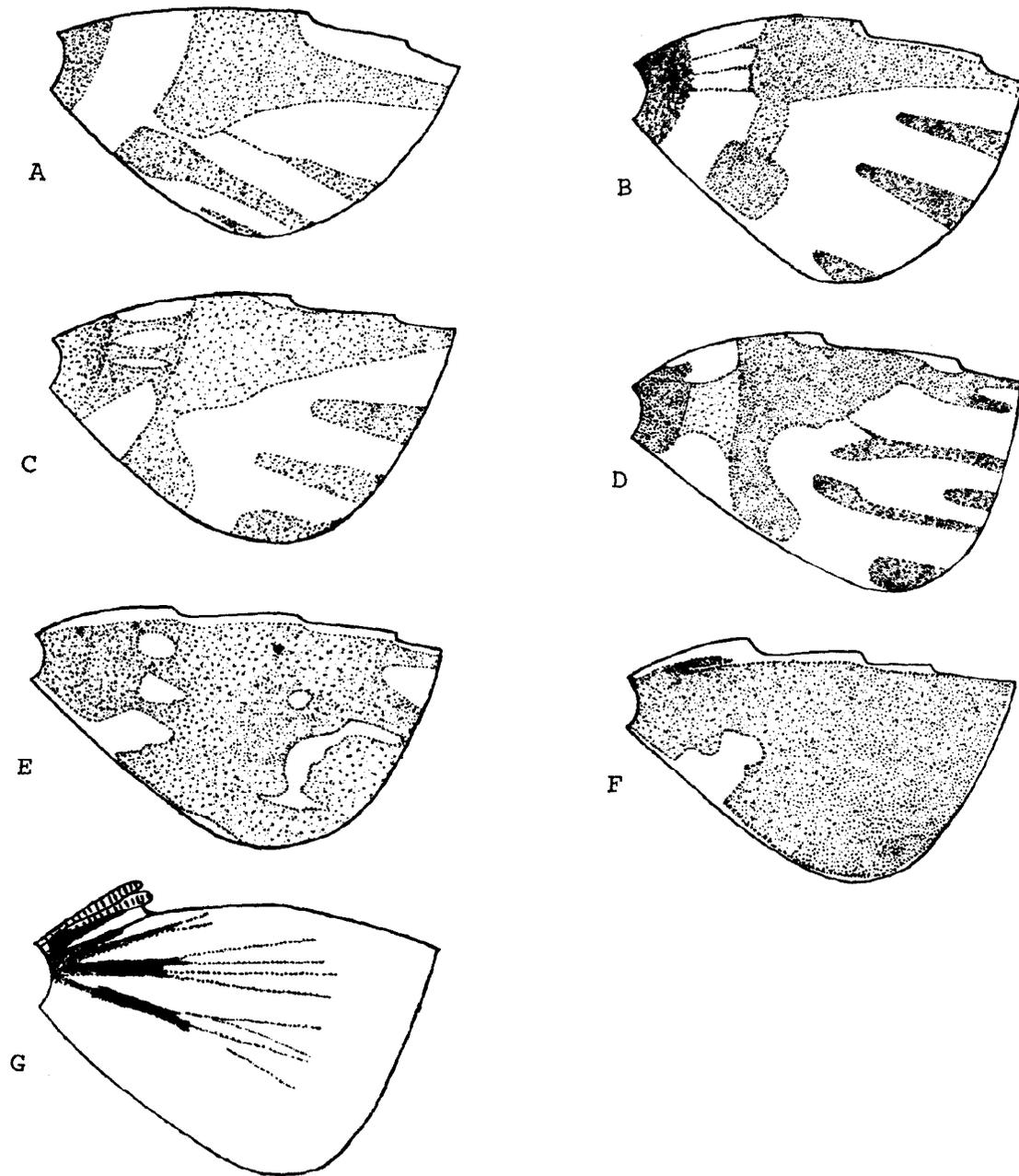


Fig. 85. *Cheilopogon heterurus*, Atlantic flyingfish. A-G. Development of pigment in pelvic fins. A. 21.5 mm SL. B. 30.3 mm SL. C. 40.0 mm SL. D. 58.7 mm SL. E. 92.7 mm SL. F. 125.2 mm SL. G. 220.1 mm SL. (A-G, Staiger, J. C., 1965: fig. 18.)

Euleptorhamphus velox
Hemiramphus brasiliensis
Hyporhamphus unifasciatus

halfbeaks
Hemiramphidae

FAMILY HEMIRAMPHIDAE

Although the halfbeaks were recently placed in the family Exocoetidae by Greenwood, *et al.* (1966), a number of researchers have continued to recognize Hemiramphidae as a distinct family. In these fishes the body is compressed laterally, the pectoral fins are not noticeably elongate, the lower lobe of the caudal fin is frequently longer than the upper, the dorsal and anal fins are relatively small and situated far back on the body, the scales are large, and the lower jaw is usually greatly extended. Halfbeaks occur in marine, estuarine, and freshwater, but are primarily schooling, pelagic, marine fishes. Some species make short aerial flights similar to the flights of flyingfishes. This characteristic is best developed in *Euleptorhamphus*, a species which is generally restricted to the open ocean. The family includes 12 genera and between 60 and 70 species.

Three species occur in the Mid-Atlantic Bight. A fourth species, *Hemiramphus balao*, has been recorded from the upper Chesapeake Bay (Musick, 1972), but the specimen on which this record is based is no longer available and the identity is questionable. *Hyporhamphus unifasciatus*, as defined here, may be a composite of two or more species (BBC). If so, information based on Caribbean specimens may actually apply to some other form.

Data summarized by Breder and Rosen (1966) suggest that, in marine halfbeaks, spawning takes place at the surface during daylight hours and the eggs are attached to aquatic vegetation or objects floating in the water. Most hemiramphids deposit eggs; some are ovoviviporous, and a few are viviporous. External fertilization is characteristic of most marine species, but some of the live-bearing, brackish and freshwater forms have modified anal rays and enlarged genital papilla which may aid in direct sperm transfer.

Hemiramphids produce both pelagic and demersal eggs. These may have chorionic filaments of various sizes or, in some species, lack filaments altogether. All halfbeak eggs lack oil globules.

In larvae of all of the regional halfbeaks the body is elongate with the dorsal and ventral profiles more or less parallel, the mouth is superior, the gut is straight, the anus is located roughly two-thirds the distance to the tip of the tail, the dorsal and anal fins develop far back on the body, and pigment develops in discrete rows, primarily along the dorsal and ventral surfaces. Larvae of *Hyporhamphus unifasciatus* (larger than 7.0 mm SL) have a striking dorsal pattern consisting of two rows of very large dark-bordered spots which tend to become confluent posteriorly. In *Hemiramphus brasiliensis* larvae (13.0 mm SL) there are two rows of dorsal melanophores, but these are obscure and the melanophores themselves are punctate and minute.

Juveniles of both *Hemiramphus brasiliensis* and *Hyporhamphus unifasciatus* have lateral fringes or folds on the anterior part of the developing beak. In *Hemiramphus* juveniles the posterior part of the dorsal fin is extended into a distinct posterior lobe and is darkly pigmented. In *Hyporhamphus* the posterior part of the dorsal is neither extended nor darkly pigmented. Juveniles of *Hemiramphus* characteristically develop a series of distinct vertical bands on the body. These bands do not occur in *Hyporhamphus*.

Euleptorhamphus velox Poey, Flying halfbeak**ADULTS**

D. 20¹⁰⁻²⁵; ¹⁷ A. 21-22; C. branched rays 7 upper, 6 lower; ^{3,5} P. 6¹⁰⁻⁷ or 8; V. 6; ^{2,3} lateral line scales ca. 139-144; predorsal scales 53-55; gill rakers on first arch 7-8 + 24-26; ⁵ vertebrae 69-73.¹⁹

Body elongate, compressed, band-like, subcarinate; ^{3,9} lower jaw greatly elongate (JDH); teeth on lower jaw longer than those on upper jaw; ⁵ pectoral fins elongate.⁴

Pigmentation: Light brown or olivaceous above; sides from upper edge of pectoral base downward bright silvery.^{3,9}

Maximum length: Ca. 610 mm.⁴

DISTRIBUTION AND ECOLOGY

Range: In the western Atlantic, Nantucket, Massachusetts^{8,13,15} south through Gulf of Mexico and the Caribbean to Recife, Brazil; in the eastern Atlantic from Cape Verde Islands and Nigeria,² also South Africa.^{16,17}

Area distribution: Coastal waters of New Jersey.^{6,11,20}

Habitat and movements: Adults—a pelagic,⁷ gliding,¹⁴ marine species recorded inshore over shallow reefs⁷ and in lagoons.¹²

Larvae—no information.

Juveniles—a juvenile 27.9 mm long recorded off south-eastern United States near 180 m depth contour.¹⁸

SPAWNING

Location: Unknown.

Season: Well-developed eggs in a female collected May 1 in Puerto Rico.¹

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LARVAE

No information.

JUVENILES

No information.

AGE AND SIZE AT MATURITY

A 190 mm female contained ripe eggs.¹⁵

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Fig. 66. *Euleptorhamphus velox*, Flying halfbeak. A. Adult, 135 mm SL. (A, Collette, B. B., 1965: fig. 2.)

Hemiramphus brasiliensis (Linnaeus), Ballyhoo**ADULTS**

D. 12–15; A. 11–15; ^{1,10} scales along body 53 ^{8,12,16}–61; ³ total vertebrae 52–55; preanal vertebrae 34–37; caudal vertebrae 16–18; total gill rakers first arch 28–38; second arch 20–30.¹

Proportions expressed as percent SL: Body length (posterior edge of opercle to base of caudal, 78.2–79.7; longest pectoral ray, 15.7–16.4; pectoral insertion to pelvic base, 42.6–43.3; pelvic insertion to caudal base, 33.3–35.3; distance from snout to tip of lower jaw, 29.1–31.6; depth at pectoral insertion, 12.9–13.7; depth at pelvic insertion, 13.1–13.6.²⁷ Proportions as times in SL: Head 4.3–4.6, depth 5.4–6.3.¹² Depth 6.75 times in length excluding jaw.¹⁷

Body rather robust,¹³ elongate, compressed,¹² deeper than wide; ¹³ sides nearly parallel and vertical; ² back more or less rounded.¹³ Head rather low,¹² mandible produced into long beak terminating with a fleshy flap.¹⁶ Teeth short,¹² in broad bands on premaxillary plate, rim of mouth, and lower jaw, lacking on beak.¹³ Air bladder cellular.^{2,13} Sensory canal on postorbital branched. Upper jaw naked.²²

Dorsal in advance of anal origin, its base 1.5–2.1 times that of anal base; ²² caudal deeply forked, the lower lobe much longer than the upper; ^{17,22} pectoral fin length less than distance from base of uppermost pectoral ray to posterior end of nasal fossa; ¹ pelvics inserted scarcely in front of dorsal ² and nearer hypural than gill opening.¹³

Pigmentation: Rich deep bluish green,^{8,17} dusky greenish brown,⁹ or dark greenish above; ¹⁶ sides and belly bright silver¹² or silver-white; however, dorsal and ventral colors may end abruptly in mid-lateral region¹⁶ and mid-lateral region may be marked with a dark streak which becomes wider and more diffuse posteriorly; midline of back with 3 narrow bands, all obscure, the central one often diffuse; ⁹ beak blackish, its tip bright orange or scarlet, and its membrane white-edged; ^{8,17} upper caudal lobe reddish orange,^{1,4} deep orange,⁸ orange,⁹ or yellow; lower lobe of caudal olivaceous; inner edge of both caudal lobes dark; ¹⁶ lobe of dorsal deep orange or orange-yellow; pelvics tipped or edged with yellow.^{8,17}

Maximum length: Ca. 381 mm TL.⁴

DISTRIBUTION AND ECOLOGY

Range: Both sides of the Atlantic; ²³ in the western Atlantic: Woods Hole, Massachusetts,^{1,16,21} to Rio de Janeiro, Brazil, and throughout the Gulf of Mexico and the West Indies; absent in Bermuda; in the eastern At-

lantic from the Cape Verde Islands and Dakar south to Luanda, Angola; ^{1,10} also elsewhere in Africa.^{25,26}

Area distribution: Coastal waters of New Jersey^{5,24} and in Maryland⁶ and Virginia waters of Chesapeake Bay.^{7,11,18}

Habitat and movements: Adults—coastal,²³ found in shallow water ⁷ and easily attracted to lights at surface at night;¹⁴ sometimes enter harbors¹⁷ and sometimes washed ashore.²⁰ In Florida inshore in November and again in January.¹⁹

Larvae—recorded from low salinity canals and creeks. Minimum salinity, 1.5–2.1 ppt.²⁷

Juveniles—pelagic;¹⁰ recorded from various Bahamian islands in March; ¹⁴ sometimes carried by Gulf Stream north of normal adult range.¹⁰ Juveniles 23.0–78.2 mm long recorded in Atlantic Ocean near 180 m depth contour.²⁸

SPAWNING

No information.

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LARVAE

Size range described, 8.0²–13.5 mm SL.²⁷

Myomeres 37 + 17 = 54.²⁷

Proportions as percent SL (at 13.0–13.5 mm SL): Posterior edge of opercle to base of caudal, 79.2–80.7; longest pectoral ray, 14.2–15.8; pectoral insertion to pelvic insertion, 38.7–39.3; pelvic to caudal base, 35.0–35.9; depth at pectoral base, 7.60–9.20; depth at pelvic insertion, 6.50–7.10.²⁷

Body elongate, shallow, compressed. Beak first evident in a specimen 13.0 mm SL, not so in another at 13.5 mm SL. Choroid fissure evident throughout stage. Preanal finfold extended well anterior to pelvic insertion. At 13.0–13.5 mm SL all fin rays ossified except ventralmost

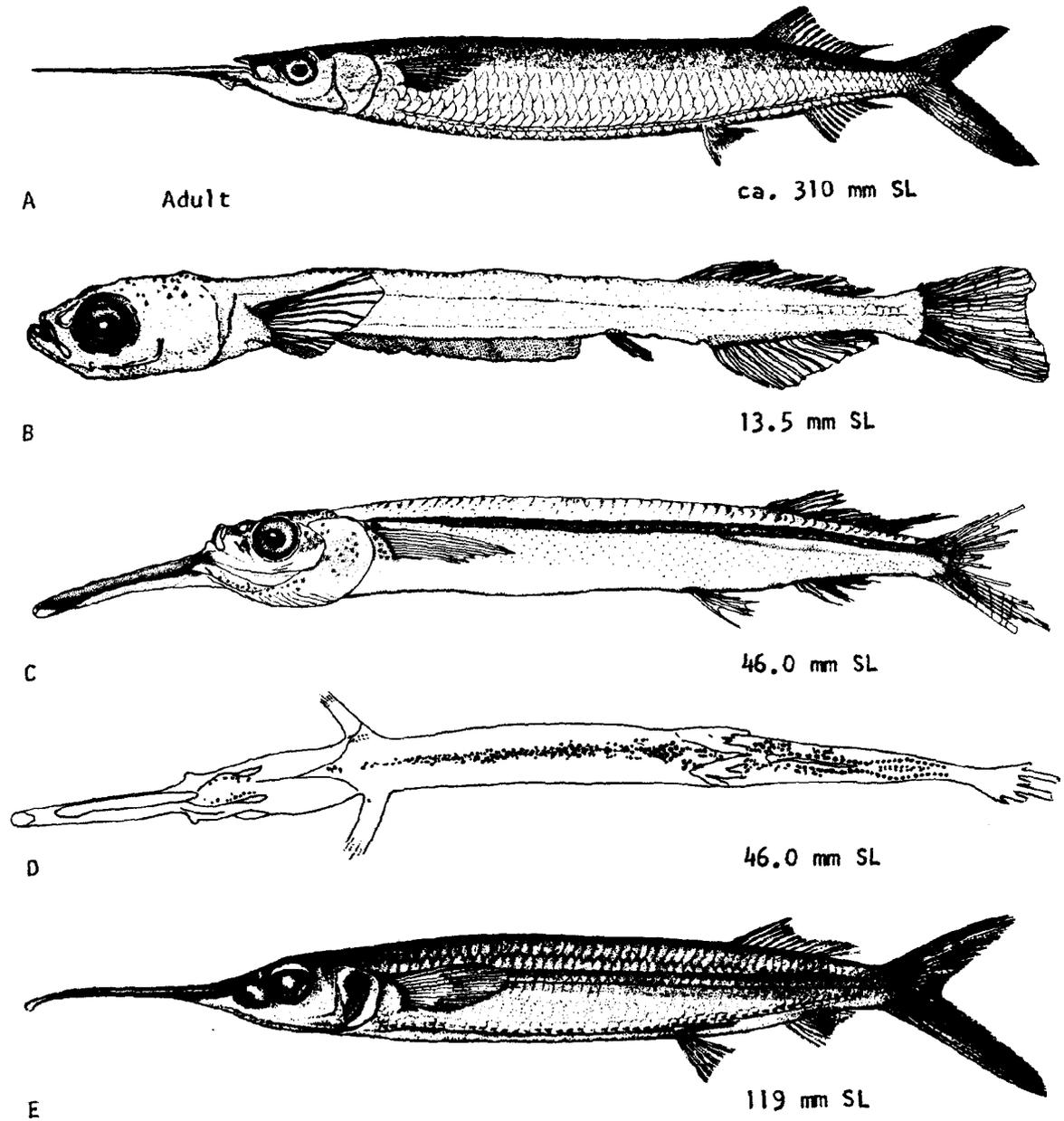


Fig. 67. *Hemiramphus brasiliensis*, Ballyhoo. A. Adult, ca. 310 mm SL. B. Larva, 13.5 mm SL. C. Juvenile, 46.0 mm SL. D. Ventral view of C. D. Juvenile, 119 mm SL. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 313. B-C, Original drawing, Hardy, J. D., Jr., and R. K. Johnson, 1974: fig. 1. E, Collette, B. B., 1965: fig. 6.)

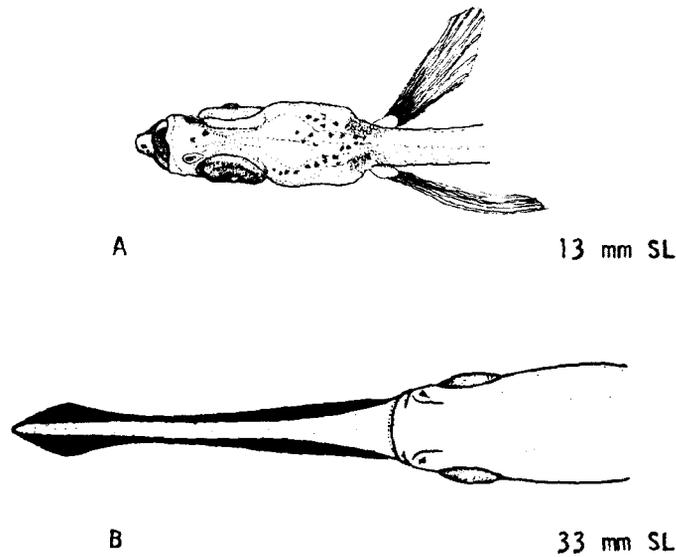


Fig. 68. *Hemiramphus brasiliensis*, Ballyhoo. Development of head. A. 13 mm SL, lower jaw not protuberant. B. 33 mm SL; lower jaw, lappets well-developed. (A. Hardy, J. D., Jr., and R. K. Johnson, 1974: fig. 2. B, Breder, C. M., Jr., 1934: pl. 6.)

pectoral rays; lower caudal lobe longer than upper. Urostyle oblique throughout stage.²⁷

Pigmentation: At 8.0–10.0 mm frequently plain brick red, fins transparent, beak with black tip.² At 13.0–13.5 mm SL scattered large melanophores on dorsal surface of head, especially on occiput; few scattered melanophores on cheeks. Pigment along middle of back limited to two obscure rows of melanophores, each row slightly lateral to dorsal midline and extending from occiput to caudal base. Scattered large melanophores on posterior-most portion of dorsal and anal fin; other fins lacking pigment except for several large melanophores at base of pectoral fin. Mid-lateral stripe present, but extremely obscure, consisting of a single row of small, widely spaced melanophores. In a 13.0 mm specimen a sheath of scattered melanophores dorsal and lateral to gut.²⁷

JUVENILES

Minimum size described: 35.0 mm.²

Gill rakers 29–31 in specimens 32.0–50.0 mm SL.¹⁰

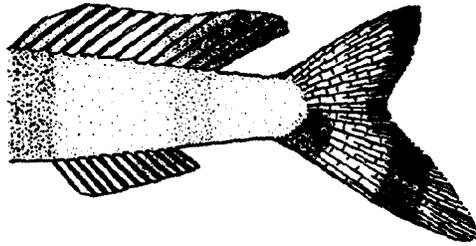
Beak of young with mandibular fold similar to that of *Tylosurus crocodilus* well-developed at least by 33.0 mm SL.³

Proportions as percent SL (at 46 mm SL): Body length (posterior edge of opercle to caudal base), 78.9; longest pectoral ray, 15.9; pectoral insertion to ventral insertion,

43.3; pectoral insertion to caudal base, 35.2; tip of snout to tip of lower jaw, 28.2; depth at pectoral fin, 12.0; depth at pelvic fin, 12.0.²⁷ Proportions as times in TL: Depth, at 35 mm, 9.2, at 38.5 mm, 7.7.⁹ Lower jaw longer than upper in specimens 40–120 mm SL, about equal at 100–200 mm SL.¹ Base of dorsal fin 1.3–1.4 times base of anal in “young.”²²

Scales fully formed in a specimen of 46 mm SL.²⁷ Posterior rays of dorsal extended into a darkened lobe at least by 38.0 mm.²

Pigmentation: In a 35.0 mm specimen from Tortugas, Florida, long vertical bars developing on sides; upper caudal lobe reddish; some individuals with median dorsal line of pigment.² In a 40.0 mm specimen from Haiti submedian dorsal lines evident as series of dots. In Haitian specimens 35.0–47.0 mm long pigmented scale edges obscured by general darkening of dorsum; top of head, snout, and lower jaw densely covered with chromatophores; opercles with few scattered pigment cells; edges of scales on dorsal surface as far down as center of sides densely pigmented; a dark band on side beginning at upper angle of gill opening, continuing to caudal fin, becoming wider and denser posteriorly; belly and under-surface with median band of chromatophores extending from isthmus to caudal fin, most intense immediately before and between pelvics, splitting in two at anus and continuing as a line of spots on either side of anal to caudal; a small black spot on body at base of ventral fin; three dark patches on middle of side, two between anal



A

33 mm SL

Fig. 69. *Hemiramphus brasiliensis*, Ballyhoo. A. Juvenile, 33.0 mm SL, median fins. (A, Breder, C. M., Jr., 1934: pl. 6.)

and dorsal, one above ventral, and a faint trace of a fourth spot just anterior to last large spot; few scattered chromatophores on lower sides; membrane of posterior part of dorsal and anal blackish; lower lobe of caudal dusky; other fins plain.⁹ In a specimen from Chesapeake Bay 46.0 mm SL, pigment well-developed on snout, inter-orbital area, occiput, cheeks, upper and lower jaws, and mandibular folds of beak. Back with 3 distinct stripes, 1 along dorsal midline and extending from occiput to caudal base, and 2, 1 on each side, lateral to it and extending only to dorsal base. Scale pockets above lateral line edged with pigment. Mid-lateral stripe well-developed, divided into 3 portions; a narrow but intense row of melanophores on horizontal septum from gill cover to caudal peduncle; a wider band of melanophores dorsal to horizontal septum likewise extending from gill cover to caudal peduncle; a similar band of melanophores ventral to horizontal septum extending from a vertical through pelvic base to caudal peduncle. A band of widely scattered melanophores covering most of ventro-lateral surface of body ventral to mid-lateral stripe. A single band of small melanophores along mid-ventral line of body, extending from isthmus to anus, dividing at anus, and continuing as a line of spots on either side of anal base to bases of procurrent caudal rays. A band

of fine melanophores at mid-ventral line of body on caudal peduncle. Pigment present at bases of all fins and extending over rays and membranes of all but pectoral fins, with especially dense pigmentation covering posteriormost portions of dorsal and anal fins and membrane between ventral caudal rays.²⁷

AGE AND SIZE AT MATURITY

No information.

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Hyporhamphus unifasciatus (Ranzani), Halfbeak**ADULTS**

D. 13-16; ⁴¹ A. 14 ²¹-18; ⁴¹ C. 23-24 (4-5+7+8+4); ³⁶ gill rakers first arch 20 ²⁷-35, second arch 18-27; ⁴¹ vertebrae 31-35 + 17-19 = 50-54. ⁴¹

Proportions expressed as times in length from tip of upper jaw to tip of tail: Depth 6 ¹⁵-13; ²³ head 4.1-4.8. ¹⁵

Body elongate, compressed; ¹ sides slightly convex; ² depth increasing with age. Mandible greatly produced, ¹⁵ its tip with a conspicuous fleshy flap. ⁸ Sensory canal on preorbital unbranched. ²⁸ Teeth small, compressed, in bands in jaws, mostly tricuspid. ¹³ Snout (upper jaw) covered with scales. ²⁸ Dense scales present, at least basally, on dorsal and anal fins. ^{21,27} Gas bladder simple. ² Dorsal fin over or nearly over origin of anal, its base and that of anal equal or subequal; ²⁸ pelvics inserted far in advance of dorsal, ² and located nearly midway between eye and base of caudal; ¹⁸ caudal moderately forked. ²⁸

Pigmentation: Pale translucent green above, sides silvery

white, venter silvery; ^{1,9,15,23} dorsal scales with dark margins; ^{1,23} 3 narrow dark streaks along middle of back; ^{13,14,15} a plumbeous or silvery lateral band, its width equal to or less than diameter of eye, from axil of pectoral to caudal base; lateral band widest posteriorly, bordered above by black, and below by paler. ^{1,9,13,14,15,21,23} Upper surface of head and mandible blackish; tip of lower jaw, including fleshy flap, a little red to bright, crimson red; mandibular flap also described as red bordered with black. ^{1,9,21,30} Anterior parts of dorsal and anal and tips of caudal dusky to almost black; caudal sometimes dark-edged. Peritoneum black. ^{1,13,14,21,23}

Maximum length: Ca. 305 mm TL or longer. ^{3,13,14}

DISTRIBUTION AND ECOLOGY

Range: Restricted to the western Atlantic; ⁴¹ recorded from New Brunswick, Canada ^{7,22} and Bermuda, to Argentina, and reported as widespread in the West Indies, ^{3,19,20} specimens from the Mid-Atlantic Bight may

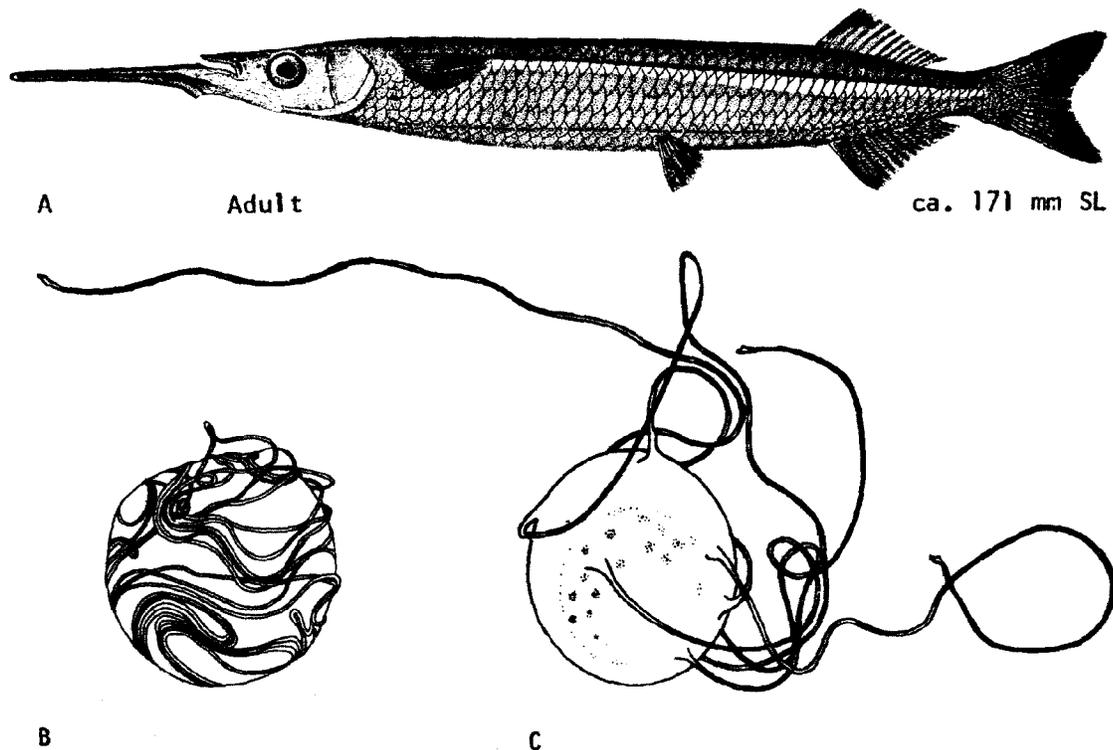


Fig. 70. *Hyporhamphus unifasciatus*, Halfbeak. A. Adult, ca. 171 mm SL. B. Ovulated egg, ca. 1.4 mm diameter. C. Fertilized egg, filaments expanded, ca. 1.2 mm diameter. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 311. B, C, Original drawings, Elizabeth Ray Peters.)

represent a distinct species. If so, its range extends southward only to mid-peninsular Florida and from the Florida panhandle to Mexico (BBC).

Habitat and movements: Adults—a pelagic schooling species^{15,35} found in surface water at night;⁴ recorded from shallow shore zones over sandy bottoms,^{5,12,24} in bays,¹⁶ in harbors near shoals and sandy islands,²³ among islands (as in Florida Keys),²⁵ in channels,²⁶ and from brackish water in lower parts of streams.¹⁵ Sometimes washed ashore in large numbers.²³ Salinity range 7.5^{11,16}–42.9 ppt. Recorded temperature range 16.0³⁷–34.9 C (although this may include some juveniles).³⁹ Apparently make inshore-offshore movements along Atlantic and Gulf coasts: in Chesapeake Bay region inshore in April, offshore (and possibly southward to warmer water) in fall.⁸ Inshore in July, August, and September in New England;²⁰ August and September in Great South Bay, New York;¹ April to November in North Carolina;¹⁰ November and September in Tampa Bay, Florida;¹¹ “late summer” to “early fall” in Texas.²⁹

Larvae—possibly on bottom¹⁵ (but this is questioned, BBC). Salinity range 0–12.0 ppt.³³

Juveniles—found in schools;³⁸ a single 23.0 mm speci-

men from near the 180 m contour in Atlantic Ocean;³⁴ specimens 39.0–46.0 mm long in inlets in vicinity of Fire Island in August;³¹ at 41.0–52.0 mm inshore along beaches;³⁸ specimens 45.0–127.0 mm long in Alligator Harbor, Florida from July until “fall.”¹⁷ Maximum recorded salinity, 31.6 ppt; maximum recorded temperature 23.3⁴⁰ or, possibly, 34.9 C.³⁹

SPAWNING

Location: In Puerto Rico, eggs found on shallow turtle-grass beds (FDM).

Season: Summer in Chesapeake Bay^{6,8} (a recently hatched specimen was recorded from the bay on July 8¹⁵); ripe female on March 5 in Haiti.⁹

Fecundity: Unknown.

EGGS

Location: Semibuoyant.¹⁵

Ripe ovarian eggs: Diameter 1.0 mm.⁹

Fertilized eggs: Diameter ca. 2.0 mm, almost transpar-

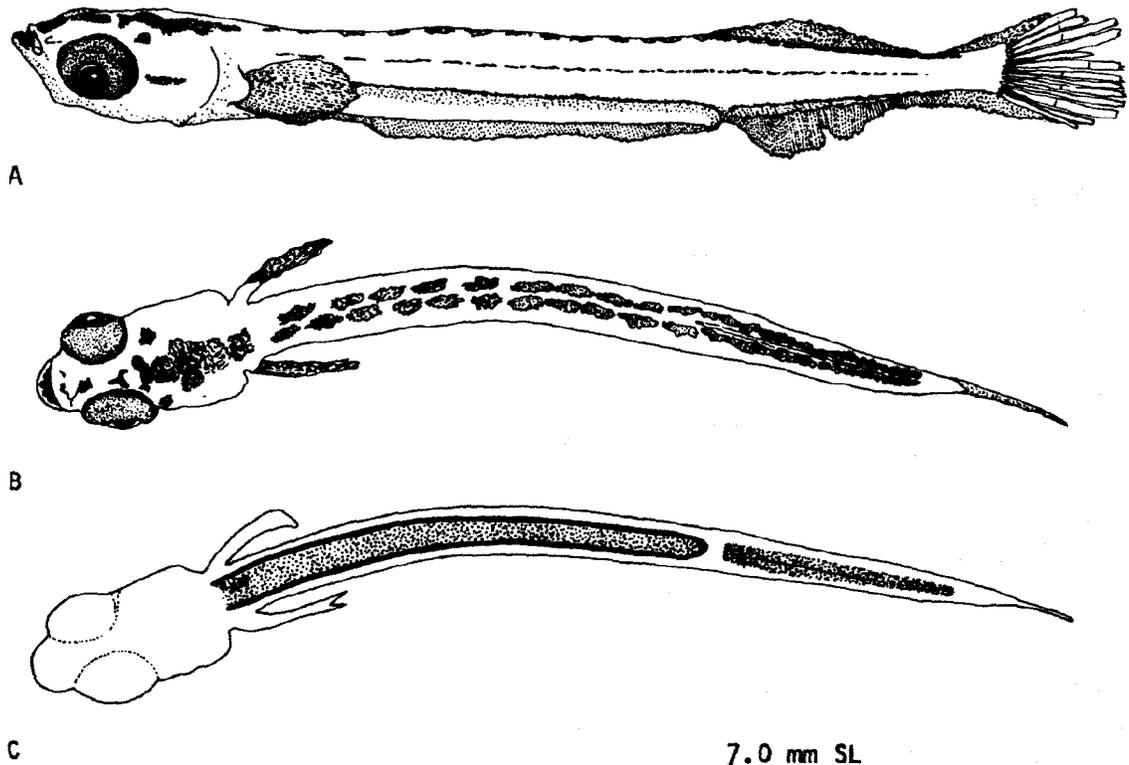


Fig. 71. *Hyporhamphus unifasciatus*, Halfbeak. A. Larva, 7.0 mm SL. B. Dorsal view of A. C. Ventral view of A. (A, B, Hardy, J. D., Jr., and R. K. Johnson, 1974: fig. 2. C, Original drawing, J. D. Hardy, Jr.)

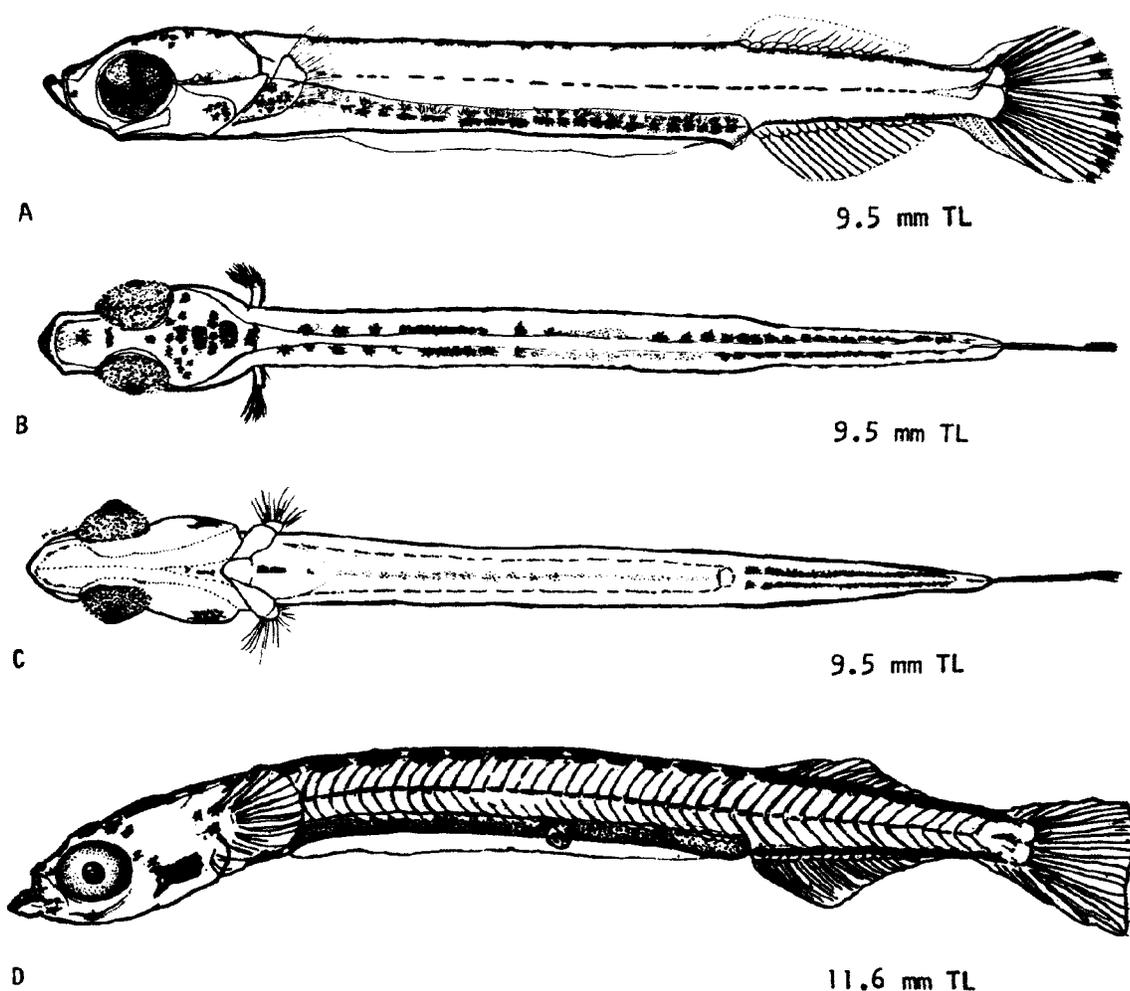


Fig. 72. *Hypothamphus unifasciatus*, Halfbeak. A. Larva, 9.5 mm TL. B. Dorsal view of A. C. Ventral view of A. D. Larva, 11.6 mm TL. (A-C, Original drawings, Nancy S. Smith. D, Original drawing, William C. Dovel.)

ent,¹⁵ chorion with several very long attachment filaments (FDM).

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

Hatching length, unknown. Smallest known specimen 3.0 mm long and recently hatched. In very young specimens beak not developed.¹⁵

LARVAE

Size range described, 7.0–15.8 mm SL.³²

Myomeres 35 + 14 (WLD).

Proportions as percent SL at 15.8 mm SL: Body length (posterior edge of opercle to base of mid-caudal rays), 79.7; pectoral length 11.6; pectoral insertion to pelvic insertion, 30.8; pelvic insertion to base of mid-caudal rays, 42.0; lower jaw length (snout to tip of lower jaw), 11.0; depth at pectoral insertion, 9.6; depth at distal tip of pectoral fin, 9.3; depth at pelvic insertion, 9.3.³²

Body elongate; upper jaw oblique to vertical;³² first evidence of elongation of beak at 15.0 mm;¹⁵ anus approximately 2/3 distance from tip of snout to end of caudal. Preanal finfold long, narrow at 7.0 mm SL, still evident at 15.8 mm. Pectorals with well-developed rays at 7.0 mm. Incipient rays in vertical fins at 7.0 mm SL.³² Anal with well formed rays at 9.5 mm (NSS). Pelvics evident at 11.6 mm (WLD). Urostyle oblique at 7.0 mm SL.³²

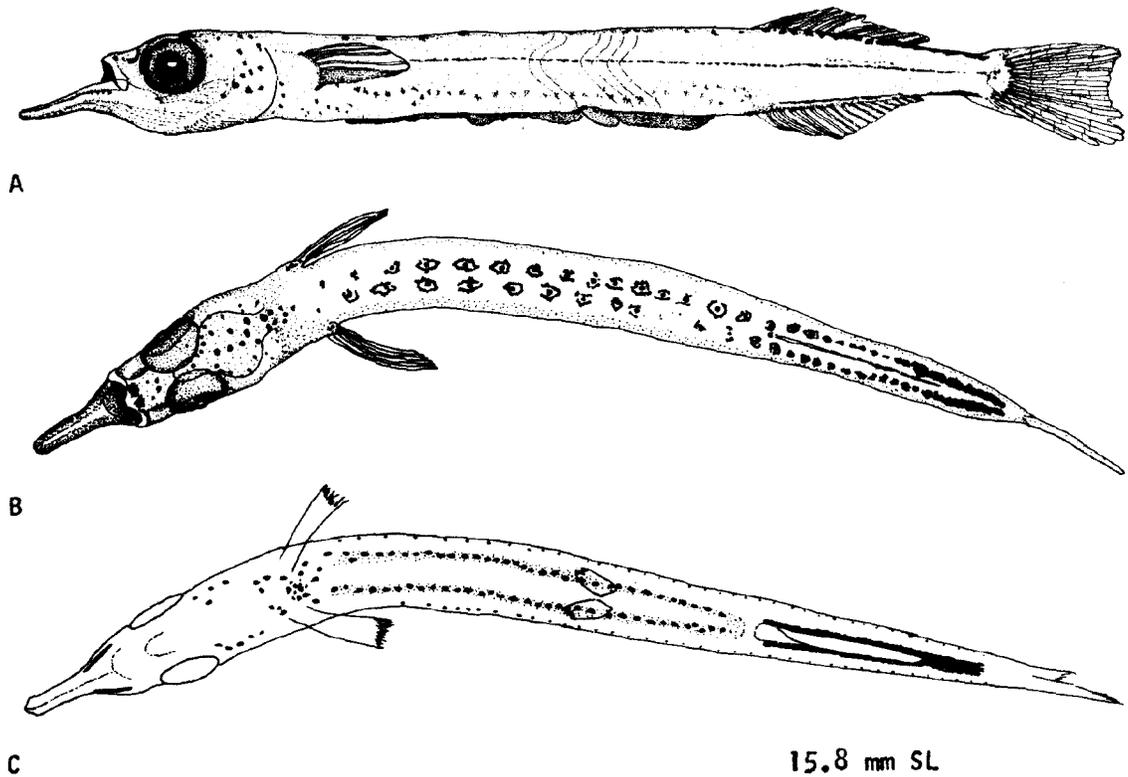


Fig. 73. *Hyporhamphus unifasciatus*, Halfbeak. A. Larva, 15.8 mm SL. B. Dorsal view of A. C. Ventral view of A. (A, B, Hardy, J. D., Jr., and R. K. Johnson, 1974: fig. 2. C, Original drawing, J. D. Hardy, Jr.)

Pigmentation: At 7.0 mm SL dorsal surface of head with 3 patches of pigment: a small patch just behind upper jaw, a somewhat larger one between eyes, and a larger one on occiput. Tip of lower jaw heavily pigmented. A row of dark spots, their borders distinctly outlined with dark pigment, along each side of midline of back from just posterior to pectoral bases to caudal base. Anterior to dorsal fin, dorsal spots oblong and usually well separated; along base of dorsal spots typically fused or separated by narrow, complete or incomplete, transverse bars of unpigmented skin. Eye heavily pigmented. A series of melanophores from posterior margin of eye to posterior margin of head. Mid-lateral stripe present as thin, dashed line from back of head to last evident caudal myomere. A dense continuous row of pigment along each side above gut connecting to each other just anterior to anus.³² Gut pigmented (JDH). A row of fused pigment spots along each side of anal fin. Three small groups of melanophores near mid-ventral line between pectoral bases. At 7.5 mm SL pigment more intense, except ventrally. At 9.5 mm TL dorsal pigment in two more or less discrete rows from head to caudal fin, melanophores on gut stellate, more numerous than in previous stages (NSS). At 11.6 mm TL dorsal pigment spots consoli-

dated posteriorly to form continuous pigment bands from dorsal origin to caudal base, gut heavily pigmented, a solid line of dark pigment ventrally from anus to caudal base; a conspicuous pigment spot on caudal peduncle and four spots on caudal base; melanophores scattered over head and beneath eye; a large bar of pigment behind and below eye (WLD). At 15.5 mm 2 submedian dorsal lines indicated by series of unconnected pigment spots (based on West Indian specimens).⁹ At 15.8 mm SL rows of pigment along gut broken into discrete spots (JDH), dorsal spots faintly outlined with dark pigment, fins without pigment.³² At 19.0 mm (West Indies) median dorsal line faintly indicated by series of small widely spaced chromatophores. In "very young fish" (stage indefinite) lateral spots apparently each formed by a single, large chromatophore.⁹

JUVENILES

Minimum length described, 22.5 mm SL.

Proportions expressed as percent SL (length range 22.5-130.6 mm): Body length (posterior edge of opercle to base of mid-caudal rays) 70.5-80.4; pectoral length 11.2-



Fig. 74. *Hyporhamphus unifasciatus*, Halfbeak. A. Juvenile, 83.5 mm TL. (A, Böhlke, J. E., and C. C. G. Chaplin, 1968: 126, © Academy of Natural Sciences of Philadelphia. Used with permission of authors and publishers.)

14.5; pectoral insertion to pelvic insertion 30.6–36.3; pelvic insertion to base of mid-caudal rays 38.4–47.2; lower jaw length (snout to tip of lower jaw) 21.4–29.8; body depth at pectoral insertion 10.4–13.4; depth at pectoral tip 9.8–14.6; depth at pelvic insertion 10.5–14.8.³²

“Young” more slender than adults; ¹⁹ beak well-developed at 25.0 mm, proportionately longer in specimens 100–200 mm long than in larger specimens; ¹⁵ mandibular lappets evident by at least 38.0 mm; posterior half of dorsal fin low, never elevated into distinct lobe.²

Pigmentation: At 23.5 mm two rows of large black spots on back; pigment developed on dorsal fin and on basal third of caudal fin.³² At 28.0 mm (West Indian specimen) number of chromatophores in median dorsal line noticeably increased. At 32.0 mm (West Indian) two submedian dorsal lines developed as elongate dashes of pigment. At 52.0 mm (West Indian) dashes of submedian lines consolidated into stripes typical of adult. At 85.0–95.0 mm (West Indian) lateral spots, seen in earlier stages, completely obliterated. In a 95.0 mm West Indian specimen scale edges pigmented.⁹

AGE AND SIZE AT MATURITY

Minimum size reported, a 147 mm female (West Indian).⁹

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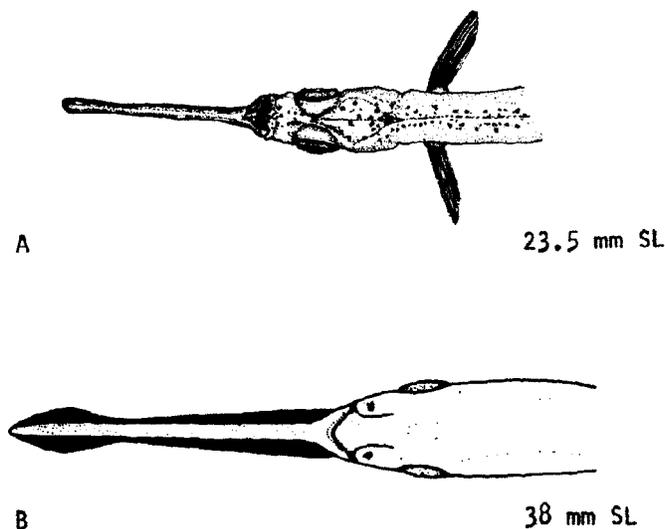


Fig. 75. *Hyporhamphus unifasciatus*, Halfbeak. Development of head. A. 23.5 mm SL. B. 38 mm SL. (A, Hardy, J. D., Jr., and R. K. Johnson, 1974: fig. 2. B, Breder, C. M., Jr., 1934: pl. 6.)

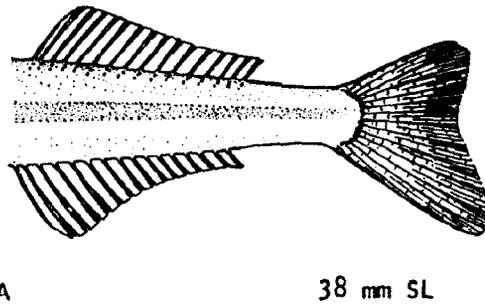


Fig. 76. *Hyporhamphus unifasciatus*, Halfbeak. A. Details of morphology and pigmentation of caudal region at 38 mm SL. (A, Breder, C. M., Jr., 1934: pl. 6.)

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Cyprinodon variegatus

Fundulus confluentus

Fundulus diaphanus

Fundulus heteroclitus

Fundulus luciae

Fundulus majalis

Lucania parva

killifishes

Cyprinodontidae

FAMILY CYPRINODONTIDAE

Cyprinodontid fishes, of which there are about 45 genera and 300 species, occur on all continents except Australia. Although they are mostly freshwater species, some occur in brackish water, and others occasionally enter coastal marine waters.

Killifishes are characterized by lack of a lateral line, a terminal and protrusible mouth, well-developed teeth in jaws, the upper surface of the head conspicuously flattened, and the dorsal fin positioned far back over the anal fin. Sex dimorphism is common in the group, especially in relation to color pattern and relative fin lengths. Males of many species develop contact organs during courtship, and, in at least one genus (*Cynolobius*), contact organs occur in the female. Although the cyprinodontids are generally regarded as strictly oviporous fishes, ovoviparity may occur in the Japanese species, *Oryzias latipes*.

Among the regional killifishes, spawning is accompanied by elaborate courtship behavior and occurs in a variety of habitats including brackish bays and river mouths, as well as ponds, lakes, marshes, streams, and creeks. Eggs may be attached to aquatic vegetation, buried in the substrate, or, in some individuals of one species, deposited inside empty mussel shells. Among extralimital species spawning habitats may be even more varied. There is evidence to suggest, for example, that at least one African species spawns pelagically. Various stratagems have been developed which may assist with protection of the eggs. In one species of *Aplocheilichthys*, for example, the eggs hang in a cluster from the anus of the female during early stages of development. In the North American *Jordanella floridae* the male guards and fans the eggs. The family includes a number of species which hatch, become mature, reproduce, and die in one year or less. These fishes, commonly called the "annuals," occur primarily in Africa and South America, although at least one North American species, *Fundulus confluentus*, also appears to belong in this group. In the annuals, eggs are generally deposited in situations where they will be subject to partial desiccation during development. This exposure, which may last up to a year or more, may be essential to optimum hatching success.

Eggs of all regional cyprinodontid fishes possess one or more oil globules. They may be adhesive or nonadhesive and their chorions may be either smooth or equipped with varying numbers of short bristles and/or long attachment filaments. Larvae are characterized by a combination of the following: the body is well-pigmented, even at hatching; the anus is at a point one-third to two-fifths the distance to the end of the tail; the mouth, which is well-developed at hatching, is either terminal or superior and oblique; fin rays are developing in the caudal and pectoral fins at or near the time of hatching; and incipient dorsal and/or anal rays are evident before the end of the yolk-sac stage.

Key to eggs of cyprinodontid fishes of the Mid-Atlantic Bight.

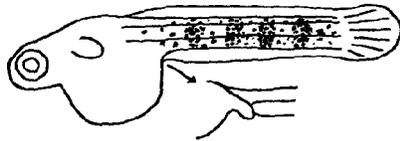
- 1A. Chorion essentially smooth, lacking bristles and/or attachment filaments, or with very small, inconspicuous filaments 2
- 1B. Chorion equipped with bristles and/or long well-developed attachment filaments 3
- 2A. Chorion perfectly smooth; egg opaque, deep amber or orange; diameter 2.0–3.0 mm *Fundulus majalis*
- 2B. Chorion essentially smooth, but usually with few poorly developed filaments; egg nearly or completely transparent; diameter 1.5–2.5 mm; limited to Atlantic coastal areas from North Carolina to Delaware *Fundulus heteroclitus*
(in part)
- 3A. Chorion with well-developed attachment filaments, but lacking bristles 4
- 3B. Chorion with both bristles and attachment filaments 7
- 4A. Attachment filaments not evenly distributed over chorion, definitely concentrated in one area; few (8–15) relatively large oil globules; diameter 1.0–1.3 mm *Lucania parva*
- 4B. Attachment filaments more or less evenly distributed over chorion 5
- 5A. Yolk with one very large oil globule and many minute ones, diameter 1.0–1.7 mm *Cyprinodon variegatus*
- 5B. Oil globules of various sizes, but no single globule conspicuously larger than the others 6
- 6A. Attachment filaments numerous, in very thick flattened mat completely surrounding eggs, egg diameter 1.5–2.5 mm *Fundulus heteroclitus*
(in part)
- 6B. Attachment filaments sparse, matted; egg diameter ca. 1.7–2.3 mm *Fundulus diaphanus*
- 7A. Chorionic bristles numerous, crowded; egg diameter 1.6–1.8 mm *Fundulus confluentus*
- 7B. Chorionic bristles sparse, widely spaced, egg diameter 1.8–2.2 mm *Fundulus luciae*

Key to yolk-sac larvae of cyprinodontid fishes of the Mid-Atlantic Bight.

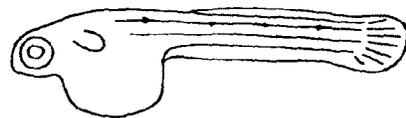
- 1A. Total myomeres 28 or less, origin of dorsal finfold in advance of anus 2
- 1B. Total myomeres 29 or more, origin of dorsal finfold behind anus 3
- 2A. Body pigment more or less evenly distributed, no lateral blotches; anus not extended beyond contour of finfold; finfold nicked at anus; myomeres 8 + 18 *Lucania parva*



- 2B. Lateral melanophores forming obscure blotches, anus extended slightly beyond contour of finfold; finfold not nicked; myomeres 8 + 16 *Cyprinodon variegatus*



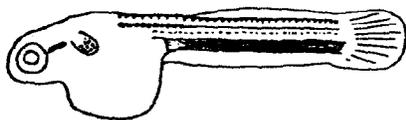
- 3A. No pigment immediately below vertebral column, pigment absent or poorly developed above notochord, no pigment in pectorals, myomeres 9-10 + 23-25 *Fundulus diaphanus*



- 3B. Pigment immediately below vertebral column 4
 4A. Entire area below vertebral column heavily pigmented, or at least darker than remainder of body; pectorals pigmented 5
 4B. Area below vertebral column with discrete bands of pigment rather than entirely pigmented 6
 5A. No mid-lateral line of melanophores, myomeres 9-10 + 21-24 *Fundulus confluentus*



- 5B. A faint dashed line of melanophores mid-laterally, myomeres 8-9 + 21 *Fundulus luciae*



- 6A. No pigment in pectoral fins; total length 7.0 to 11.0 mm (at minimum size, yolk sac large, conspicuous); myomeres 10 + 24 *Fundulus majalis*



- 6B. Pectoral fins pigmented; total length 4.0 to 7.3 mm (at maximum size, yolk nearly absorbed, inconspicuous); myomeres 9+24 *Fundulus heteroclitus*



Cyprinodon variegatus Lacépède, Sheepshead minnow

ADULTS

D. 9–13; A. 9–12;^{12,16,22,53} C. total rays 28–29,⁷² principal rays 14–16; P. 14–17; V. 5–7; lateral scale rows 24–29^{12,16,22,53} (counts of 20–22⁶¹ are questioned¹⁶); predorsal scales 4–7;⁷⁰ scales in transverse series 13,²³ between dorsal and anal 10–12, around body 26–32, around caudal peduncle 14–16;¹⁶ total vertebrae, including hypural 25¹⁶–27,⁷² preanal vertebrae 12,²² caudal vertebrae 14–15;⁷² gill rakers 18–23;¹⁸ branchiostegals 5–6;²² mandibular pores 0–2; preopercular pores 6–8; lacrymal pores 3–4;¹⁶ postorbital pores 4.⁵⁵

Proportions expressed as times in SL: Depth in males 2.2–2.7 (mean 2.38), in females 2.3–3.0 (mean 2.58); head in males 2.8–3.2 (mean 3.06), in females 2.8–3.3 (mean 3.01).¹²

Body short, compressed,^{7,45} deep, the depth increasing with age, especially in males; upper profile evenly elevated in females, with concavity at occiput in males; head short, little depressed;⁷ snout blunt; mouth small, terminal; premaxillaries strongly protractile.¹⁴ Teeth large, in single series, tricuspid.^{9,14,59} Height of dorsal equal to length of dorsal base in females, much higher in males; origin of dorsal midway between base of caudal and end of snout, and in advance of anal;^{7,12,54} anal and pelvics longer in males than in females;⁸⁸ pelvics to anus in females, to front of anal fin in males;⁵⁴ caudal fin broadly rounded,⁴⁵ nearly straight-edged; a large, elongate “humeral” scale just above pectoral base.¹⁴ Breeding males with minute spinules along edges of scales of head, in predorsal region, on posterior sides of trunk or above anal fin, on front side of caudal peduncle,¹⁸ and on anal rays; spawning females with slightly developed spinules, primarily on posterior margins of lateral scales.⁶⁴

Pigmentation: Males olivaceous above with lustrous steel blue or bluish green area on back from nape to dorsal^{7,26,26} or beyond;¹⁴ a series of poorly defined dark bars on sides;^{26,53} belly yellowish white³⁸ to deep orange;¹⁴ cheeks and opercles slate gray⁷ to salmon.²³ Dorsal ocellus lacking or developed as faint dusky spot,²⁶ rarely bordered with pale;⁵³ anal fin yellow, orange, or dusky, bordered with bluish black or orange; caudal fin dull green or olive with narrow dusky or black bar at base and black margin; pectorals yellow to yellow-orange or dull orange, black at tip, sometimes brownish red near insertion; pelvics yellow to orange or dusky, margined with bluish black or orange.^{14,23,26,38,48,53}

Females light olive,⁷ brown,²⁶ brassy¹⁴ or light orange above; 14 dark crossbars on lower sides alternating with 7–8 crossbars on back;²³ lower sides and venter yellow-

ish or white;^{14,26} cheeks brassy; lower jaw blue.²³ Dorsal olive or dusky with 1 or 2 prominent dark ocelli on posterior rays; anal and pelvics usually clear or pale yellowish with white margins; pectorals clear, dusky, or orange; caudal greenish, dusky, or dull reddish with dark basal bar and plain margin.^{11,14,23,26}

Both sexes capable of changing intensity of color with background.⁴¹

Maximum length: 93 mm,^{6,36} with males usually somewhat longer than females.^{9,11}

DISTRIBUTION AND ECOLOGY

Range: Massachusetts to Yucatan, Mexico, and throughout West Indies to South America; unsuccessfully introduced into Olympic Peninsula, Washington.^{15,21,35,39,51,52}

Area distribution: Virginia,⁶² Maryland,¹⁴ Delaware,⁴ and New Jersey;³ north in Chesapeake Bay to vicinity of Annapolis.¹⁴

Habitat and movements: Adults—a schooling,¹⁴ euryhaline^{4,5,28,37,47,50} species inhabiting shallow water^{14,38} (typically less than 76 mm deep⁶⁴) in coves, bays, ponds, inlets, harbors, and salt marshes;^{14,38,56} also recorded from salt ditches^{30,40} and ponds,²⁴ pools,⁴³ and creeks;^{14,44} shallow bayous;²⁴ tide pools;¹⁰ lakes;⁵² small streams;⁵³ rivers;⁴⁵ springs;⁶³ passes between islands;¹⁷ and along open beaches.² In Florida, usually over clear, firm sand bottoms, rarely over flocculent organic debris.⁶⁴ Sometimes associated with large mats of *Ulva* or other aquatic vegetation,^{47,57} in Yucatan on *Cladophora* mats (NRF), at other times and places in areas completely devoid of vegetation.²⁰ Capable of living in extremely foul water,⁴⁷ and able to withstand oxygen levels of 0.00 to 0.81 ppm in anerobic springs;⁶³ also recorded from sulfurous saline water.⁶⁴ Burrow in mud during winter^{1,13} and sometimes in mud, plant debris, or other detritus during unusually low tides.^{12,20} Markedly diurnal, “roosting” among plant roots at night.⁴² Maximum salinity 142.4 ppt,^{8,12} preferred salinity less than 20 ppt.²⁰ Maximum depth 1.5 m.⁵⁷ Apparently make limited inshore and offshore movements in April, May, and November on Texas coast,⁶ in Florida tend to enter bayous during cold months, bays during warmer months.⁸

Larvae—specimens ca. 4.0 mm long at outlet of springs at exact edge of water over hard white sand bottom, extremely active at this stage.⁶⁴ Specimens 7.0 mm long (9 days old) remain at or near bottom.⁴⁰ Newly hatched larvae found in salinities in excess of 90.0 ppt;⁴⁶ offspring may be less tolerant of increased salinities than adults.⁵⁸

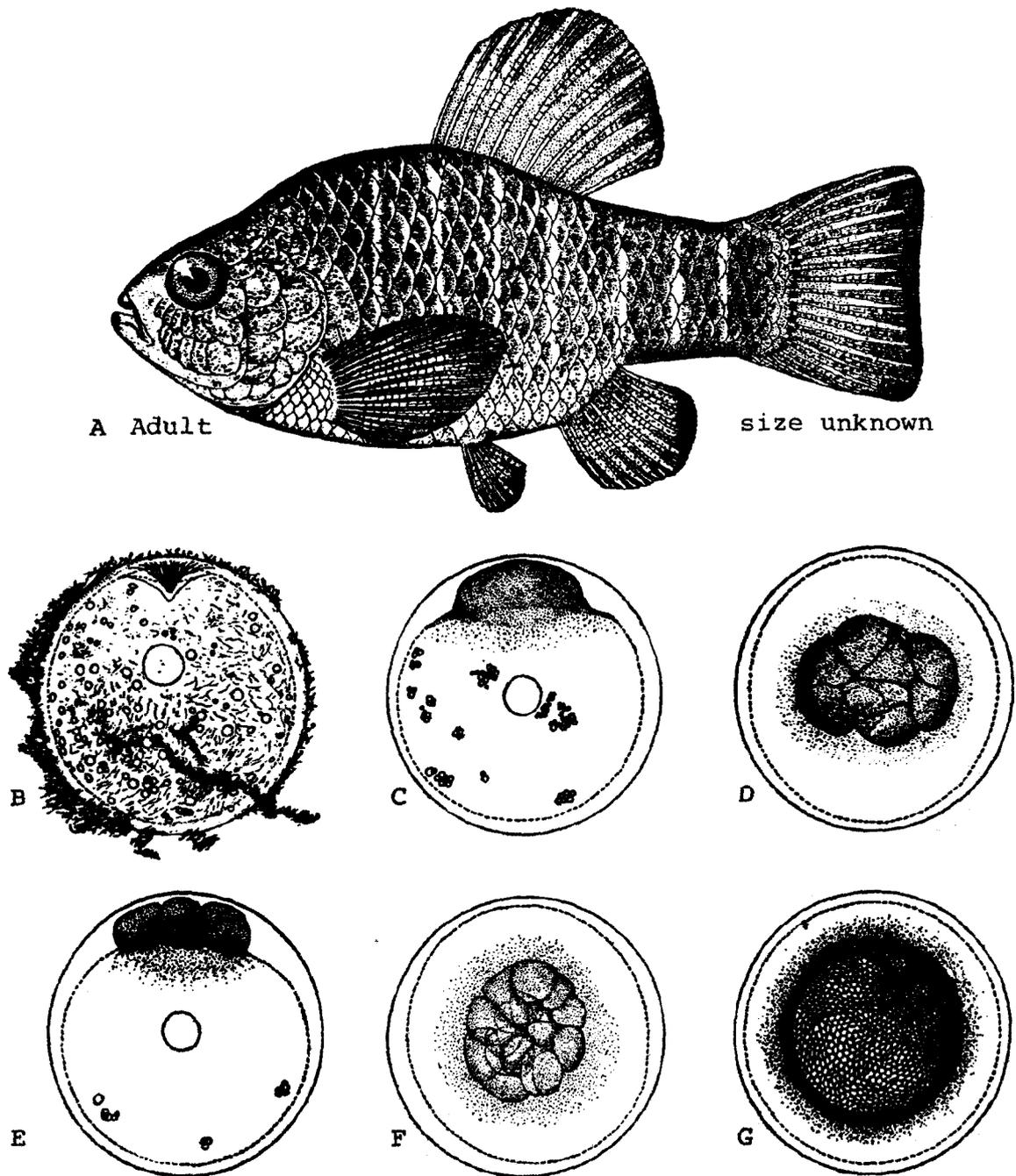


Fig. 78. *Cyprinodon variegatus*, Sheepshead minnow. A. Adult, size unknown. B. Mature, unfertilized egg, showing attachment filaments and micropyle. C. Blastodisc fully developed. D, E. 8-cell stage. F. 16-cell stage. G. Late cleavage. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 296. B-C, Kuntz, A., 1916: figs. 1-6.)

Juveniles—large schools of “young” often left in shallow depressions in sand by receding tide; ⁴⁰ “juveniles” sometimes bury in bottom; salinity range (may include some advanced larvae), 0.08-97.3 ppt.⁶⁵

SPAWNING

Location: At depths of 2.5 to 61 cm in shallow arms of small bays; large tide pools; mangrove lagoons; and pools

in shallow, gently flowing streams over bottoms of sand, black silt, or mud. Males occupy territories up to 0.3–0.6 m in diameter and may or may not construct nest pits. Pits, when constructed, 10–15 cm in diameter and 2.5–3.8 cm deep. Spawning may actually take place out of both pit and territory. Spawning territories typically situated adjacent to bank or up to 3 m from shore and usually associated with submerged logs or rocks. Density of territories may approach 100 per 0.9 square meters area.^{26,28,32,48}

Season: On Andros Island, Bahamas, courtship observed in January;⁴⁴ on the Gulf coast of the United States, possibly throughout the year;²⁰ variously observed in Florida, as in late December in southern Florida,²⁶ in summer in Tampa Bay,⁸ and from February to June in St. John's River;⁶⁴ in Texas breeding colors late April through July,⁴⁹ ripe eggs specifically as late as July 24 and 25, small fish added to population from June to January,¹² females with ripe eggs noted in every month except January;⁶⁸ in North Carolina ripe females April to October;⁶⁰ in Chesapeake Bay throughout summer;¹⁴ in Delaware Bay May (or possibly April) to August;⁵⁷ in New Jersey breeding colors May to September;⁴⁸ in New York May to September;²⁶ in Massachusetts June to mid-July;⁸² under laboratory conditions in December⁴⁶ and from mid-March to October.²⁰

Time: Morning (0800 hours)¹¹ and afternoon¹³ (1400–1840 hours), with activity diminishing as darkness approaches.²⁶

Temperature: 22.8⁴⁶–28.9 C.²⁶

Salinity: 0.08–63.1 ppt, with sudden drops in salinity apparently initiating spawning activity.⁶⁵

Frequency: A single female may spawn a number of times during a single season at intervals of 1²⁶–7 days,⁴⁶ average 4 spawnings per nest entry,⁷¹ and deposit 1¹³–3⁴⁶ eggs per spawning; one female produced eggs 15 times between April 28 and August 16; a female may produce 2–24 sets of eggs during a single season.⁶⁰

Fecundity: Maximum published total for a single individual, 140, of which half "seemed to be of one size and generally nearly mature";⁶⁰ ripe ova 41–51.⁶⁴

EGGS

Location: Demersal,⁵ adhesive⁴⁸ or semi-adhesive, sticking to plants,³⁷ the sides of aquaria,⁴⁸ and each other;³¹ sometimes stuck to plants near surface,⁵⁸ and other times partially buried in bottom;¹³ in laboratory experiments eggs most often found near base of spawning mops⁶⁶

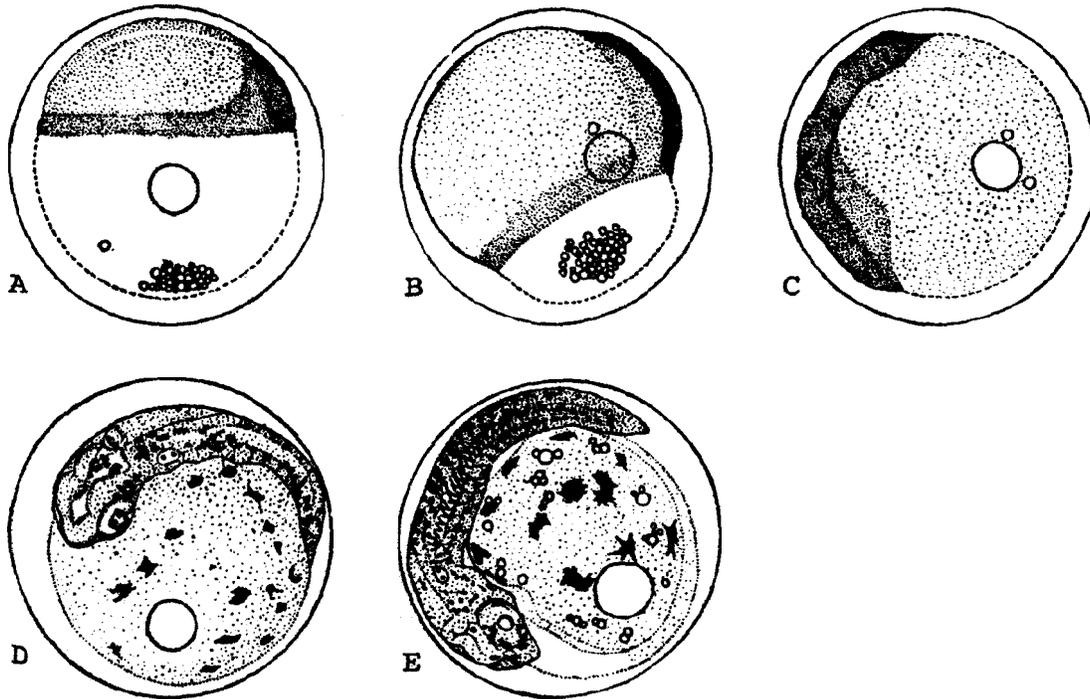


Fig. 79. *Cyprinodon variegatus*, Sheepshead minnow. A. Germ ring formed, embryonic shield developing. B. Blastoderm over 3/4 of yolk, yolk noticeably constricted. C. Early embryo. D. Embryo 48 hours after fertilization, pigment on yolk sac and body, otoliths formed. E. Tail-free embryo, 72 hours. (A-E, Kuntz, A., 1916: figs. 7–11.)

(although other eggs were probably eaten by adult fishes, NRF).

Unfertilized eggs: Micropyle single, a cone-shaped funnel without clearly defined edges and which indents slightly into the yolk; attachment structures or adhesive filaments in vicinity of micropyle enlarged and arranged in star-shaped configuration.^{13,31}

Fertilized eggs: Spherical;^{5,31,32} diameter 1.0⁴⁶-1.73

mm¹³ (reported averages ca. 1.3⁵¹ and ca. 1.5 mm); colorless, nearly colorless,^{25,27} or yellowish;^{31,32,33,61} clear,^{13,46} the transparency increasing after differentiation of blastodisc; egg membrane thick, horny,³¹ covered with fibrous sticky coat²⁷ comprised of evenly distributed microscopic filaments attached by club-like structures;¹ yolk with one large oil globule and several groups of much smaller oil globules;^{5,33,38} perivitelline space narrow (JDH).

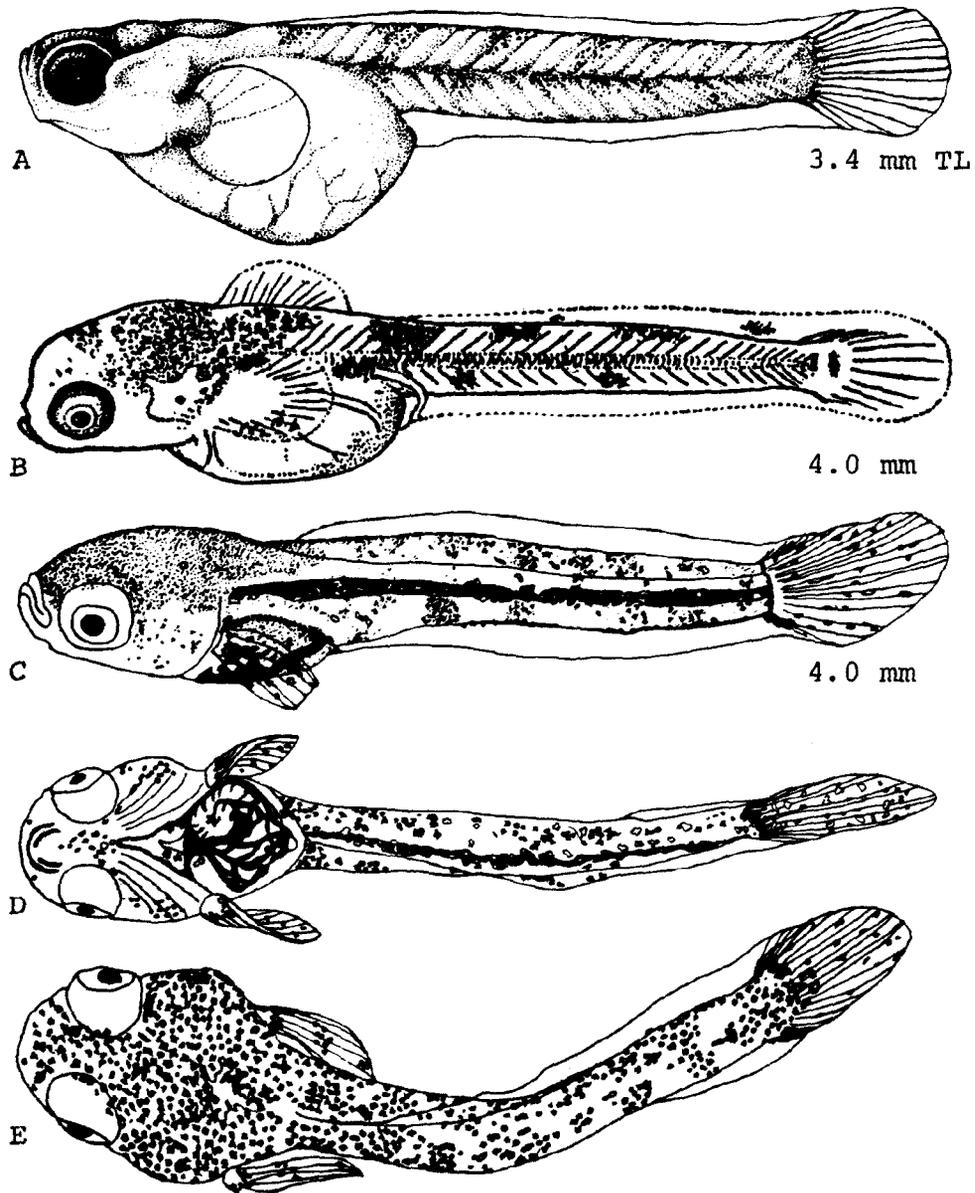


Fig. 80. *Cyprinodon variegatus*, Sheepshead minnow. A. Yolk-sac larva, 3.4 mm TL. B. Yolk-sac larva, 4.0 mm. C. Yolk-sac larva, 4.0 mm, illustrated from a living specimen. D. Ventral view of C. E. Dorsal view of C. (A, Foster, N., 1974: 131, but photographed, with permission, from the original drawing by R. Lynn Moran. B, Kuntz, A., 1916: fig. 12. C-D, Original drawings, Linda L. Hudson.)

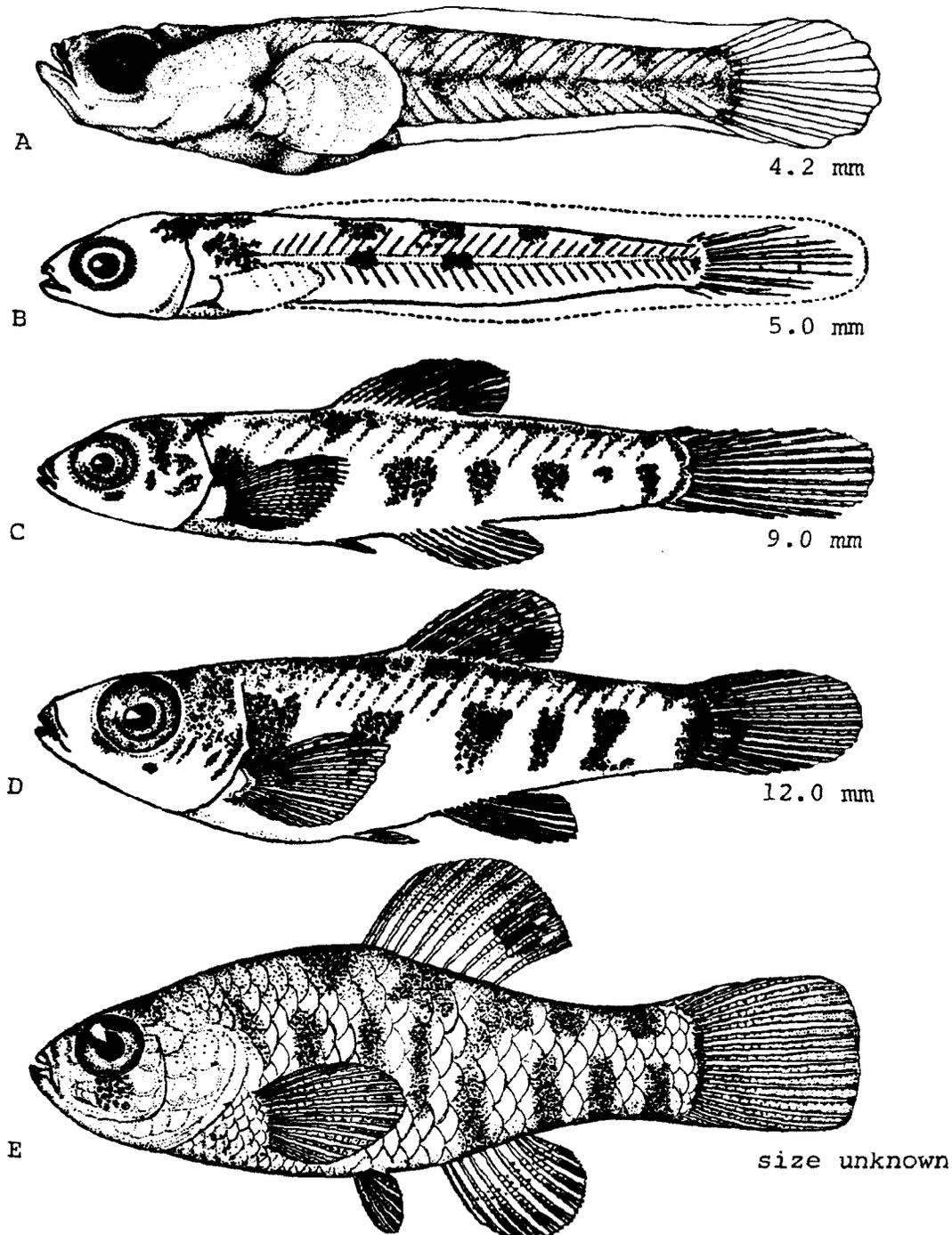


Fig. 81. *Cyprinodon variegatus*, Sheepshead minnow. A. Yolk-sac larva, 4.2 mm TL. B. Yolk-sac larva, 5.0 mm. C. Larva, 9.0 mm. D. Juvenile, 12.0 mm. E. Juvenile, size unknown. (A, Foster, N., 1974: 131, but photographed, with permission, from the original drawing by R. Lynn Moran. B-D, Kuntz, A., 1916: figs. 13-15. E, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 296a.)

EGG DEVELOPMENT

Development at unspecified temperature:

Blastodisc stage—blastodisc of nearly uniform thickness throughout central area, thinning out abruptly near periphery.

About 1 hour, 30 minutes—first cleavage.

About 2 hours—2nd cleavage, blastomeres approximately equal in size and symmetry.

By time of 4th cleavage—arrangement of blastomeres distinctly irregular.

At less than 24 hours—blastoderm completely around yolk; blastopore closed; embryo less than 1/2 around yolk, short, thick, non-segmented, non-pigmented and somewhat irregular in outline.

Soon after closure of blastopore—large melanophores sparsely scattered over surface of embryo and throughout extra-embryonic blastoderm.

Somewhat later—yellow chromatophores appear on embryo and in extra-embryonic blastoderm.

48 hours—embryo fully segmented; otoliths formed; circulation established; chromatophores in extra-embryonic blastoderm aggregating along major blood vessels.

72 hours—embryo large, plump; tail free; movement established.

Just before hatching—yolk mass one half original size; length of embryo not exceeding circumference of egg.³¹

Incubation period: 4¹⁹–8²⁷ days; 4–5 days at ca. 28 C and 30 ppt salinity; 5–6 days at 23.3 C⁴⁶–27.8 C.⁴⁸ (A report of 21 days at 23 C¹³ is questioned, JDH.) Hatching can be delayed for isolated eggs, especially if dissolved oxygen is high (NRF).

*Note on development: under laboratory conditions eggs have been reared at salinities as high as 37.6 ppt.*⁶⁵

YOLK-SAC LARVAE

Hatching length 3.7–4.3 mm.⁶⁷ Maximum size described, 5.0 mm. Duration of stage, at least 5 days.³¹

Myomeres, 8 + 16.⁶⁷

At 4.0 mm body plump; head straight, not deflected over yolk; yolk mass oval at 4.0 mm, nearly absorbed at 5.0 mm. Mouth apparently open at hatching, terminal at 5.0 mm; gape extended to anterior margin of eye at 5.0 mm. Caudal and pectorals with incipient rays at hatching; dorsal, anal, and pelvics completely absent at 5.0 mm. Notochord hyaline at hatching; urostyle oblique at 5.0 mm.⁶⁷

Pigmentation: In a living specimen 4.0 mm TL, orange pigment on head and in obscure lateral blotches on body;

a row of orange and black chromatophores (predominantly black) along ventral edge of notochord; a series of more or less evenly spaced orange spots along dorso-lateral surface of body; large stellate leucophores on body, caudal fin (where they are the dominant pigment), the underside of the head, and in dense clumps at pectoral bases; bright yellow chromatophores on ventral aspects of head and in thoracic region.⁶⁷

Hatchlings otherwise described as yellowish throughout; posterior half of body with lighter and darker vertical bars; and with chromatophores scattered over head and anterior part of body. At 5.0 mm vertical bars somewhat more developed.^{31,38} Some specimens of unspecified length, however, "almost entirely unmarked."¹⁴

LARVAE

Specimens described, 7.0⁴⁶–9.0 mm.³¹

At 9.0 mm body relatively slender, dorsum not conspicuously elevated. Dorsal, anal, caudal, and pectorals fully formed; pelvics apparently incomplete.¹⁴

Pigmentation: Some specimens of less than 8.0 mm almost entirely unmarked.¹⁴ At 7.0–9.0 mm vertical bands, typically on adult female, usually evident but not fully developed.^{31,46}

JUVENILES

Minimum size described, 12.0 mm.³¹

"Young" proportionately more slender than adults;³⁶ at 12.0 mm depth increasing, back becoming elevated; caudal more rounded than in adult.³¹ Occipital concavity (always present in adult males) absent in "young" males.¹⁴

Pigmentation: At 12.0 mm, colors characteristic of adult, but lighter; vertical bars more conspicuous.³¹ At 15.0 mm pattern of both sexes like that of adult female^{14,46} including dorsal ocellus;³⁴ "small" males may have orange shading on sides along with female pattern.⁵⁴ At ca. 18.0 mm body silvery white with ca. 8 irregular cross-bars and rounded blotches, some of which extend downward and contact lateral bars; a narrow blackish bar at base of caudal; posterior dorsal ocellus black, rounded.⁴⁶ Juvenile pattern retained to lengths of ca. 30¹⁴–32 mm.⁶¹

AGE AND SIZE AT MATURITY

Mature at 4 months^{46,58} to 1 year;³² males at 24–25 mm, females at 27–28 mm.⁵⁷

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Fundulus confluentus Goode and Bean, Marsh killifish**ADULTS**

D. 8³⁹-13,²⁷ mode 11; ⁴ A. 7¹⁵-12; C. (branched rays) 13-20; ²⁷ P. 13²⁷-18; ²⁶ V. 6; ²³ lateral line scales 30²⁷-42; ³⁹ oblique scale rows between upper angle of gill opening and dorsal origin 18-19,¹⁶ from anus forward to middle of back 15, from nape to dorsal origin 18²³-22; scales around caudal peduncle 15-18; mandibular pores 6-10; gill rakers 4-9; ²⁷ branchiostegals, possibly 5.²²

Proportions as times in SL: Depth 3.5²⁷-5.5; ³⁹ head 2.8-3.6; caudal peduncle depth 6.0-8.2; caudal length 3.6-5.0; dorsal length 3.2-5.7; anal length 3.6-5.6; pectoral length 5.0-6.5; dorsal origin to caudal base 2.5-3.2.²⁷ Proportions as times in HL: Eye 3.0-4.0,³⁹ snout 3.3-3.5.³³

Body rather slender, compressed; caudal peduncle strongly compressed; head depressed,¹⁶ small, narrow; ²³ mouth slightly superior, mostly transverse.¹⁶ Teeth villiform, in narrow bands in each jaw, the outer series slightly enlarged.²⁰ Postorbital canal series uninterrupted.²⁴ Humeral scale not enlarged; ²³ in females 1 or 2 modified, triangular scales between pelvic fins; anal sheath along approximately one-third length of first anal ray.²⁷ Male contact organs on lower parts of opercle, sides of body between dorsal and anal fins, on anal fins, and, sometimes, on rays in anterior part of dorsal.³⁵

Pigmentation: Quite variable,^{16,21} general ground color described as gray,¹⁷ dark olive,¹³ brownish,¹⁹ brownish yellow,¹⁵ or yellowish gray; ²² highly melanistic specimens reported from Florida.³² Males dark olive brown²³ or dark green above,¹⁶ with a dark predorsal stripe from first enlarged interorbital scale to dorsal fin origin; blue or olive brown dorsolaterally. Sides typically brownish with posterior parts blue,²⁷ sometimes very dark⁸ and thickly sprinkled with blackish brown spots,³⁰ also sometimes golden. Sides with 13²³ to ca. 20 or more³⁰ white²⁷ or silvery³⁴ vertical bars which do not extend onto belly, but almost reach mid-ventral line behind pelvics, and with numerous small pearly spots posterior to dorsal fin origin; ^{16,23} lateral bars inconspicuous in very dark males.⁸ Ventral surfaces white, yellow,²⁷ golden,²³ yellow-orange, or orange.³⁸ Numerous melanophores on operculum and cheeks, and operculum with a large, dark blotch bordered with silver.²⁷ Dorsal fin usually with,¹⁶ but sometimes without,³⁰ a conspicuous, black ocellus; ¹⁶ ocellus sometimes bordered with bright orange; ³⁴ outer edge of dorsal white,³⁸ yellow,³⁵ orange,²³ or reddish orange; ³⁵ base of dorsal dark⁸ and sometimes with pearly spots.¹⁶ Anal fin base dark⁸ and with pearly spots; ¹⁶ margin with yellow,³⁵ orange,^{23,34} reddish orange,³⁵ or pinkish pigment.¹⁶ Caudal fin dusky, light orange, its base indistinctly barred²³ and with pearly spots¹⁶ and its border bright yellow or reddish orange³⁵ (although in breeding

males dark to tip³⁸). Pectorals orange, slightly dusky,²³ and with melanophores along rays.²⁷ Pelvics plain orange.²³

Females brown or olive above,^{16,27} the back sometimes with small dark blotches.²³ Sides with vertical bars, spots, spots and bars,²⁷ or horizontal streaks; vertical bars entirely lacking in some populations.³⁴ Ventral surfaces pale,²³ dusky white, yellowish,²⁷ or slightly greenish. Head with irregular sprinkling of black dots.¹⁶ Dorsal fin dusky,²³ milky white, yellow,²⁷ or golden dusky; ¹⁶ dorsal ocellus well-developed, reduced, or absent; ²⁷ when present, ocellus bordered, at least above and below, with "pale"⁸ or white; ²³ sometimes noticeably elongate.¹⁶ Anal milky white, yellow,²⁷ or wine colored¹⁶ and with some melanophores.²¹ Caudal plain dusky, milky white, yellow,²⁷ or dusky golden.¹⁶ Pectorals transparent,²⁷ dusky golden,¹⁶ and with melanophores along rays. Pelvics similar to pectorals.^{23,35}

Pigmentation varies both ecologically and geographically. Males in brackish water typically blue posteriorly, with pearly spots on body and median fins and light vertical stripes; in freshwater, body brown or olive, spots yellowish or dusky white. Females west of the Mississippi River²⁷ (and apparently also along Atlantic coast, JDH) without vertical bars or dorsal ocellus.²⁷

Maximum length: Females 81.0 mm, males 65.0 mm²⁷ (a reported maximum length of ca. 100 mm¹⁹ is questioned. JDH).

DISTRIBUTION AND ECOLOGY

Range: Lynnhaven, Virginia¹⁶ to Key West, Florida and west along the Gulf coast to Corpus Christi, Texas.³⁵

Area distribution: Lynnhaven, Virginia¹⁶ (all records from Maryland,³ Delaware,²⁵ and New Jersey⁴⁵ are questioned).³⁷

Habitat and movements: Adults—a euryhaline,^{7,9,17,25} shallow water¹⁶ species found over soft, muddy bottoms²⁷ in pools,^{5,6,35} brackish marsh ponds,³⁶ barrier beach ponds³¹ (by implication, JDH), tide pools on mud flats,⁸ freshwater ponds,¹⁴ salt marshes,^{7,10,12,19} lakes,³² swamps,³³ bays,^{14,18} rice fields,²⁷ bayous,^{5,35} streams (both tidal²⁰ and, presumably, nontidal²⁸), creeks,³⁶ clear spring runs,²⁷ freshwater rivers,^{13,36} and vicinity of salt springs in freshwater areas. Sometimes in turbid²⁷ or muddy water,¹⁶ and sometimes found in drying mud.²⁷ Often associated with cypress, willow,²⁹ mangrove,¹⁰ and saw grass,³⁵ and sometimes with aquatic vegetation, at least in rivers.²⁷ Salinity range 0.0^{1,32,36}-53.9 ppt.³⁵ Recorded temperature range 12.0-25.6 C.⁴¹

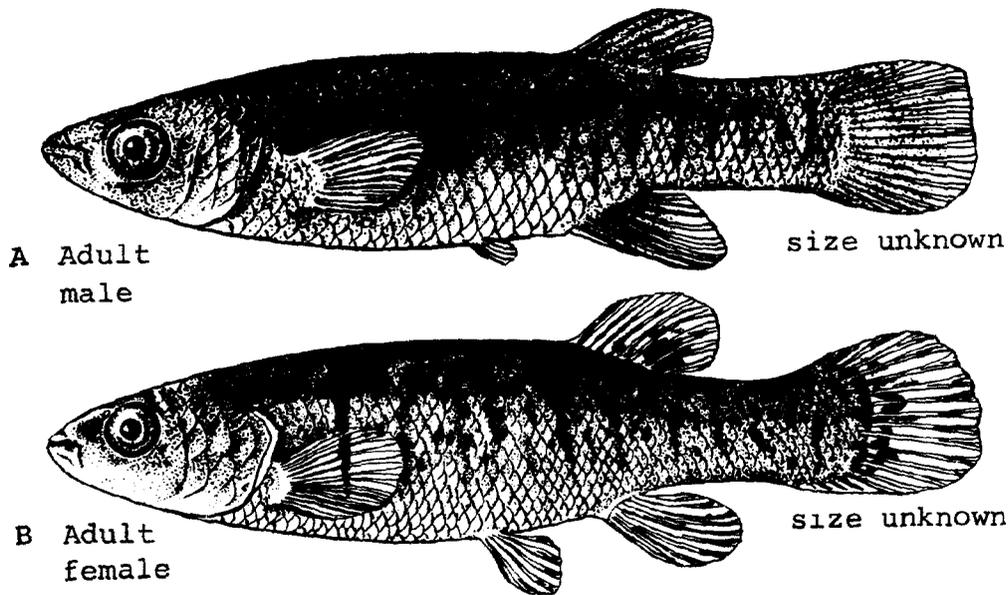


Fig. 82. *Fundulus confluentus*, Marsh killifish. A. Adult male, size unknown. B. Adult female, size unknown. (A, B, Hildebrand, S. F., and W. C. Schroeder, 1928: figs. 74-75.)

Larvae—no information.

Juveniles—maximum recorded salinity, 3.7 ppt; maximum recorded temperature, 28.3 C.⁴² Specimens 19.0 mm long from tidal streams in Florida.¹¹

SPAWNING

Location: In nature among "plants"³⁰ (including algae masses³⁵) in both fresh and brackish water in rainfilled swales^{7,27} and pools, as well as the fluctuating margin of brackish tidal water.² Under laboratory conditions directly over bare substrate of sand (which may be preferred spawning site for subspecies *F. confluentus confluentus*),^{37,44} over clumps of spanish moss,³⁸ randomly on submerged spawning mops,³⁷ and at or near surface near corals of floating spawning mops.³⁴ Drewry listed spawning sites of *F. confluentus pulvereus* in decreasing order of preference (under laboratory conditions) as finely divided plant material of any sort, vertical or overhanging solid surfaces, and loose sand or gravel.³⁸

Season: In Florida ripe individuals reported in all months, and apparently continuous at least in Everglades and Florida Keys.^{7,10,27,32} In Texas ripe males year round, ripe females recorded in all months but November and December; spawning period 10, or possibly 12, months.³⁸ Because of possible misidentifications, reports of spawning in April and May in Chesapeake Bay and from April to October at Beaufort, North Carolina¹⁶ are questioned (JDH).

Temperature: Spawned in aquaria in which temperatures varied from 23.3-27.2 C.³⁷

Fecundity: 34-61 ripe ova.³²

EGGS

Location: Demersal (JDH), possibly attached to plants³⁰ or algae masses;³⁵ under experimental conditions buried in substrate, or attached randomly to spawning mops from bottom^{37,44} to near surface;³⁴ sometimes stranded out of water on ground surface among plant litter or in moist matted algae.^{2,7}

Ripe ovarian eggs: Yellowish, diameter 0.8 to ca. 1.5 mm.^{10,32,35,40}

Fertilized eggs: Diameter 1.6-1.8 mm;³⁵ usually (JDH), but not always, round;³⁰ chorion with both attachment filaments and "chorionic bristles"⁴⁴ or "minute punctae"³⁵ (scanning electron micrographs of these structures show them as small, spherical nodules³⁷); yolk with 10-15 oil globules.³⁵

EGG DEVELOPMENT

Embryos "well developed" in 5 days at unspecified temperature.³⁰

Incubation: Variously stated as 10-14 days "with the aid of some microorganism culture" to assist with hatch-

ing;³⁰ "up to 28 days";³⁵ 3-4 weeks in the subspecies *pulvereus*.^{34,35} At 28.2-29.5 C, 11-17 days (GED). When developed out of water, hatching may be delayed for up to 95 days; such eggs hatch in 15-30 minutes after immersion in tap water.^{2,7}

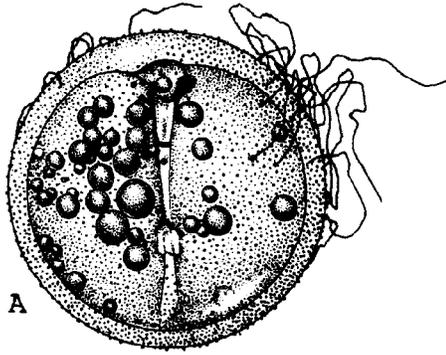


Fig. 83. *Fundulus confluentus*, Marsh killifish. A. Developing egg, showing chorionic bristles and attachment filaments. For comparison to closely similar chorion of *Fundulus luciae* see fig. 106. (A, Original drawing, Elizabeth Ray Peters.)

YOLK-SAC LARVAE

Hatching length, 4.0-5.6 mm. Length at end of stage, unknown.

Myomeres 9-10 + 21-24.⁴³

Caudal fin with 12 rays formed at hatching.³⁵

Pigmentation: In life at 5.5 mm (recently hatched *F. confluentus confluentus*) dark brown pigment on head, along back, in anterodorsal region of notochord, ventrally throughout area below notochord, over yolk sac, and along developing caudal rays; dorsal pigment band serrated (but this pattern lost soon after hatching); a conspicuous row of bright golden spots from region of posterior end of yolk sac to base of tail, the posterior-most of which is conspicuously larger than the rest; small yellow blotches over yolk sac, and single yellow chromatophores on cheeks; small areas of white pigment on yolk sac, head, and base of pectoral fins; two orange spots on caudal fin, one dorsally and one ventrally, and scattered orange chromatophores on yolk sac; a conspicuous pigment band behind eye, and melanophores in pectoral fin.⁴³

In preserved yolk-sac larvae of *F. confluentus pulvereus* of unspecified size, mid-dorsal and mid-ventral rows of melanophores well-developed and a series of small melanophores mid-laterally between epaxial and hypaxial muscle masses.³⁵

LARVAE

Undescribed, but "young" from eggs reared out of water hatch without visible yolk, and at sizes equal to individuals from water-hatched eggs 2 to 4 weeks old.^{2,7}

JUVENILES

Minimum size, unknown.

Pigmentation: In "young" of 30 mm or less the color is uniformly that of the adult female;¹⁶ this is especially true of the basal melanophore layer of *pulvereus* populations;³⁸ juvenile males may have a dorsal ocellus.²⁷

AGE AND SIZE AT MATURITY

Age unknown, but entire life-span may be limited to a single season;⁶ specimens 26-40 mm TL have been regarded as adults; otherwise 29 mm SL³⁵ or ca. 35 mm TL in *F. confluentus pulvereus*, ca. 40 mm TL in *F. confluentus confluentus*.²⁷

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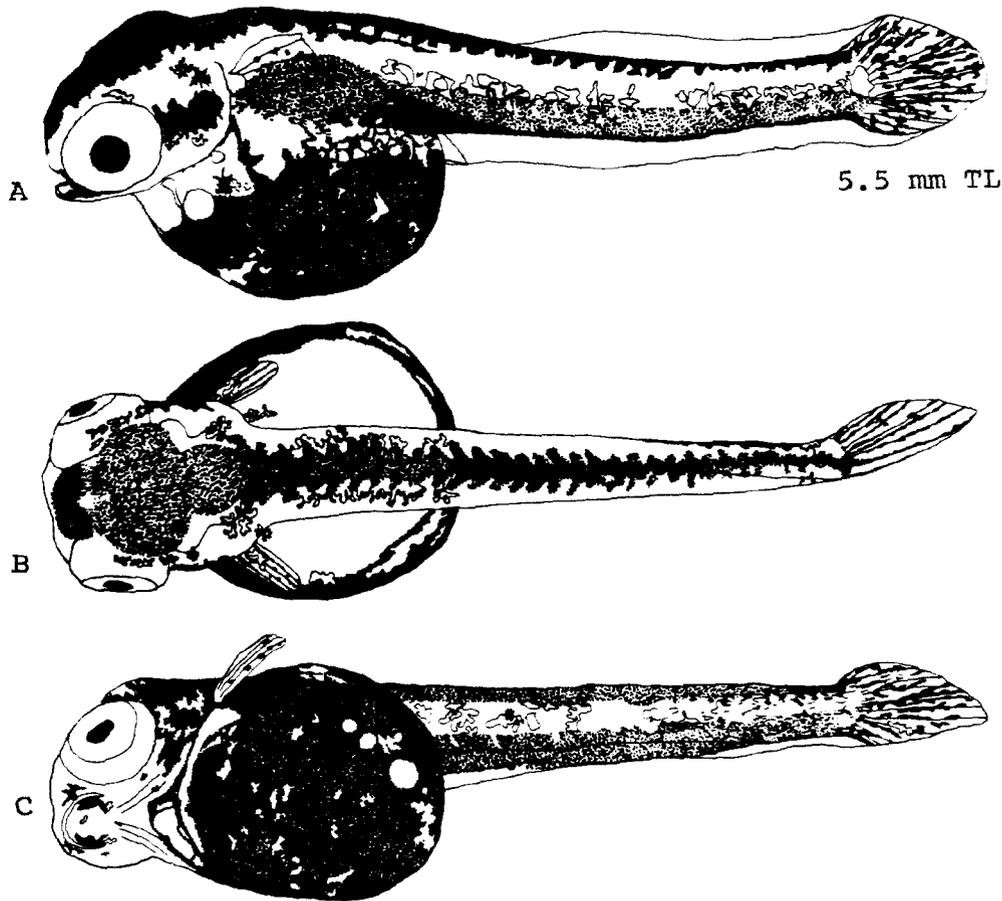


Fig. 84. *Fundulus confluentus*, Marsh killifish. A. Yolk-sac larva, 5.5 mm TL. B. Dorsal view of A. C. Ventrolateral view of A. (A-C, Original drawings, Linda L. Hudson.)

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Fundulus diaphanus (Lesueur), Banded killifish**ADULTS**

D. 9⁷⁰-16;¹⁸ A. 9¹²-13;^{9,18} C. 14-17;⁷⁴ P. 13-19;^{12,71} V. 6;²² scale rows along body 40-55,¹² counts of 31-33⁷⁰ and 60⁶⁶ doubted (JDH), scales around body in advance of dorsals and pelvics 27-42,^{10,71} oblique scale rows between upper angle of gill opening and dorsal origin 14-18,¹³ predorsal scales 21⁹-29, scales between dorsal fin origin and anal fin origin 16-18;²¹ transverse scale rows on body ca. 12⁶³-15;²⁷ vertebrae 35-36^{23,90} (17+18²²); gill rakers 4⁸-7;²¹ branchiostegals, usually 6, 6, but vary from 5, 6-7, 7;⁹⁶ preopercular pores 7; mandibular pores 4; postorbital pores 4.^{10,68}

Proportions at times in SL: Depth 3.8-4.8.²³ As times in TL: depth 4.1-5.7, head 3.3-4.0.⁴⁵ Proportions as percent TL: depth 12.9-17.2, head 21.3-24.2; as percent HL: Eye 23.6-31.7, snout 30.3-35.7.^{7,11,74}

Body elongate, slender, not elevated, somewhat flattened at back of head and nape region, compressed posteriorly;^{7,11,74} head depressed; mouth mostly transverse, slightly superior;⁴⁵ cheeks and opercles scaled.⁴¹ Dorsal fin origin in advance of anal origin;^{40,61} anal of male much longer than that of female;¹⁵ pelvics scarcely reaching vent in female, somewhat longer in male.⁶³ Males with contact organs on anal rays,¹⁷ also on a broad area from the dorsolateral region above the pectoral fins, broadening posteriorly to include most of the scales between dorsal and anal bases and onto the caudal peduncle, also on top and sides of head and on dorsal, anal and pelvic fins.⁷⁸

Pigmentation: Olivaceous,⁷⁸ olive yellow, or yellow-brown above,^{7,11,69} somewhat iridescent;⁵ sides silvery^{7,11} or yellowish; venter yellow or silvery white; a dark brown mid-dorsal stripe;⁶⁹ back sometimes spotted;^{11,27} sides with 12⁷⁴-30⁶ vertical dark bars;⁵ dorsal usually colorless,¹⁵ sometimes mottled with dark and light spots;⁹ other fins light olive, olive yellow,⁶⁹ or bright yellow; scales edged with fine dark spots;⁹ peritoneum silvery,¹⁰ silvery and lightly speckled, or dark on dorsolateral surface and silver on lateral and ventral surfaces.⁷⁴ Males olivaceous above,²⁷ white below;⁴⁵ 15-30 vertical dark^{6,42} or silvery bars;^{7,27,40,45,51} caudal peduncle bluish white beneath;⁴⁵ a dark spot on opercle opposite eye;²⁷ dorsal usually plain, occasionally faintly mottled with black and white^{15,21,27,45} or with black posterior ocellus;⁹ caudal dusky; anal and pectorals more or less yellowish; pelvics mostly bluish white tinged with yellow;⁴⁵ breeding males (subspecies *menona*) vivid iridescent green with pink tinges and golden cross stripes.⁶⁷ Females olive above, silvery white on lower sides, white below;⁴⁵ 15-20^{7,11,27,51} dark or greenish bars narrower

and shorter than those of male;^{27,45} interspaces between bars sometimes black-spotted;⁴⁵ dorsal, caudal, and pectorals yellow; anal and pelvics translucent.⁴⁵

Maximum length: Ca. 112 mm.³³

DISTRIBUTION AND ECOLOGY

Range: Manitoba and Newfoundland southward along the Atlantic slope to South Carolina; eastern parts of Dakotas, southeastward across Minnesota, Wisconsin, Michigan, and northern parts of Iowa, Illinois, Indiana, and Ohio to southernmost Ontario, New York, and eastern Pennsylvania.^{1,2,8,19,20} Introduced in Allegheny River system in Pennsylvania and as far down the Ohio River as Cincinnati.^{20,78,79}

Area distribution: Coastal waters of New Jersey,³ Delaware,¹⁴ Maryland,⁴⁸ and Virginia;⁷² northward in Chesapeake Bay to Havre de Grace.⁴⁵

Habitat and movements: Adults—a schooling^{24,62} shallow water species^{20,24} found in fresh, tidal fresh, and brackish water,^{2,4,8,58,65} and apparently sometimes in "salt water."² In estuarine areas along open, sandy shores,²⁸ particularly near mouths of freshwater streams,¹⁶ and in tide pools and ditches.⁶⁰ Recorded from freshwater ponds,⁸ lakes,^{10,26,40,47} pools,^{50,64} streams,^{4,8,19,42} brooks,^{27,53} springs,^{27,63} sheltered bays,³² inundated flood plains and marshes.^{33,35} Found over bottoms of sand, fine gravel, boulders, marl, and organic debris,^{24,25,41,62,69} in areas with heavy,⁶⁹ moderate,^{20,33,41,69} or no vegetation.²⁵ When in rivers found in sluggish⁶⁷ to moderate current.⁴⁹ Maximum recorded salinity, 5.6 ppt,²⁵ although also reported to occur occasionally in undiluted seawater. Seldom in water over 300 mm deep.²⁴ Large schools congregate in autumn in some lakes;⁵² in winter apparently remain in ice-free areas.⁴⁵

Yolk-sac larvae—remain at bottom.⁶⁷

Larvae—specimens 5.5-13.0 mm long at bottom in water 3-6 m deep.⁵⁴

Juveniles—among low weeds, sometimes in water ca. 6.3-12.6 mm deep.²⁴

SPAWNING

Location: Fresh and brackish water^{4,48,56,73} in pools,³¹ ponds,³⁸ streams,⁵⁵ and brooks⁴³ in shallow water associated with aquatic vegetation^{33,37,41} such as *Vallisneria*.²⁴ Spawning observed in water ca. 150⁷⁸-200 mm²⁴ deep.

Season: In Chesapeake Bay, April to September;⁴⁵ in

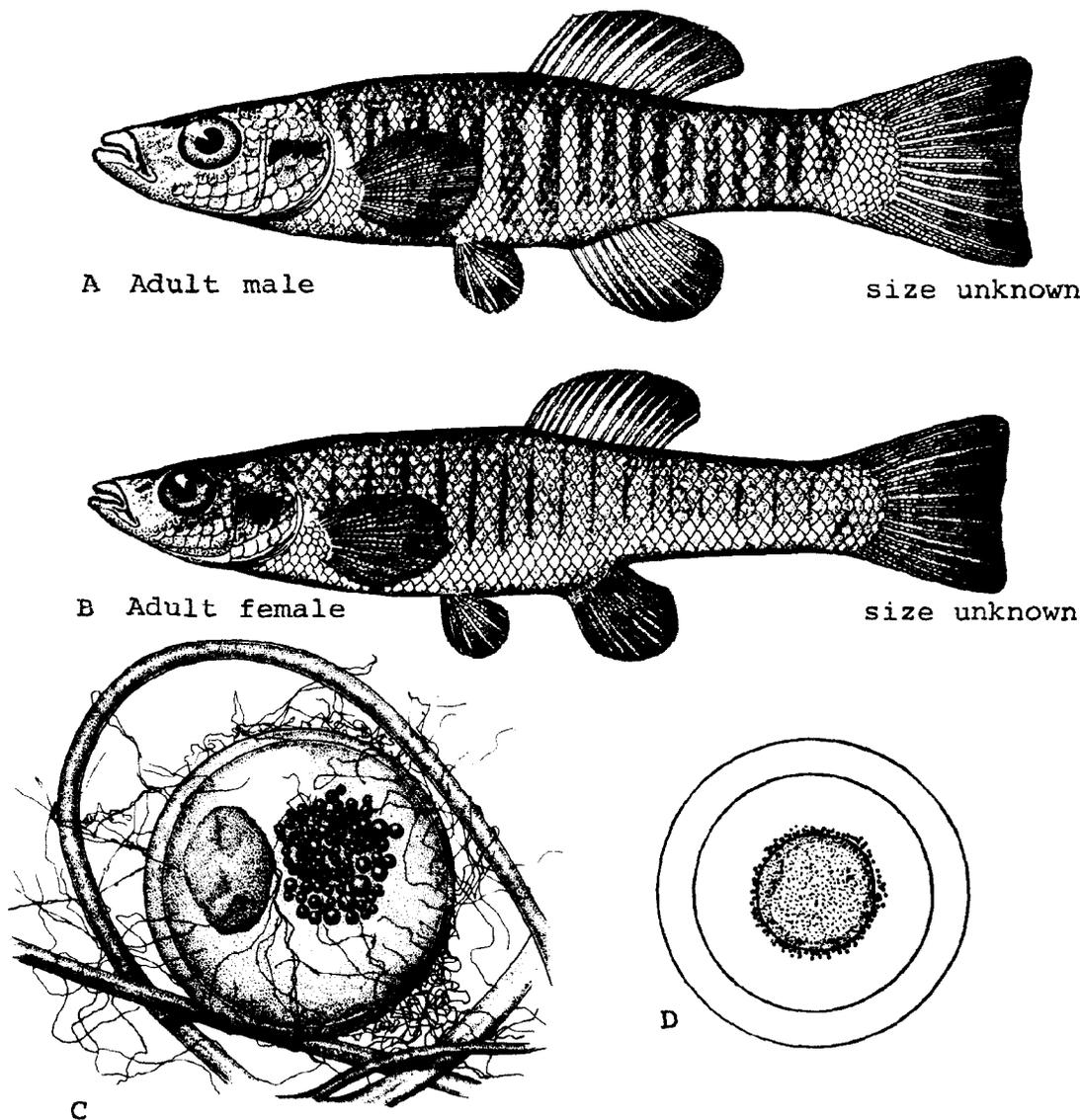


Fig. 85. *Fundulus diaphanus*, Banded killifish. A. Adult male, size unknown. B. Adult female, size unknown. C. Recently fertilized egg, showing attachment filaments. D. Egg 20 hours after fertilization, showing developing blastoderm. (A, B, Smith, H. M., 1892: pl. 19. C, Adapted from Foster, N. R., 1971: 10, Elizabeth Ray Peters, delineator. D, Newman, H. H., 1914: pl. 3.)

New York, spawning observed late May and mid-June;⁶⁰ in Connecticut, mid-June through mid-August;²⁴ in Indiana, late June to late July;⁵² in Illinois, spawning observed June 24 and August 3;⁴¹ in aquaria (subspecies *menona*) as early as March 10.⁶⁷

Time: Afternoon⁶⁰ (actual times reported 1400²⁴ and 1635 hours⁷⁸).

Temperature: Territorial combat at minimum of 21 C;⁴³ spawning at 22⁶⁰-32.2 C.²⁴

Fecundity: Ca. 200^{24,50}-252 mature ova (with smaller eggs also present).⁴⁵ Three to 10 eggs are released at each spawning act.^{43,55,67}

EGGS

Location: Demersal,^{36,67} attached to weeds,²⁴ filamentous algae,³⁸ or other aquatic vegetation^{30,78} by attachment filaments;^{24,78} also in algae at edge of large stones;^{60,78}

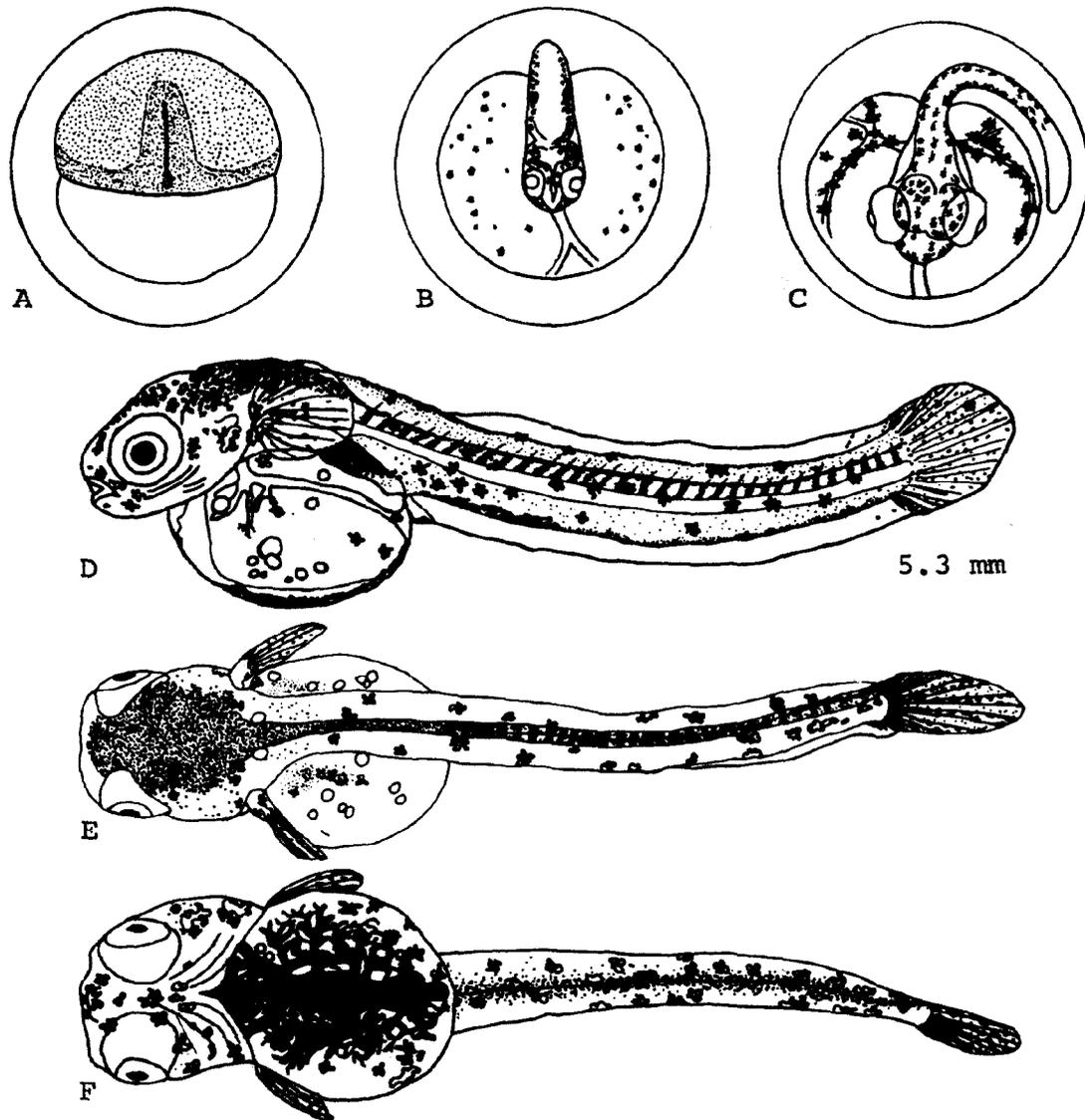


Fig. 86. *Fundulus diaphanus*, Banded killifish. A. 48 hours, germ ring, embryonic shield formed. B. 96 hours, pigment on yolk and body, vitelline vessels formed. C. 168 hours, advanced embryo, pigment developed along vitelline vessels. D. Yolk-sac larva, 5.3 mm TL. E. Dorsal view of A. F. Ventral view of A. (A-C, Newman, H. H., 1914: pl. 3. D-F, Original drawings, Linda L. Hudson.)

sometimes bound together in clumps;³⁶ in aquarium studies placed randomly throughout spawning mops.⁷⁷

Ripe ovarian eggs: Ca. 2.0 mm in diameter.⁴⁵

Freshly extruded eggs: Light yellow,⁵² ca. 1.5 mm in diameter.⁶⁷

Fertilized eggs: Diameter ca. 1.7 mm⁷⁸-2.3 mm (but minimum diameter based on preserved eggs);⁷⁸ perivitelline space ca. 1/4 egg radius;²⁹ pale yellow (by implication); egg membrane with adhesive threads^{24,34,43} which appear to vary greatly in number and distribution

in different localities (JDH); yolk with 10 to 15 medium-size oil globules⁷⁸ (although the total number of oil globules appears to be considerably greater than this. JDH).

EGG DEVELOPMENT

Development at unspecified temperature:²⁹

2 hours—first cleavage.

6 hours—advanced cleavage.

- 20 hours—blastoderm with germ ring faintly defined, embryonic shield barely visible.
- 48 hours—germ ring halfway around yolk, embryonic axis well defined, no neural tube.
- 72 hours—blastopore closed, embryo with short tail, midbrain broadly open, no heart beat, chromatophores under hindbrain and on yolk.
- 96 hours—heartbeat established; dark stellate chromatophores on top and sides of brain; yolk with many melanophores and few dull orange chromatophores.
- 120 hours—circulation well established; head with small brownish melanophores; large black melanophores along vitelline vessels; dull reddish brown stellate chromatophores on yolk.

216 hours—embryo light-colored; tail long, slender.
312–360 hours (13–15 days)—hatching.²⁹

Incubation: 11–12 days at 22.0–26.5 C; ³⁸ 16–18 days at 12–14 C; ⁶⁷ newly laid eggs hatched in 9 days at unspecified temperature.⁷⁸

YOLK-SAC LARVAE

Hatching length 5.3–6.4.^{54,76} Maximum length, 7.1 mm.³²

Myomeres 9–10 + 23–25.⁷⁶

Proportions expressed as times in TL at 7.1 mm: Snout-vent length 2.5, head length 4.44, greatest depth 6.5.³² At 7.1 mm rays developed in caudal, origin of dorsal finfold at 13th myomere.⁷⁶

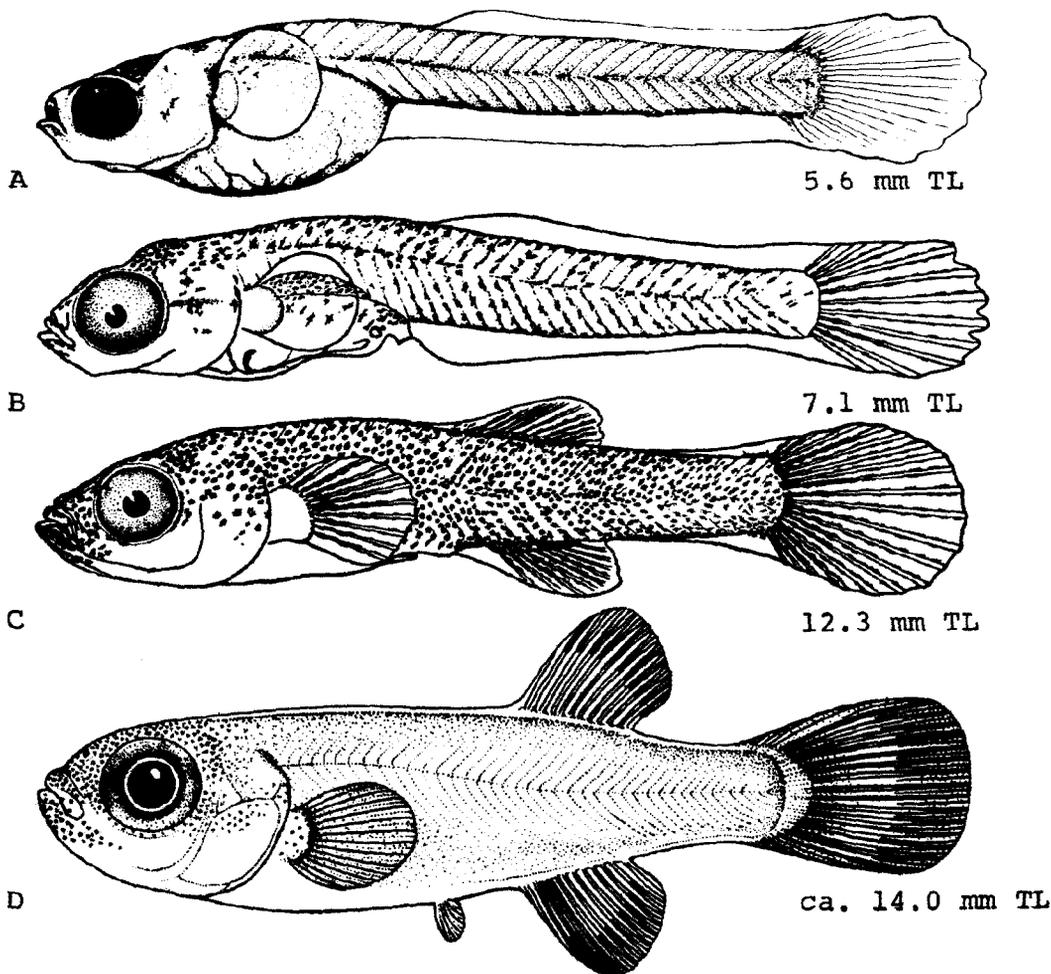


Fig. 87. *Fundulus diaphanus*, Banded killifish. A. Yolk-sac larva, 5.6 mm TL. B. Yolk-sac larva, 7.1 mm TL. C. Larva, 12.3 mm TL. D. Juvenile, ca. 14.0 mm TL. (A, Foster, N., 1974: 133, but photographed, with permission, from the original figure by R. Lynn Moran. B, C, Fish, M. P., 1932: figs. 74–75. D, Fowler, H. W., 1945: fig. 170.)

Pigmentation: At 5.3 mm (described from life) dorsal aspects of head dark; an indefinite row of dark pigment dorsally along body and a similar row along dorsal edge of notochord; ventrally dark pigment sparse, limited to series of small dots along mid-ventral line, no pigment immediately below notochord; dark pigment along developing caudal rays and on yolk sac; no pigment in developing pectoral fins; very large stellate white chromatophores on head and body and at bases of pectoral fins; smaller white chromatophores on yolk sac; few orange chromatophores on ventral aspects of body and yolk. In preserved specimens of this size no pigment immediately below notochord or in pectorals, absent or poorly developed above notochord.⁷⁶ At 7.1 mm, chromatophores over entire body, especially on top of head and in an irregular series on dorsal and ventral ridges; lateral chromatophores stellate, delicate, more numerous along lateral line and myosepta; heavy pigment on isthmus, continuing along mid-ventral line to stomach; few chromatophores on pectorals and along caudal rays.³² Pigment along developing caudal rays variable: apparently lacking in some populations;⁷² well-developed in others.⁷⁶

LARVAE

Size range described, 6.0⁶⁷-12.3 mm.³²

Preanal myomeres 10, postanal myomeres 20-22.³²

Proportions expressed as times in TL at 12.3 mm: Snout-vent length 2.1, head length 3.6, greatest depth 5.13.³²

At 12.3 mm mouth more superior than in earlier stages, finfold nearly obliterated; pelvics first evident.³²

Pigmentation: At 12.3 mm body covered with stellate chromatophores except beneath stomach; chromatophores along rays of dorsal, anal, pectorals, and caudal.³²

JUVENILES

Specimens described, up to ca. 50 mm.^{27,45,51}

Pigmentation: Young or immature with dark vertical bars^{7,11,59,62} on pale olivaceous background. Differentiation of adult pattern occurs at ca. 50 mm^{27,45,51} although specimens below this size may be mature.⁶⁹ With a 14-hour photoperiod and a temperature of 26.1 C, sexes can be distinguished 87 days after hatching.⁷⁸

AGE AND SIZE AT MATURITY

During third summer,³⁸ although specimens 70 mm and 6 1/2 months have been reported approaching maturity;⁷ ca. 38 mm in subspecies *menona*, 52.5 mm in *diaphanus diaphanus*.⁶⁹

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Fundulus heteroclitus (Linnaeus), Mummichog**ADULTS**

D. 10¹⁵⁶-14,³⁸ A. 9¹⁵⁶-12,³¹ C. 17-22; P. 16¹⁵⁶-20;¹⁶⁰ V. 6⁵⁰-7;¹⁵⁶ scales, lateral rows 31⁴³-39,⁸ predorsal 18-22, between dorsal origin and anal origin 14-16;⁴⁵ in transverse series 13-15;⁵³ gill rakers 7¹⁴¹-12; branchiostegal rays usually 5,5 sometimes 5,4 4,5 5,6, or 6,6;^{50,83,156} vertebrae 32-35¹⁵⁶ (decreasing in number with increasing developmental temperature¹¹⁰); precaudal vertebrae 14-15; caudal vertebrae 19-20;⁵⁰ 6 paired canals on head, each with 2-7 external pores;³⁰ total mandibular pores, 8;^{19,88} preopercular pores, 7.¹²⁰

Proportions expressed as times in SL: Head length 2.8-3.7,¹⁹ average depth 3.2-4.0,²¹ depth at pectoral base 4.4.⁸³ Proportions as percent TL, greatest depth 15.8-20.0, head length 20.6-25.0; as percent HL, eye 21.6-28.3.¹⁴¹

Body robust,⁶ short, deep;¹⁸ back elevated;⁸ caudal peduncle strongly compressed.³¹ Head short, broad, depressed;^{18,31,104} mouth small, terminal, mostly transverse;³¹ lower jaw projecting beyond upper;⁹³ premaxillary protractile.¹⁵⁶ Teeth pointed, in villiform bands, the outer ones enlarged.³¹ Dorsal fin origin somewhat anterior to anal fin origin;^{31,93} dorsal and anal fins of male larger than those of female;^{23,66} pelvic fins usually equidistant from tip of snout and caudal base;²¹ caudal fin broadly rounded.^{31,93} Males with contact organs on side of head, on body below and behind dorsal,¹³² and, possibly (identity questioned, JDH), on anal rays, during and within eight weeks after spawning.^{36,76} External oviducts varying seasonally from 45-65% of anterior margin of anal in southern New England populations.⁸³

Pigmentation: Typically olivaceous to dark green above, pale to yellow-orange below.⁹³ Color highly variable,^{17,67,89} depending on external stimuli,^{75,97,101,121} and assuming tints of pink, yellow, green, or blue.¹¹⁸ Scales of both sexes sometimes with white spots⁴³ arranged either in short vertical bars and scattered at random on body or in longitudinal or diagonal stripes.¹³⁸ Males dark green^{17,18,53} or blue-green above,¹³¹ yellow below; sides with narrow silvery white bars, between which are numerous small whitish or yellowish spots; head yellow below;⁵³ dorsal with or without dark ocellus on posterior rays,^{43,53,131} dorsal ocellus present year round in some populations,⁴³ present seasonally in others,¹⁰⁹ otherwise dorsal fin dusky or spotted; anal and caudal fins dusky or spotted; pelvic fins dusky, edged with yellow-gold.^{23,131} Body of spawning males with extensive bluish or orange reflections;^{88,112} blue-black above, yellow or greenish yellow below;¹³¹ sides with ca. 15 narrow silvery vertical bars and numerous white or yellow spots extending on to vertical fins; head brownish between eyes; oper-

culum dusky above, golden below; chin olive; anal and pelvic fins golden.³¹ Females brownish green to nearly plain olive above,^{8,131} lighter below;⁵³ fins plain tan,¹³¹ the vertical ones sometimes with greenish tinge. Smaller females with 13-15 dark crossbars narrower than interspaces.³¹ Spawning females very pale.¹⁴⁴ Peritoneum of both sexes almost uniformly black.¹⁴¹

Maximum length: Largest specimen from Chesapeake Bay region 122 mm,¹⁶² with females slightly larger than males.¹²⁴

DISTRIBUTION AND ECOLOGY

Range: Newfoundland⁹ and Nova Scotia⁴⁰ to Mantanzas Inlet in northeastern Florida;^{2,42} introduced in Ohio drainage of western Pennsylvania.¹²⁶ (Records from Labrador^{41,127} are apparently in error.⁹)

Area distribution: Coastal waters of New Jersey,^{6,135} Delaware,⁷ Maryland,⁵ and Virginia;^{133,134} north to Havre de Grace in Chesapeake Bay.³¹

Habitat and movements: Adults—a schooling species^{5,142} found in fresh,^{80,85,97,98} tidal fresh,^{77,108} brackish,^{19,27,31,40,92} and salt water,^{31,40,125} and capable of withstanding abrupt salinity changes.¹⁰³ Recorded from nontidal portions of large rivers;¹⁰⁰ freshwater streams,⁹³ and creeks;¹ lakes;^{100,157} salt marshes;^{1,7,71,161} barrier beach ponds;⁵⁵ tidal streams,⁸⁶ creeks, and ditches;¹⁶¹ near tributary inlets in bays;^{12,27} in shallow brackish coves;³¹ near docks; along beaches;^{5,14} and in ocean surf.⁸⁶ Frequently associated with vegetation such as eelgrass, *Salicornia*, and *Spartina*.^{27,35,54,87,112} Apparently ubiquitous in some areas,²² but preferring muddy water^{53,144,159} and muddy bottom elsewhere.³¹ Capable of moving overland or burrowing in mud when stranded in small ponds above tide,^{87,161} and can remain out of water for at least four hours without apparent injury.¹¹¹ Sometimes found in extremely foul, polluted water.^{33,44,90,105,112} Migratory,⁶⁵ moving to marshes and freshwater creeks in late March (at water temperature of 15 C), with peak of migration occurring in mid-April. Run in and out with tide during summer months until temperature of pools reaches ca. 24 C (during August), then cease running for over two weeks, reappearing in early September and continuing to run until temperature is down to 10 C.^{1,17,35,111,144} May retire to deep mud holes near mouths of creeks in winter, but also hibernate inshore, burrowing 15-20 cm in mud in salt marsh pools and sheltered lagoons.^{1,17,87,111,112} Maximum distance from shore, seldom more than 90 m; maximum depth, seldom deeper than "a couple of fathoms";⁸⁷ salinity range (natural), 0.0^{80,85,157}-41.0 ppt;¹⁵⁹ experimental, up to 106.0-120.3 ppt.¹⁵⁸ Minimum recorded temperature (experimental), -1.5 C.^{149,150,151,152}

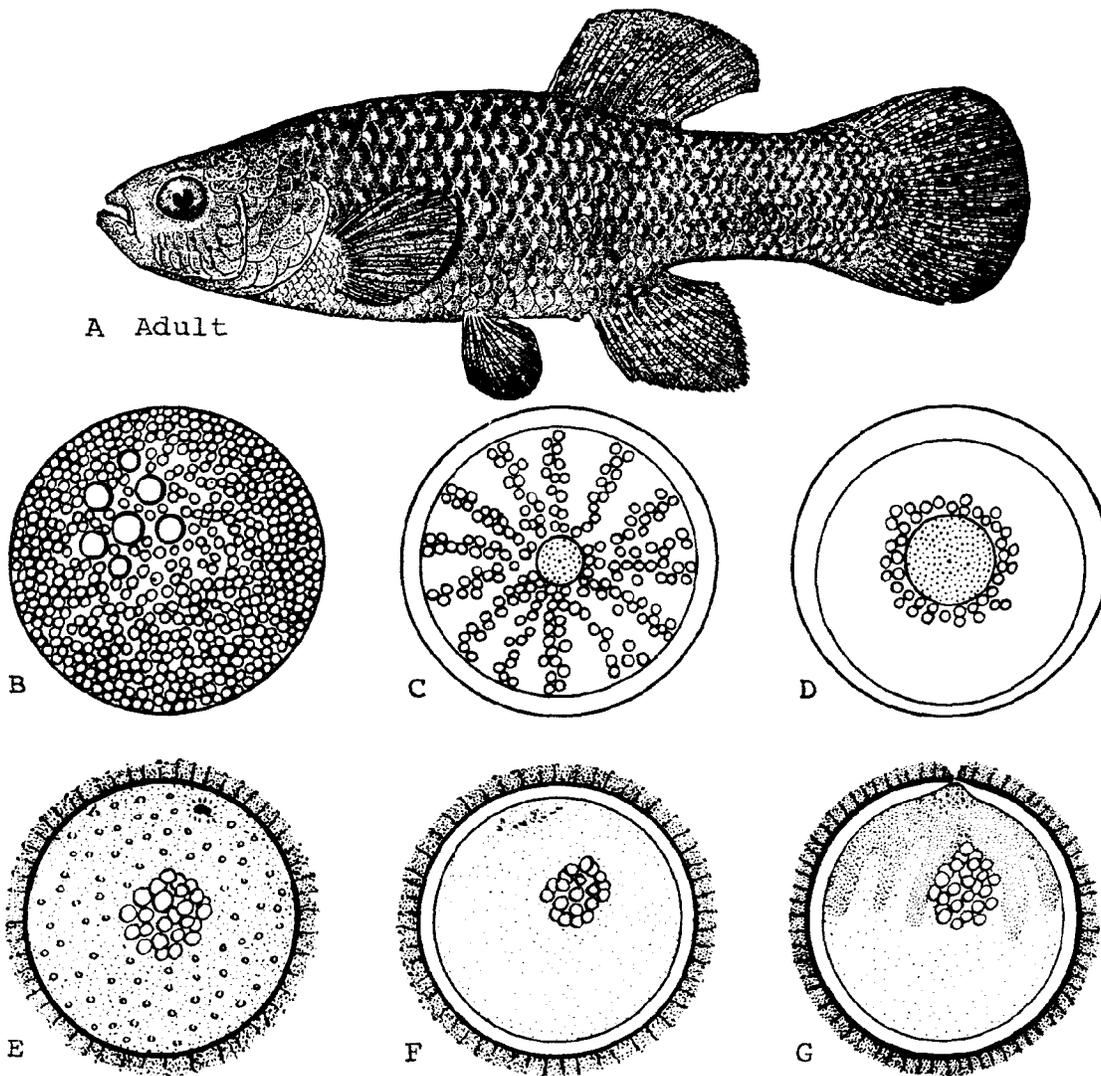


Fig. 88. *Fundulus heteroclitus*, Mummichog. A. Adult, size unknown. B. Freshly stripped unfertilized egg showing large platelets. C. Unfertilized egg one hour after stripping showing streaming of platelets toward small blastodisc, and formation of perivitelline space. D. An unfertilized egg 1 hour and 15 minutes after stripping showing relative size of blastodisc. E. Unfertilized egg showing platelets and chorionic fibrils. F. Contraction of egg from vitelline membrane shortly after fertilization. G. Migration of peripheral cytoplasm toward point of sperm entrance (micropyle) and formation of polar cap. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 174. B, C, D, Kagan, B. M., 1935: pl. I. E, F, G, Nelsen, O. E., 1953: fig. 122.)

Maximum recorded temperature (natural), 32.5 C.¹⁵⁹ Upper lethal temperature, ca. 33.5 C.¹⁵⁶

Larvae—yolk-sac larvae apparently remain off the bottom and are attracted to light;³ specimens as small as 7.1 mm have been recorded in salinities which varied from 1.66-3.21 ppt.⁶⁹ Larvae commonly swim at surface, but will swim to bottom if disturbed.⁷³ Loeb has pointed

out that freshly hatched larvae die in solutions of NaCl equal in strength to seawater, but live indefinitely in distilled water.¹¹⁵

Juveniles—"Young" and "immature" recorded from growths of eelgrass along sandy beaches;⁵² in warm, shallow pools;¹⁶¹ and in ditches associated with salt marshes.⁸⁰

SPAWNING

Location: Salt, brackish, and freshwater^{13,71,112,134} in ponds,^{23,161} shallow pools,⁶² rivers,¹³⁴ and "pure sea water."⁶⁵ Spawning takes place in shadowed areas⁵¹ over shallows above gravelly^{135,161} or hard bottoms having sparse⁷¹ to dense¹⁰⁷ vegetation; also among emergent vegetation in intertidal zone,^{78,135} among *Spartina* roots,¹⁴⁴ and sometimes so close to shore that eggs may be washed ashore and left above water line by receding tide.^{78,135} Observed spawning in large numbers in pools not over 9 square m in area of more than a few centimeters deep.⁶² Individuals depositing nearly a filamentous eggs spawn over tidal flats inside empty shells of the ribbed mussel, *Modiolus demissus*.¹⁴³

Season: In North Carolina early May to late August;⁵⁴ in Virginia (reduced filament population), eggs observed May 3 to September 3;¹⁴³ in Chesapeake Bay, April to August;^{31,131} in Delaware Bay, May 4 through mid-August with several peaks at or near new moon high tide;¹²⁴ in New Jersey, April to late August, peak late May;^{1,17} in New York, males with breeding colors April 27;⁷¹ in Rhode Island, June to July;²⁷ in Connecticut, May to July;^{73,123} in Massachusetts, nuptial colors of males, April through August,¹⁰⁹ spawning mid-May through early August,^{26,63,79,95,96,128,129} peak June and July;⁵⁴ in Gulf of Maine, June to early August.¹⁴⁴ Spawning colors may begin to develop in early February in aquaria,¹¹⁹ and may be evident until October (by implication, JDH) in natural populations.¹⁰⁹ One female may produce several groups of eggs during a single spawning season.^{31,124}

Time: During daylight hours (by implication, JDH),²³ mid-day.^{107,144}

Temperature: 16.5¹⁵⁹–25.0 C.¹⁰⁷

Fecundity: 460–800 mature ova;^{31,47,61,124,131} one female from a population having reduced egg filaments deposited 123 eggs in 4 days (68+53+1+1);¹⁴³ female of unspecified egg type, 30 eggs at one laying.⁸⁴

EGGS

Location: Demersal.^{11,15} Presumably normally filamented eggs (JDH) attached to seaweed,^{44,46,117} algae,²⁰ and other plants⁸⁶ as well as to sand,^{87,131} stones,⁴⁴ and rocks,¹¹⁷ and in clumps to one another;^{20,27,46,87} sometimes deposited in sand at waters edge at high tide,²⁷ and found beneath mats of filamentous algae above waterline when tide recedes;⁷⁸ also deposited in mud,^{17,68} and sometimes buried in mud by spawning activities.²³ Eggs with greatly reduced filaments inside vertically oriented shells of ribbed mussel, *Modiolus demissus*, having gape of ca. 2.0 mm at posterior ends (each shell may contain

1–718 eggs in various stages of development). Eggs in shells sometimes exposed and dry, yet hatch when submerged.¹⁴³ Under experimental conditions normally filamented eggs placed randomly on spawning mops in nonflowing water,¹⁵⁵ reduced filament eggs preferentially placed against nylon screen in flowing water.¹⁴⁷

Immature ovarian eggs: At 0.16 mm diameter filaments visible as hyaline dots; at 0.4 mm filaments longer than diameter of egg in one northern population.⁶⁴

Mature ovarian eggs: 1.2–2.0 mm diameter, spherical, translucent, and with small oil globules;¹²⁴ filaments present on chorion in some populations, absent or nearly so in others.⁵⁴

Freshly stripped unfertilized eggs: Diameter ca. 2.0 mm, with eggs from smaller females commonly smaller than those of larger females;⁷³ pale brown,¹³⁵ clear yellow,⁷³ or slightly opaque;²⁹ yolk platelets and oil globules aggregated at yolk surface;^{47,73} yolk mass contained within a single membrane-bound sac enclosed in a layer of cytoplasm with an external limiting membrane on its surface;¹⁴⁵ filaments, when present, in a loose network over chorion;^{64,116} micropyle funnel-shaped,^{37,47} located at animal pole;^{29,114} egg membrane very glutinous.^{23,73}

Fertilized eggs: Spherical,⁷¹ yellowish,^{11,87,94} amber⁷¹ or almost colorless, nearly or completely transparent^{33,51,117} (a report of opaque eggs⁷² is questioned, JDH). Diameter ca. 1.5^{11,72}–2.5 mm,^{44,114,145} average ca. 2.0 mm.^{33,112} When developed in seawater perivitelline space increased as yolk used; in distilled water yolk increases in size and perivitelline space completely obliterated as development proceeds.⁷³ Oil globules opaque,¹¹ small,²⁰ unequal,⁷² and numerous^{11,20,117} (maximum number reported "more than 50"¹⁴⁴), characteristic in number and size for eggs derived from a single spawning of a particular female,²⁹ initially grouped together,⁷² but gradually carried over yolk by advancing blastoderm.²⁰ Chorion heavy, firm,^{15,87} and apparently thicker in reduced filament eggs;^{82,143} adhesive when first deposited,^{27,33,59} but ultimately losing stickiness.⁷³ Chorionic filaments in many populations long, elastic, adhesive, and sometimes forming a fibrous coat,^{11,15,20,48,59} filaments sometimes absent or greatly reduced.^{54,143}

EGG DEVELOPMENT

Following activation of egg and cytoplasmic streaming to animal pole (blastocap formation) some cytoplasm remains over yolk forming "yolk cytoplasmic layer" which ultimately becomes continuous with the periblast.¹⁴⁵

Development at 20 C±0.2 C (the Armstrong and Child series):

- 1 hour, 45 minutes (Stage 2)—one-cell stage.
- 2 hours, 30 minutes (Stage 3)—first cleavage.

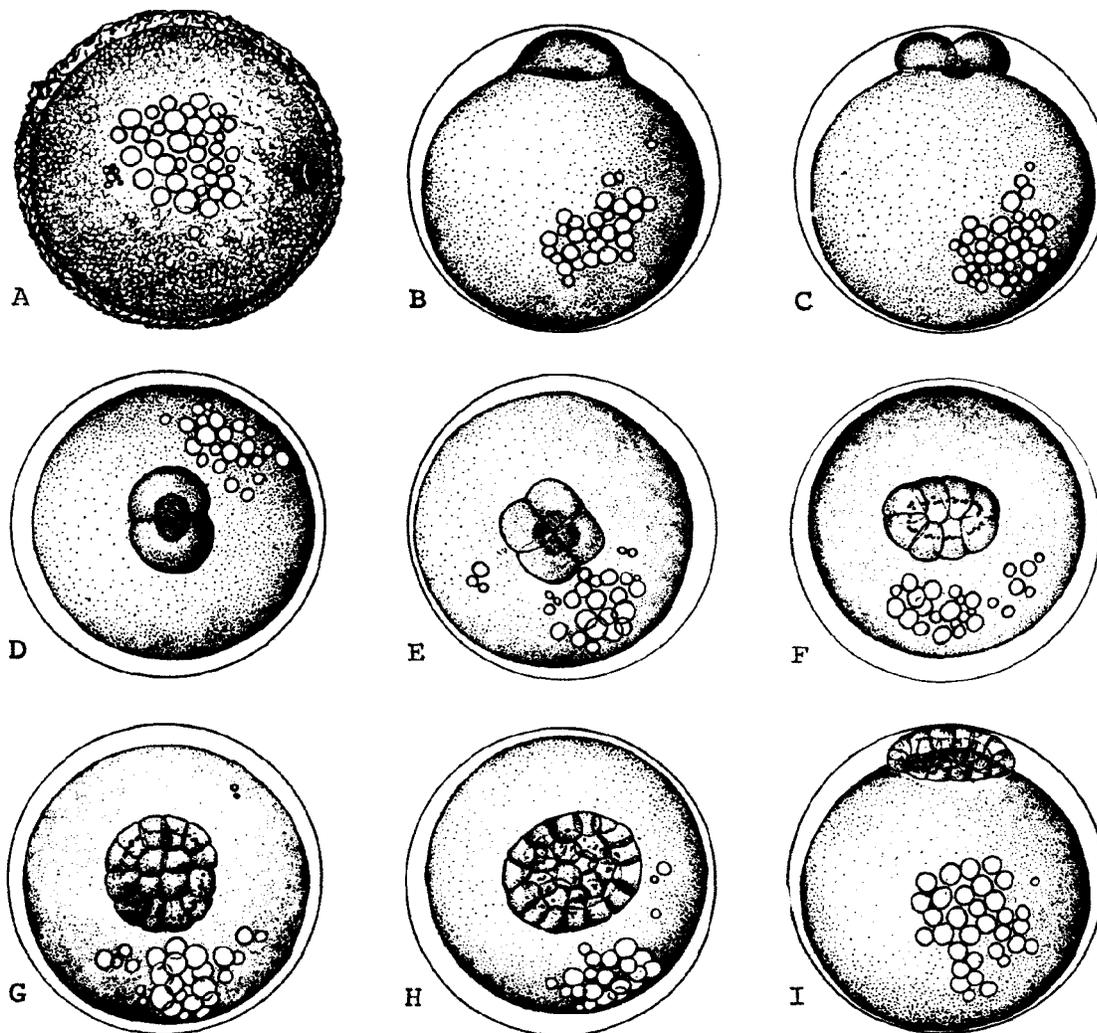


Fig. 89. *Fundulus heteroclitus*, Mummichog. A. Unfertilized egg showing matted chorionic fibrils. B. Blastodisc formation, 1 hour and 45 minutes after fertilization. C. 2-cell stage, lateral view, 2 hours and 30 minutes. D. Same as C, dorsal view. E. 4-cell stage, 3 hours and 15 minutes. F. 8-cell stage, 4 hours and 15 minutes. G. 16-cell stage, 5 hours. H. Late cleavage stage, dorsal view, 6 hours. I. Same as H, lateral view. (A-I, Armstrong, P. B., and J. S. Child, 1965: figs. 1-7.)

3 hours, 15 minutes (Stage 4)—second cleavage, 4 blastomeres of approximately equal size.
 4 hours, 15 minutes (Stage 5)—8-cell stage, with blastomeres usually arranged in parallel rows.
 5 hours (Stage 6)—16-cell stage.
 6 hours (Stage 7)—blastomeres appear columnar, with central cells forming a two-layered structure.
 7 hours, 30 minutes (Stage 8)—early morula.
 10 hours (Stage 10)—late morula.
 11 hours (Stage 11)—blastoderm flattened over yolk, its margins serrated; blastocoel not yet evident.
 15 hours (Stage 12)—marginal periblast nuclei forming circumferential band about one-fourth diameter of blastoderm (not shown in drawing).

20 hours (Stage 13)—blastoderm somewhat more flattened and expanded; blastocoel barely evident; fine droplets surround animal pole, marking future site of closure of blastopore.
 24 hours (Stage 14)—blastocoel conspicuously enlarged; periblast somewhat reduced in width.
 27 hours (Stage 15)—germ ring formed, narrow; embryonic shield rudimentary, frequently overlapping oil globules; blastocoel further enlarged, not necessarily bilaterally symmetrical.
 30 hours (Stage 16)—embryonic shield enlarged; embryonic axis lengthened; increased number of droplets at vegetal pole in region of future closure of blastopore.

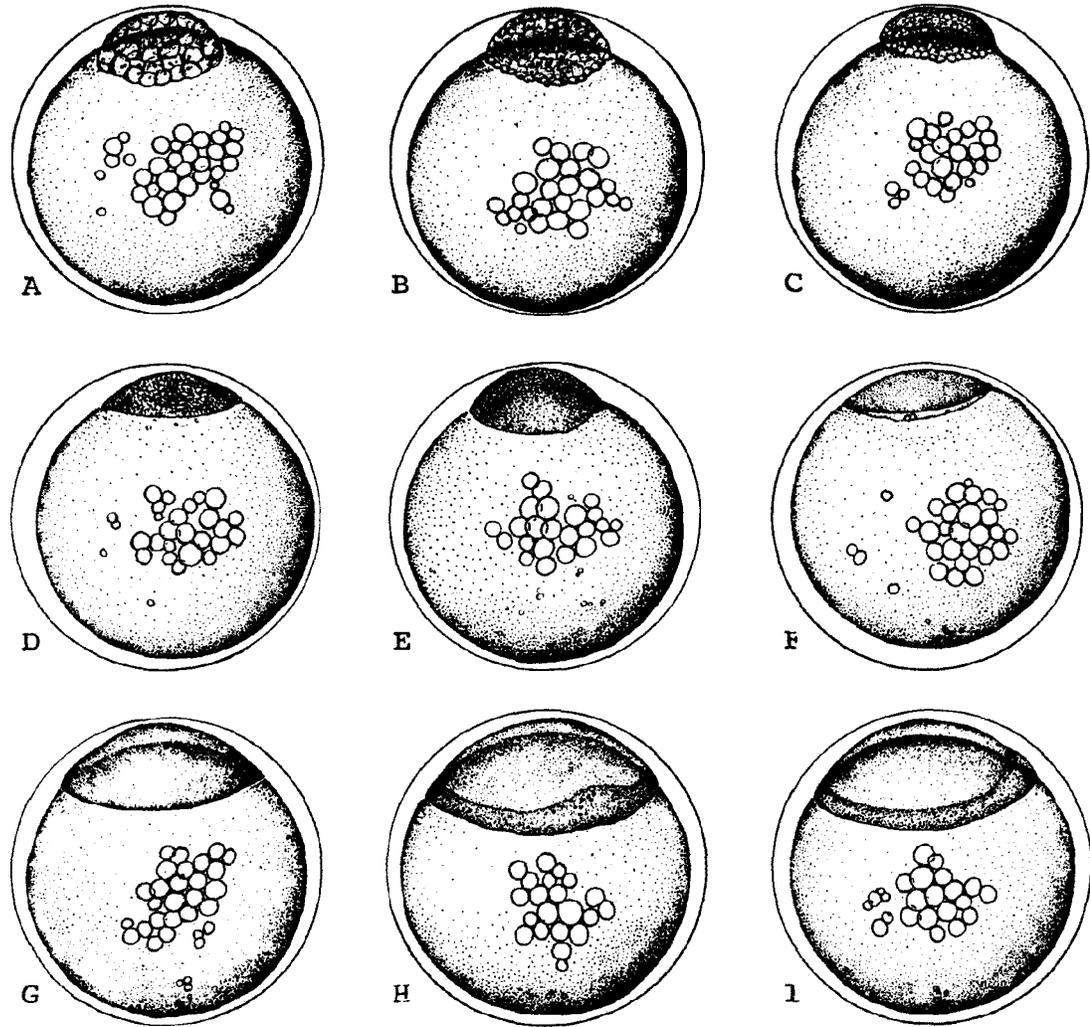


Fig. 90. *Fundulus heteroclitus*, Mummichog. A, B, C. Morulas, 7 hours and 30 minutes, 9 hours, and 10 hours old, respectively, showing late of lateral growth of blastoderm. D. Early blastula, blastoderm flattening over yolk, 11 hours. E. Continued expansion of blastoderm, 15 hours. F. Blastocoel formed, ill-defined; 20 hours. G. Advanced blastula, 24 hours. H, I. Early gastrula, germ ring around entire margin of blastoderm, embryonic shield rudimentary, 27 hours. (A-I, Armstrong, P. B., and J. C. Child, 1965: figs. 8-15.)

33 hours (Stage 17)—gastrula over half of yolk; embryonic axis one-sixth circumference of yolk.
 37 hours (Stage 18)—extra-embryonic ectoderm over three-fourths of yolk.
 40 hours (Stage 19)—blastopore reduced to small opening; embryonic keel prominent; optic vesicles present, rudimentary.
 46 hours (Stage 20)—blastopore closed; forebrain, midbrain, and hindbrain distinguishable; an evident condensation of cells lateral to embryonic axis in area of future anterior somites; Kupffer's vesicle and possibly anlagen of pericardial cavity evident.

52 hours (Stage 21)—3-4 pairs of somites.

56 hours (Stage 22)—optic cup present, lens absent; pericardial cavity definitely formed; condensation of tissue at future site of pectoral fin; blood islands forming on yolk.

66 hours (Stage 23)—anlagen of lens, olfactory placode, and heart present; small pigment cells present on yolk sac and occasionally on dorso-lateral aspect of hindbrain.

74 hours (Stage 24)—brain ventricles, otic vesicles forming; 14 somites formed; cardiac contractions evident; condensation of tissue on lateral aspects of hindbrain anterior and posterior to

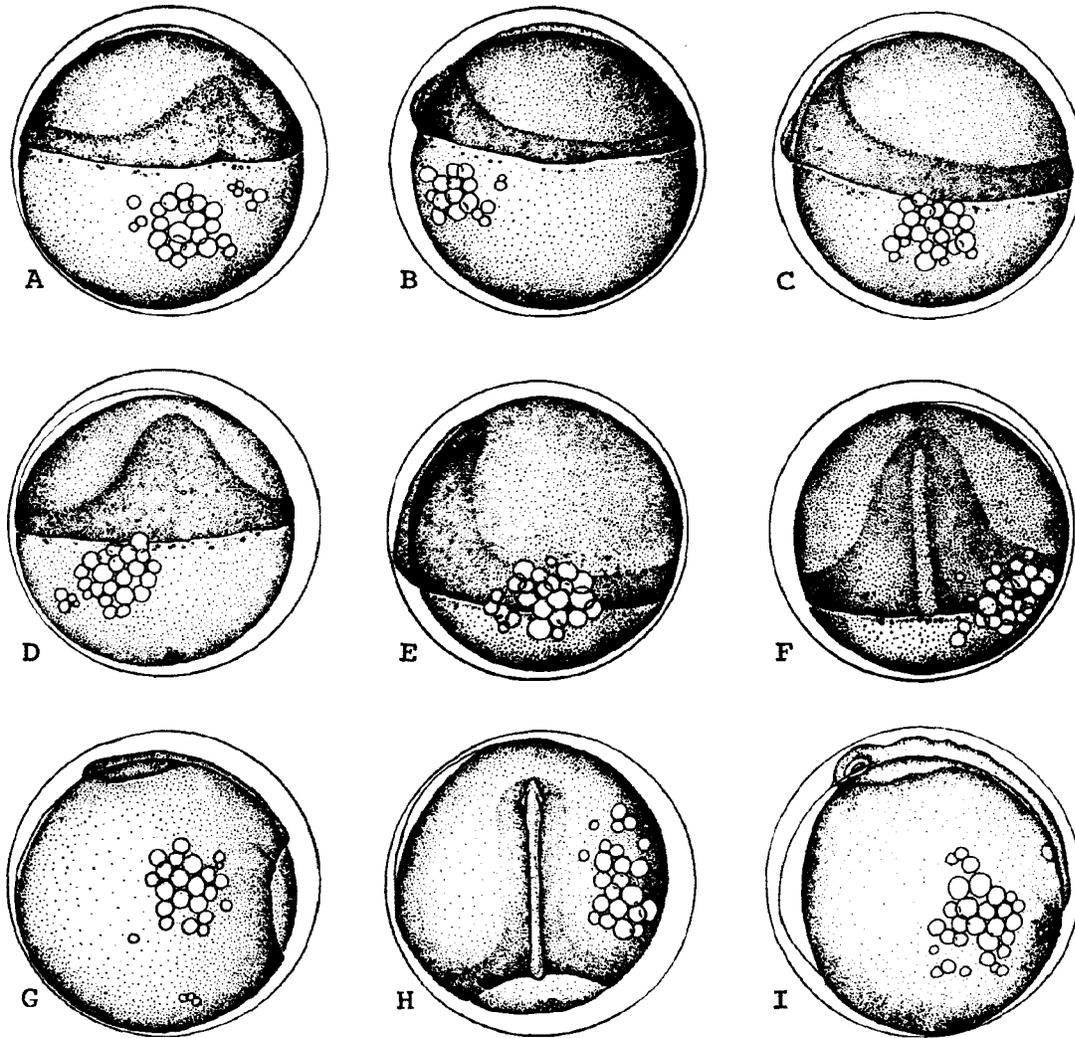


Fig. 91. *Fundulus heteroclitus*, Mummichog. A, B. Embryonic axis increased in length, 30 hours. C, D. Blastoderm over one-half of yolk, 33 hours. E, F. Extra-embryonic ectoderm over three-fourths yolk, 37 hours. G, H. Embryonic keel prominent, optic vesicles rudimentary, blastopore evident as small opening, 40 hours. I. Blastopore closed, main divisions of brain formed, Kupffer's vesicle evident, 46 hours. (A-I, Armstrong, P. B., and J. S. Child, 1965: figs. 16-20.)

otic vesicles; blood islands of yolk forming a syncytium; circulation not yet established; tail tip rounded, attached; melanophores increased in number, especially on yolk; erythrocytes evident under hindbrain and on trunk.

84 hours (Stage 25)—circulation established; contractions of somatic muscles evident; 19 somites present; tail free; melanophores more numerous and extended onto optic lobes.

92 hours (Stage 26)—anterior end of heart curved; future otoliths evident as aggregations of very fine granules; incipient urinary bladder evident as condensation of cells near base of tail; a few

contracted erythrocytes on yolk sac.

112 hours (Stage 27)—ventricle of heart differentiated; otoliths evident as dense concrete bodies; pronephros functional; urinary bladder not yet formed; yolk melanophores expanded.

128 hours (Stage 28)—developing pectoral fin evident as mass of tissue jutting upward above surface of yolk sac; urinary bladder small, bilobed; pigment present on retina imparting dusky tone to eye.

144 hours (Stage 29)—eye conspicuously increased in size and pigmentation; pectoral fin still small, acuminate.

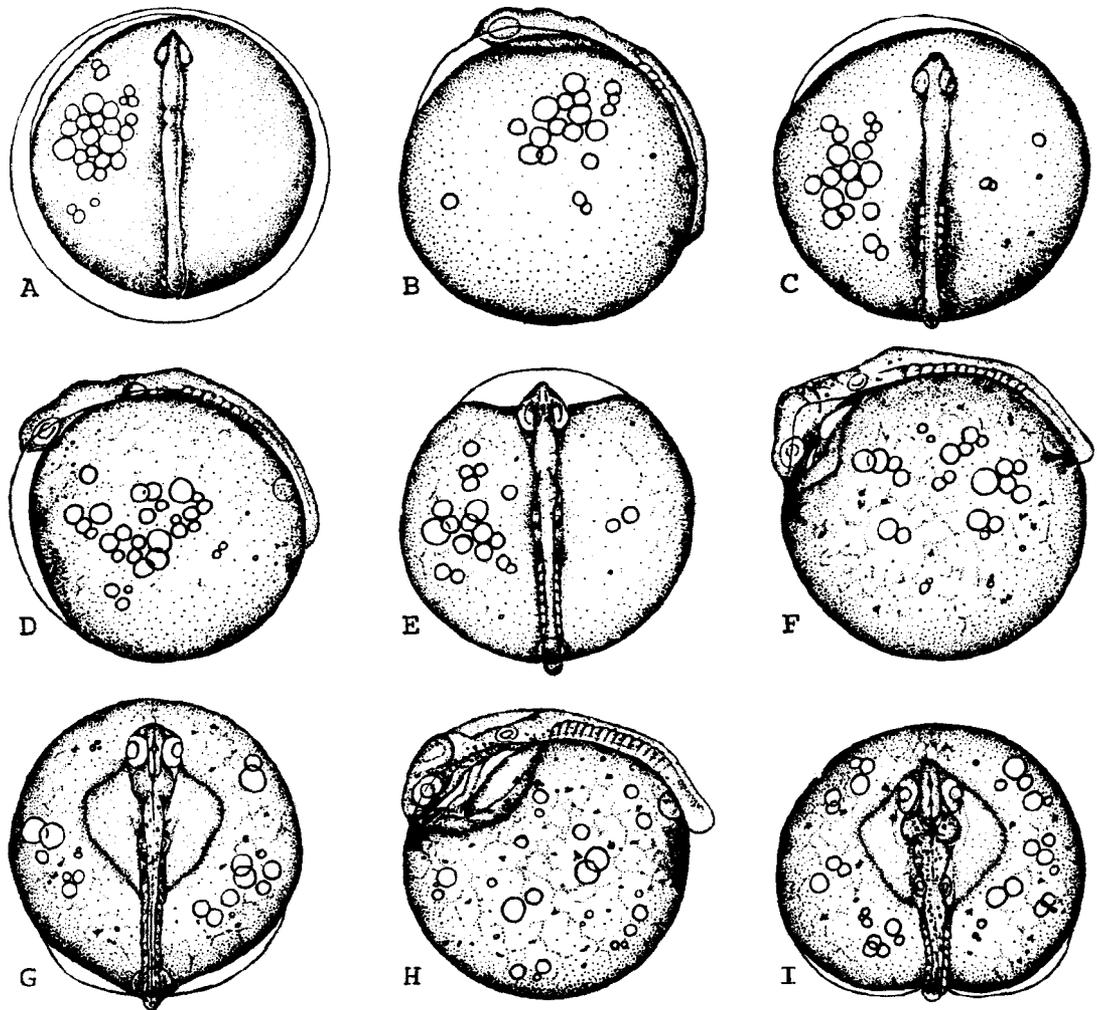


Fig. 92. *Fundulus heteroclitus*, Mummichog. A. 46 hour embryo, somites not yet developed, tail rounded. B, C. 52 hour embryo, lateral view, 3-4 somites. D, E. 56 hour embryo, optic cups, pericardial cavity formed. F, G. 66 hour embryo, lens olfactory placodes formed; pigment present, mainly on yolk. H, I. 74 hour embryo, ca. 14 somites, cardiac contractions observed. (A-I, Armstrong, P. B., and J. S. Child, 1965: figs. 20-24.)

- 156 hours (Stage 30)—pectoral fin extended slightly above lateral line; incipient caudal fin flattened; tail tip, when flexed, extending over hindbrain.
- 168 hours (Stage 31)—all heart chambers differentiated; liver evident.
- 192 hours (Stage 32)—posterior margin of operculum forming below anterior margin of otocyst.
- 216 hours (Stage 33)—flexure of head markedly developed; lower jaw forming; sporadic movement of fins; caudal rays barely evident and marked with few unexpanded pigment cells.
- 228 hours (Stage 34)—lower jaw well-developed, movable; mouth open; caudal rays well-developed; swim bladder small, inconspicuous⁷³ (presumed pre-hatching stage, JDH).

A number of authors have presented additional developmental sequences of *Fundulus heteroclitus*. These are briefly reviewed below.

Development at 20 C (the Hyman series): 4-6 hours, 2- to 4-cell stages; 6-8 hours, 32-cell stage; 26-29 hours, blastoderm one-third over yolk; 34-37 hours, eyes formed; 84 hours, circulation established.¹⁰

Development at 22 C (the Spitz and Burnett series): 56 hours, main brain divisions differentiated, optic lobes prominent; 66 hours, integumentary melanophores first evident; 84 hours, circulation established; 112 hours, dendrites of melanophores clearly visible; 144 hours, eye pigment developing; 168 hours, heart chambers differentiated; 216 hours, ectoderm of yolk sac detached anteriorly

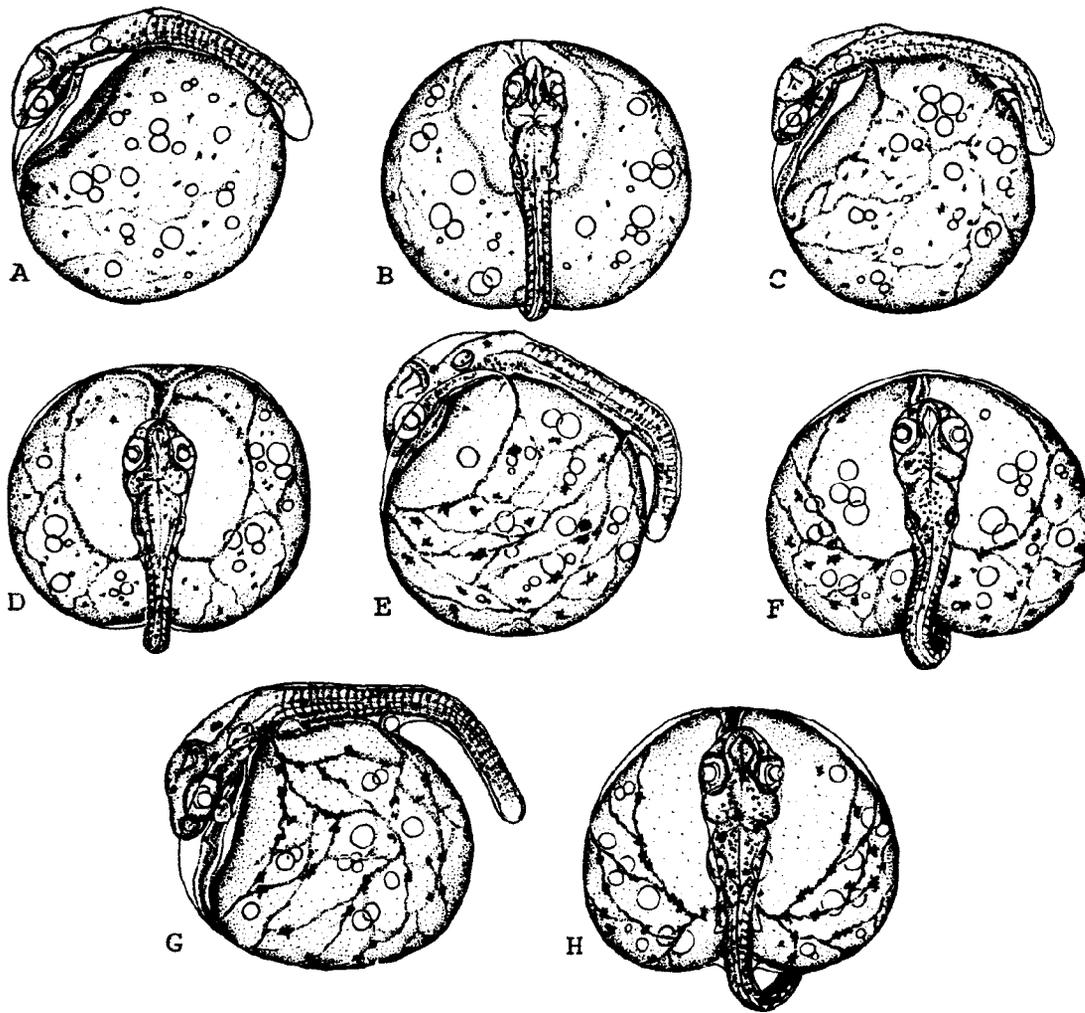


Fig. 93. *Fundulus heteroclitus*, Mummichog. A, B. 84 hour embryo, circulation established, 19 somites formed, tail tip free, first somatic contractions observed. C, D. 92 hour embryo, otoliths formed, erythrocytes evident on yolk sac. E, F. 112 hour embryo, pectoral buds forming. G, H. 128 hour embryo, pigment forming in eye. (A-H, Armstrong, P. B., and J. S. Child, 1965: figs. 25-28.)

at lower level of forebrain; 228 hours, hatching.¹⁴⁶

Development at 22-27 C (the Manery, Warbritton, and Irving series): 20 minutes, blastodisc formed; 3 hours and 30 minutes, 32- and 64-cell stages; 26 hours and 15 minutes, germ ring at equator, embryonic shield well-defined; 49 hours and 45 minutes, heart, brain, optic vesicles, lenses, and 16 somites formed, chromatophores on body; 73 hours and 30 minutes, circulation established; 120 hours, 35 somites; 192 hours, pectoral buds formed; 216 hours, posterior part of brain obscured by dense pigment, eye pigmented, caudal rays developing; 264 hours, body length ca. 3/4 yolk circumference; 360 hours, eyes and body heavily pigmented; 432-528 hours (18-22 days), eye pigment metallic.⁵⁹

Development at 25 C (the Solberg series): 1 hour, blastodisc formed; 1 hour and 30 minutes, 2-cell stage; 2 hours, 4-cell stage; 2 hours and 30 minutes, 8-cell stage, blastocoel forming; 3 hours, 16-cell stage; 3 hours and 30 minutes, 32-cell stage; 4 hours, 64-cell stage; 4 hours and 3 minutes, 128-cell stage; 5 hours and 30 minutes to 6 hours, early high blastula; 7-9 hours, late high blastula; 10-12 hours, blastula flattened into yolk; 13 hours, blastula beginning to expand; 16 hours, periblast formed; 17 hours, embryonic shield, primitive endoderm formed; 18 hours, blastoderm ca. one-third over yolk surface; 19 hours and 30 minutes, blastoderm over one-half of yolk; 21 hours, blastoderm over ca. two-thirds yolk; 22 hours, blastoderm over ca. three-fourths yolk; 24 hours, eyes and

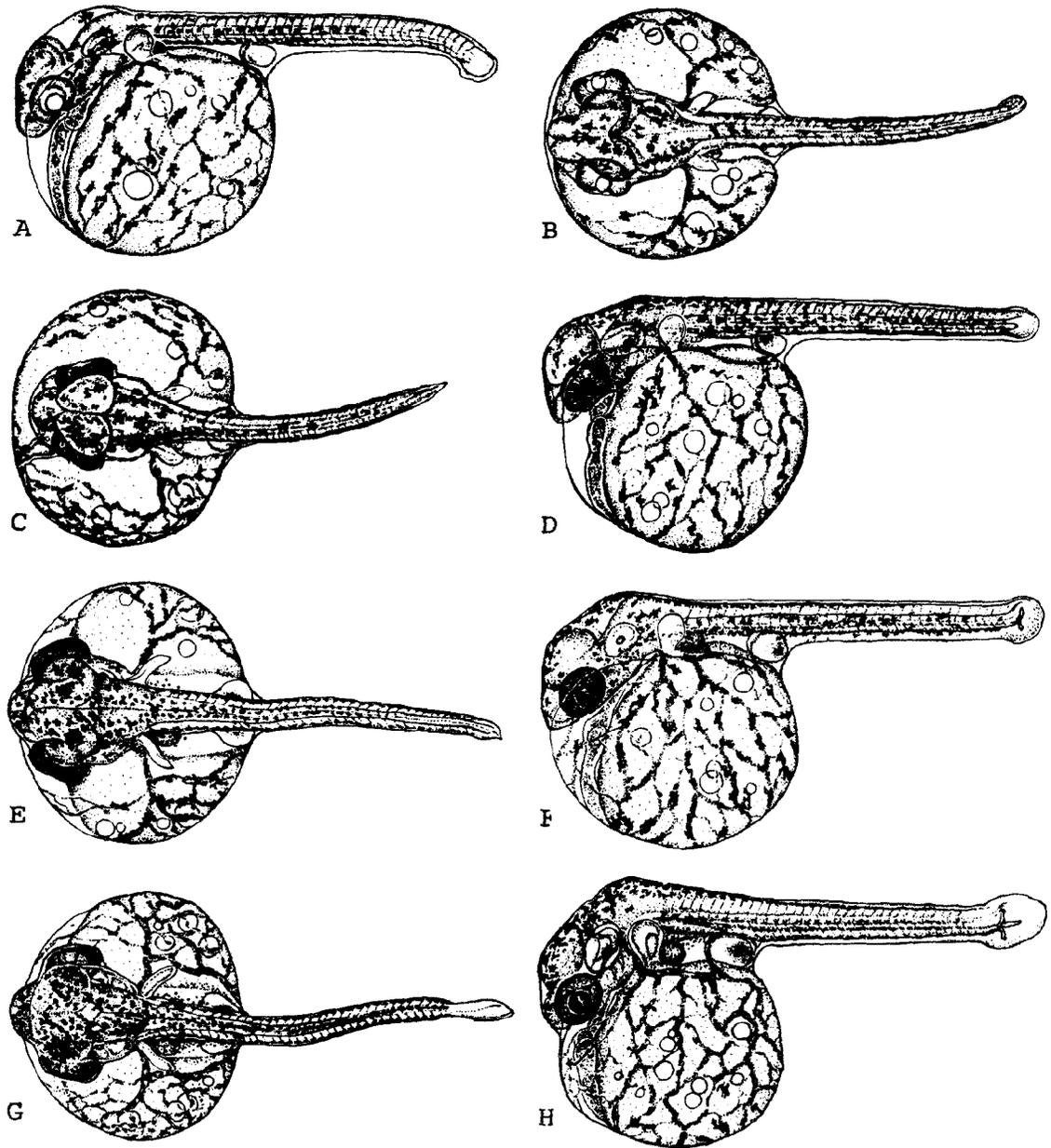


Fig. 94. *Fundulus heteroclitus*, Mummichog. A, B. 144 hour embryo, ventricle well defined, eye pigment increased. C, D. 156 hour embryo, pectoral fin slightly above lateral line. E, F. 168 hour embryo, all heart chambers differentiated, liver formed. G, H. 192 hour embryo, retina heavily pigmented, posterior margin of opercle forming. (A-H, Armstrong, P. B., and J. S. Child, 1965: figs. 29-32.)

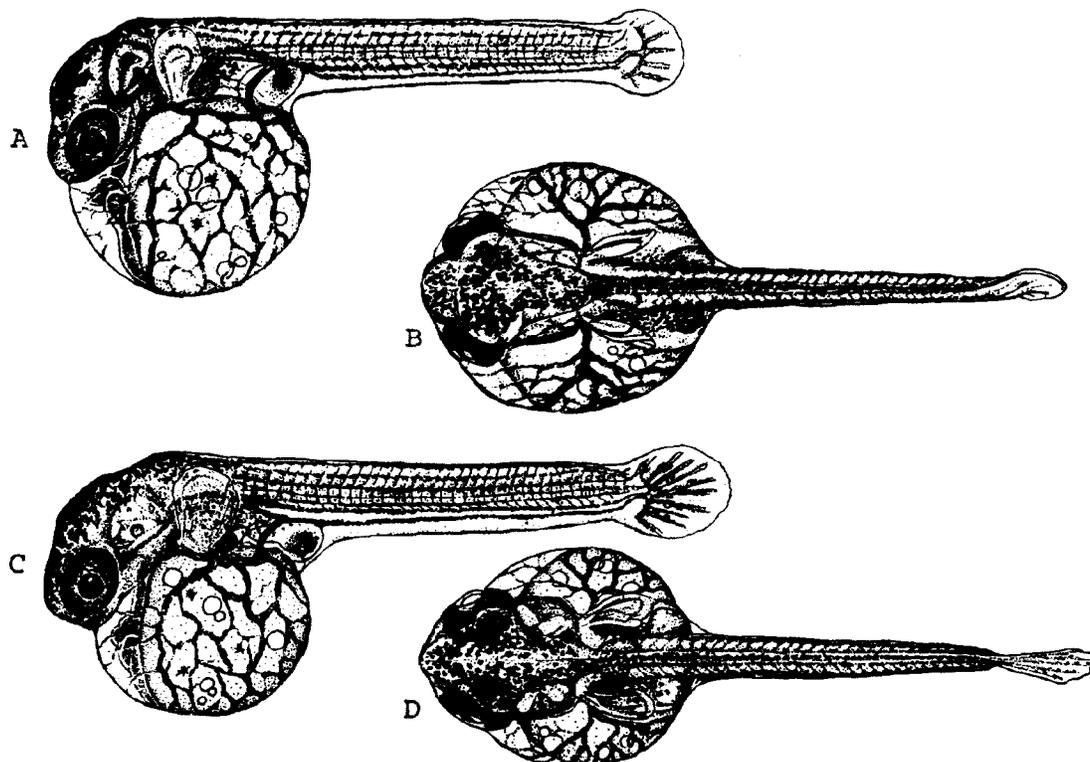


Fig. 95. *Fundulus heteroclitus*, Mummichog. A, B. 216 hour embryo, head greatly flexed; incipient rays, some with unexpanded pigment cells, in caudal fin. C, D. 228 hour embryo, lower jaw movable, caudal rays well-developed; hatching imminent. (A-D, Armstrong, P. B., and J. S. Child, 1965: figs. 33-34.)

brain divisions forming, yolk plug large; 26 hours, blastopore closed; 27 hours, first somites; 28 hours, 4 somites; 31 hours, optocoele formed; 33 hours, auditory placodes formed; 34 hours, optic cup, lens formed, ca. 10 somites; 38 hours, optic lobes formed, midbrain greatly enlarged; 40 hours, melanophores on yolk; 42 hours, melanophores on embryo; 44 hours, heart pulsating, olfactory pits formed, primitive kidney distinct; 46 hours, circulation established; 60 hours, otoliths developed; 72 hours, 35 somites; 78 hours, pectoral buds evident; 84 hours, pigment on retina, urinary vesicles evident; 90 hours, liver evident, cartilage forming; 102 hours, pectorals rounded; 108 hours, lens obscured by retinal pigment; 114 hours, peritoneum pigmented; 126 hours, caudal rays forming; 144 hours, gas bladder formed (although possibly formed as early as 78 hours); 168 hours, neural and haemal arches in caudal vertebrae; 192 hours, head beginning to straighten; 240 hours, mouth open; 264 hours, hatching.^{96,97,117}

Development at unspecified temperature (the Jones series): Embryonic shield stage, germ ring beyond equator of yolk and distinct from 2-layered embryonic shield; yolk plug stage, embryonic shield sharply differentiated, mesoderm, notochord, and anlagen of neural cord de-

veloped; closure of blastopore stage, 3 brain regions evident, optic vesicles differentiated, mesodermal plates distinct; 7-somite stage, anlagen of optic cups, incipient sense organs, auditory sacs, and lateral line organs evident; 10-somite stage, anlagen of lens evident; 15-somite stage (80 hours old), tail free, lens complete and enclosed, pectoral buds evident, chromatophores scattered over yolk and periblast.¹

Development at unspecified temperature (first Newman series): 2 hours and 20 minutes, 50% of eggs in 4-cell stage; 24 hours, germ ring nearly around yolk, embryonic shield evident; 48 hours, optic vesicles large and hollow, 3-4 somites in most specimens; 54 hours, lens developed, ca. 12 somites; 72 hours, melanophores on body and yolk, trunk opaque; 96 hours, eye pigment developing; 114 hours, large chromatophores on head above brain and on upper surface of eye, yolk reduced; 168 hours, pigment increased on body and yolk, pectoral fins formed, movable; 288-326 hours (12-14 days), hatching.³³

Development at unspecified temperature (second Newman series): 2 hours, first cleavage; 4 hours, 32- and 64-cell stages; 20 hours, advanced cleavage; 52 hours, blastopore closed or nearly closed, pale chromatophores

under hindbrain and few red chromatophores near head; 72 hours, heart pulsating, no vitelline circulation, few melanophores on yolk and head; 96 hours, vitelline circulation established, body and yolk well-pigmented; 312-336 hours, hatching.⁵⁵

Development at unspecified temperature but as specific stages (the Oppenheimer series): Stage 1, unfertilized egg; stage 2, blastodisc formed; stage 3, 2-cell stage; stage 4, 4-cell stage; stage 5, 8-cell stage; stage 6, 16-cell stage; stage 7, 32-cell stage; stage 8, early high blastula; stage 9, late high blastula; stage 10, flat blastula; stage 11, expanding blastula; stage 12, early gastrula; stage 13, middle gastrula, blastoderm over about one-half of yolk; stage 14, later gastrula; stage 15, closure of blastopore, central nervous system formed, occasionally somites and optic vesicles evident depending on rearing environment; stage 17, optic vesicles hollow, 1-4 somites; stage 18, auditory placodes visible, first indication of extra-embryonic coelom, 4-14 somites; stage 19, neural cavity, lens, olfactory pits, 14-20 somites formed; stage 20, optic lobes formed, ear vesicular, blood islands on yolk, heart pulsating, pericardium differentiating, pectoral buds evident, melanophores on yolk and anterior part of body, 20-25 somites; stage 21, muscular contractions evident, optic lobes formed, ca. 28 somites; stage 22, circulation established, cerebral hemispheres forming, ca. 35 somites; stage 23, otoliths formed, melanophores on pericardium; stage 30, caudal rays visible, lower jaw formed; stage 31, swim bladder evident as diverticulum from gut, eyes and mouth movable; stage 32, hatching.^{28,29}

Development at unspecified temperature (the Richards and Porter series): 10 hours, blastodisc lenticular, segmentation cavity formed; 14 hours, embryonic shield just forming; 18 hours, germ ring ca. one-third around yolk; 24 hours, germ ring to equator of yolk, embryonic shield elongated, anlagen of embryonic axis and neural furrows evident; 30 hours, germ ring nearly closed, optic bulbs evident, mesoderm thickened into lateral plates, notochord forming.¹⁶

Development at unspecified temperature (the Stockard series): ca. 2 hours, 2-cell stage; 18-20 hours, blastoderm flattened; 24 hours, blastoderm one-fourth to one-third around yolk; 48 hours, yolk plug, 2 somites formed; 48-72 hours, pigment granules on yolk; 72 hours, large chromatophores on yolk; 76 hours, heart contractile, Kupffer's vesicle formed; ca. 96-108 hours, stellate chromatophores along walls of yolk vessels and on surface of pericardial space; ca. 120 hours, small brownish melanophores on yolk.^{48,51}

Miscellaneous comments on development:

Nelsen pointed out that the polar cap forms in the region of the micropyle.¹¹⁴

Kagen found that at 20 C the yolk platelets were oblit-

erated and the perivitelline space was formed 5 minutes after fertilization.⁴⁷

Moenkhaus noted the following variations in developmental sequences at unspecified temperatures: 2-cell stage, 47 minutes to 2 hours and 20 minutes; 16-cell stage, 2 hours and 15 minutes to 4 hours and 5 minutes; closure of the blastopore, 40 hours and 35 minutes to 86 hours and 30 minutes.^{50,61}

Bancroft stated that, at the time of initial heartbeat, melanophores appear on the yolk, the forebrain lacks a lumen, and there are ca. 12 somites.⁵⁶

Gilson described 7-day embryos as having large melanophores close to and above the neural tube and beneath the musculature of the tail, and numerous small melanophores in several distinct series on the tail. The posterior melanophores were strikingly metameric although irregularities were noted.²⁵

Shepard concluded that the pigment cells on the yolk sac are not of neural crest origin, but appear to arise from the extra-embryonic germ ring.⁷⁰

Stockard found that at 5 C, 20 hours were required for development of 2- and 4-cell stages, while at "unusually warm temperature" the germ ring was one-third to one-half over the yolk, the embryonic shield was well-formed, and the embryonic axis was indicated in only 22 hours. In a later series 10-12 somites were formed in 48 hours, the heart was pulsating in 53 hours, and circulation was established in 72 hours.⁴⁶

Rogers noted the optic cups, lenses, and optic stalks in embryos 63 hours old which had been reared at 22-26 C. The optic tract was formed in 99 hours.⁸¹

Bancroft observed a continuous mid-lateral line of red chromatophores in embryos just prior to hatching.⁵⁶

Russell found that melanophores first appear on the head 4 days after fertilization. On the sixth day melanophores of the yolk sac migrate to the yolk-sac vessels. Advanced embryos usually have 8-18 (average 13) melanophores on the dorsal surface.⁹⁶

Milkman found that, just prior to hatching, the mouth and anus are functional and the yolk is reduced by two-thirds. Seven and one-half minutes before hatching interchorionic summersaults begin and the chorion becomes rough, weak, thin, and flaccid.⁵⁷

Denny stated that just before hatching the lateral line organs have not yet broken through the epidermis, but that a small vesicle is frequently present at the summit of each developing organ.¹²²

Brummett pointed out that the tail bud usually appears just after the closure of the blastopore.⁸²

Incubation period: 9^{27,87,110,131,136}-ca. 47 days.^{32,140} At

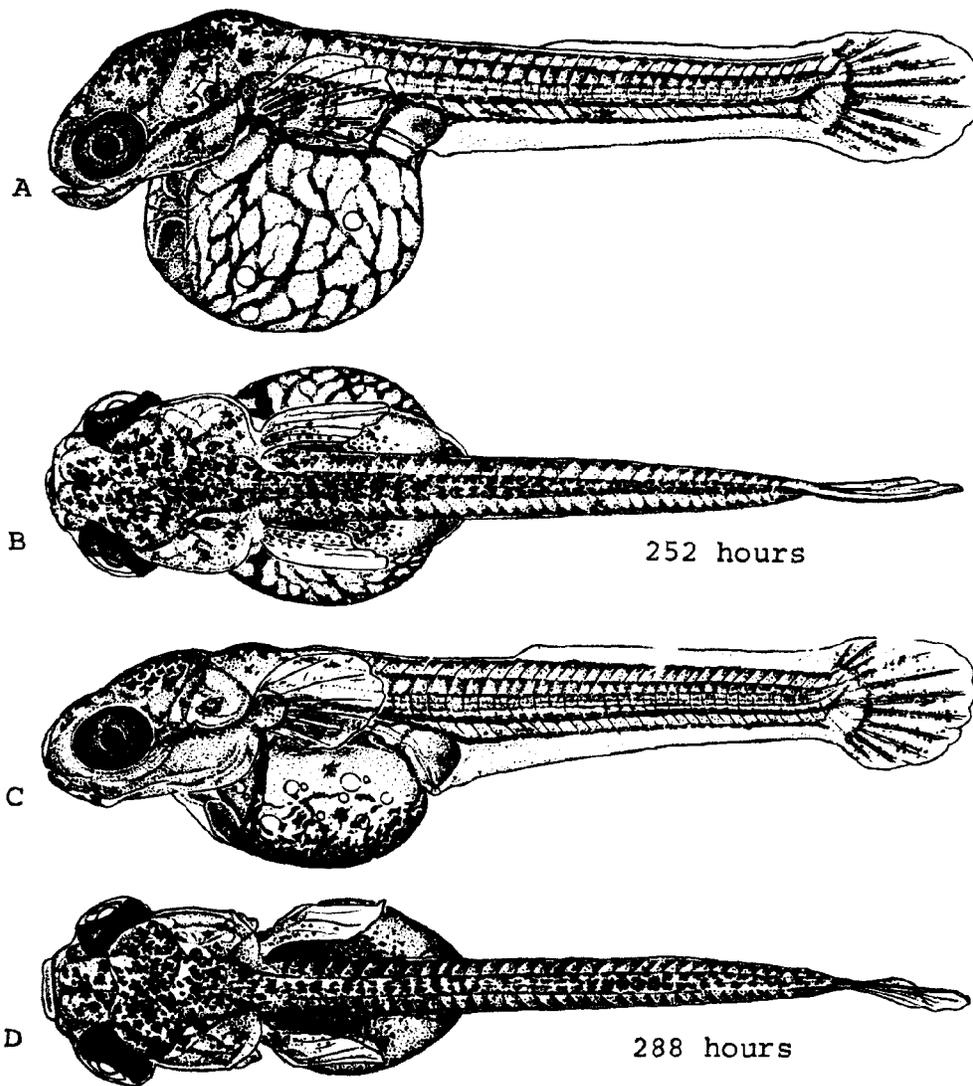


Fig. 96. *Fundulus heteroclitus*, Mummichog. A, B. Newly hatched yolk-sac larva, size unknown, 252 hours after fertilization, head somewhat extended, opercular margins well defined. C, D. Yolk-sac larva, size unknown, 288 hours after fertilization. (A-D, Armstrong, P. B., and J. S. Child, 1965: figs. 35-36.)

12.8-17.2 C, 24 days;¹⁵⁶ at 15.0 C, 1032-1143 hours based on median hatching time;¹⁴⁰ at 18.0 C, 14-17 days;¹⁵³ at 18.3 C, ca. 40 days;¹⁴⁴ at 19.4-21.4, average 17 to more than 40 days (varying with oxygen level³²); at 20.0 C, 395-525 hours based on median hatching time;¹⁴⁰ at 22.0-26.0 C, 11-13 days;⁸¹ at ca. 23.0 C, 10-18 days¹⁴³ (also reported as "after 12 days"⁸⁴); at ca. 24 C, 13 days;¹⁵⁰ at 24.5 C, 9-20 days;¹¹⁰ at 25.0 C, 11 days¹¹⁷ (also 264-400 hours based on median hatching time); at 30 C, 244-311 hours based on median hatching time.¹⁴⁰ Averages based on unspecified tem-

peratures have been stated as 11⁶⁷ and ca. 14 days.²⁵ Incubation varies with both temperature and oxygen concentration³² and tends to be slower when eggs are crowded.³⁹ Eggs develop more rapidly out of water, but will not hatch unless submerged. Such eggs, after 33 days of "dry" incubation, take up to 27 minutes to hatch after submersion.²⁶ After hatching begins, hatching of a single group of eggs may continue for 96 to 744 hours.¹⁴⁰ Hatching apparently more nearly synchronous if clumps of eggs are separated.⁴⁶ Hatching time under natural conditions 14-18 days.¹⁴³

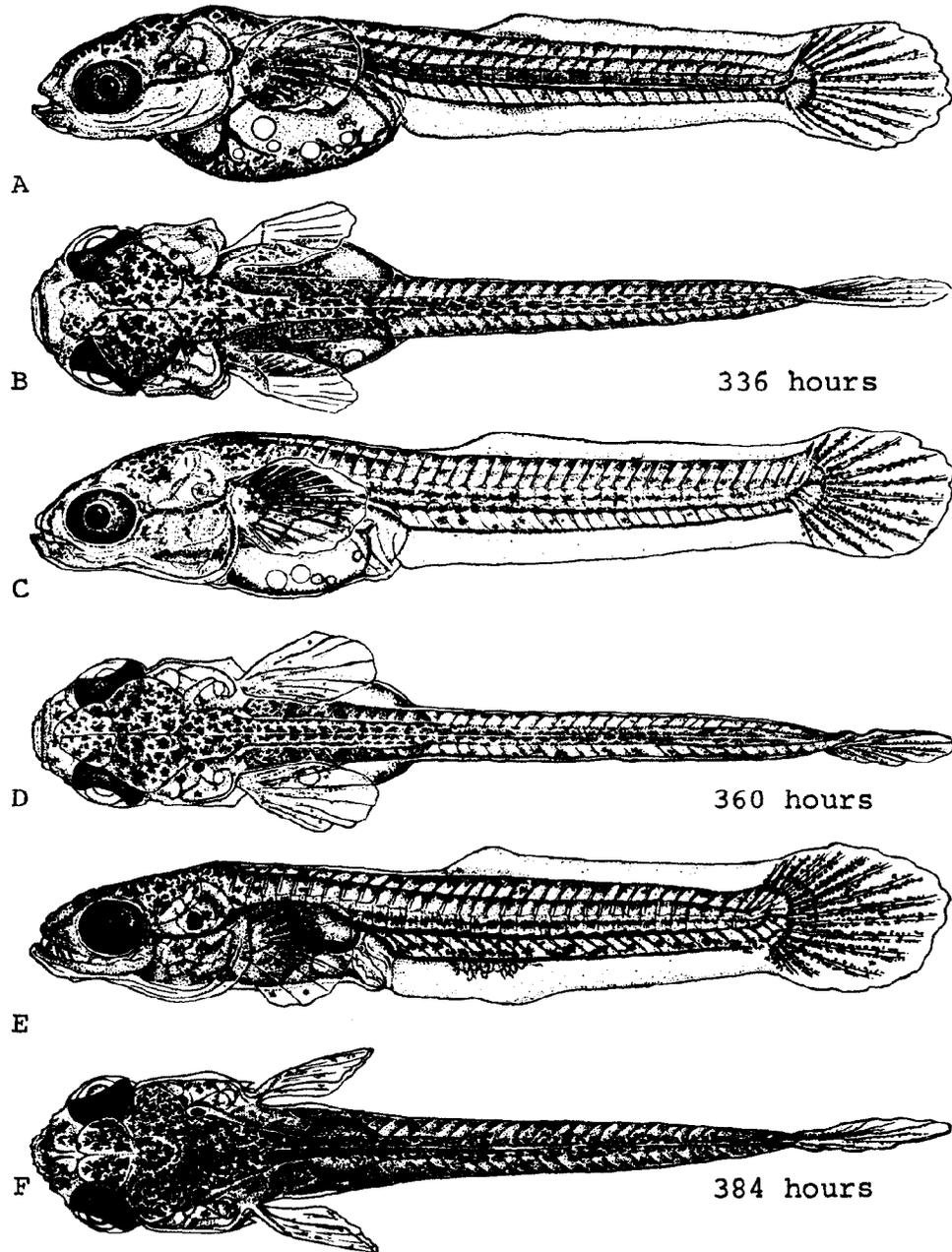


Fig. 97. *Fundulus heteroclitus*, Mummichog. A, B. Yolk-sac larva, size unknown, 336 hours after fertilization. C, D. Yolk-sac larva, size unknown, 360 hours after fertilization. E, F. Yolk-sac larva, size unknown, 384 hours after fertilization. (A-F, Armstrong, P. B., and J. S. Child, 1964: figs. 37-39.)

Temperature tolerances: 12¹¹⁷–30 C.¹⁴⁰ During early development eggs are killed or develop abnormally when subjected to reduced temperatures (0 C to possibly 10 C). Advanced embryos can survive temperatures of 0–2 C for rather prolonged periods.^{49,60}

Salinity tolerances: Eggs will develop in distilled water, seawater, or "concentrated sea water";¹⁰⁶ those hatched in freshwater are typically 2–5 days behind those in seawater,²⁴ although at 60 ppt onset of hatching is retarded.¹⁴⁰

Note: Eggs can be kept under "complete vacuum" for 4 days.⁷⁴

YOLK-SAC LARVAE

Hatching length 4.0 mm or less^{102,154} to 7.7 mm¹⁵⁶ (larger specimens may hatch as larvae^{71,87,112}). Average hatching length, 5.0 mm.¹⁴⁸ In one set of experiments hatching length varied 5.13 ± 0.06 to 6.85 ± 0.04 mm.¹⁴⁰

Yolk retained for 24⁶⁶ to 156 hours after hatching¹⁴⁶ or to length of 7.0–10.0 mm.¹⁵³

Myomeres 33¹⁵⁴–ca. 35,¹¹⁷ also reported as 9 + 24.¹⁵⁴

Head initially flexed over yolk, straightened by end of stage. Opercular margins well defined at hatching. Yolk sac variable, large and round at hatching⁷³ or greatly reduced;^{26,117} oil globules retained throughout stage.⁷³ Skeleton well ossified,¹¹⁰ urostyle oblique,⁷³ pectoral rays evident³³ at hatching. Typical lateral line cupulae present one day after hatching.¹²² Gas bladder considerably enlarged as stage progresses.²⁹ Origin of dorsal finfold at midpoint of TL at beginning of stage, somewhat more forward at end of stage;⁷³ origin of anal finfold about one-third distance from tip of snout to tip of tail.¹⁴⁴

Pigmentation: At hatching a series of melanophores on each side of mid-dorsal and mid-ventral lines, typically restricted to the somites; a continuous mid-lateral series of red chromatophores and 0–2 large mid-lateral melanophores^{25,56} (although in some populations the mid-lateral

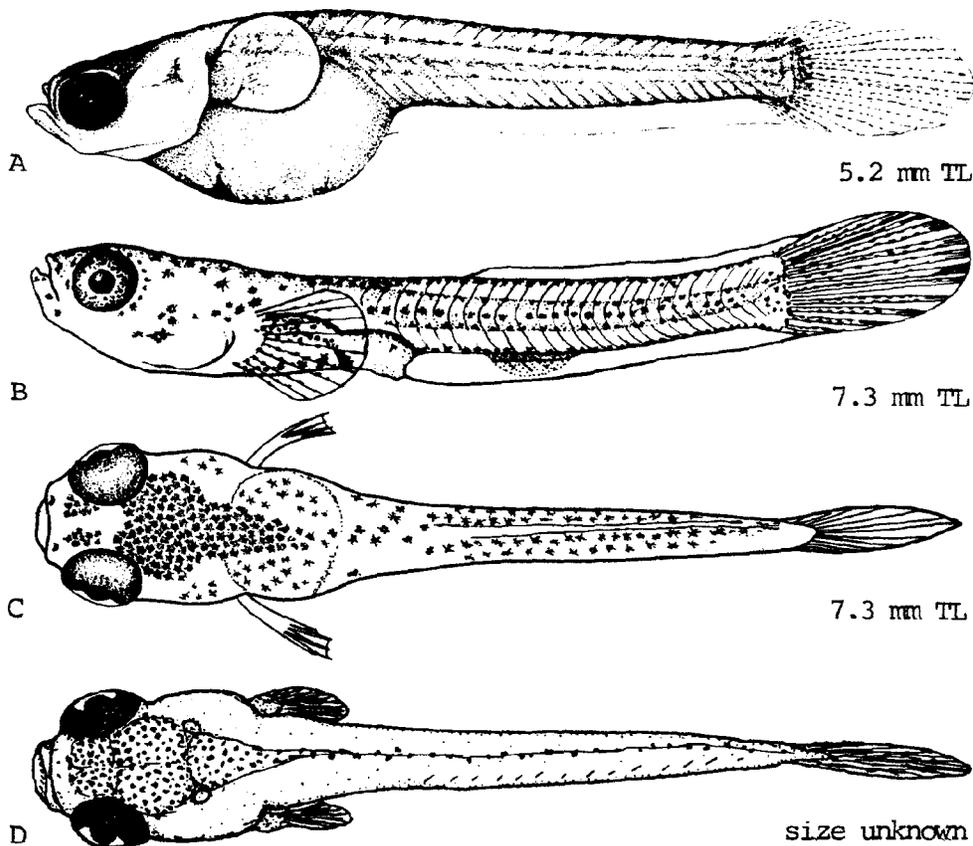


Fig. 98. *Fundulus heteroclitus*, Mummichog. A. Yolk-sac larva, 5.2 mm TL. B. Larva, 7.3 mm TL, dorsal view. C. Larva, 7.3 mm TL, dorsal view. D. Larva, 8 days old, dorsal view, size unknown. (A, Foster, N., 1974: 135, photographed, with permission from the original illustration by R. Lynn Moran. B, Original drawing, Oscar E. Sette. C, Newman, H. H., 1908: pl. 5. D, Stockard, C. R., 1909: fig. 1.)

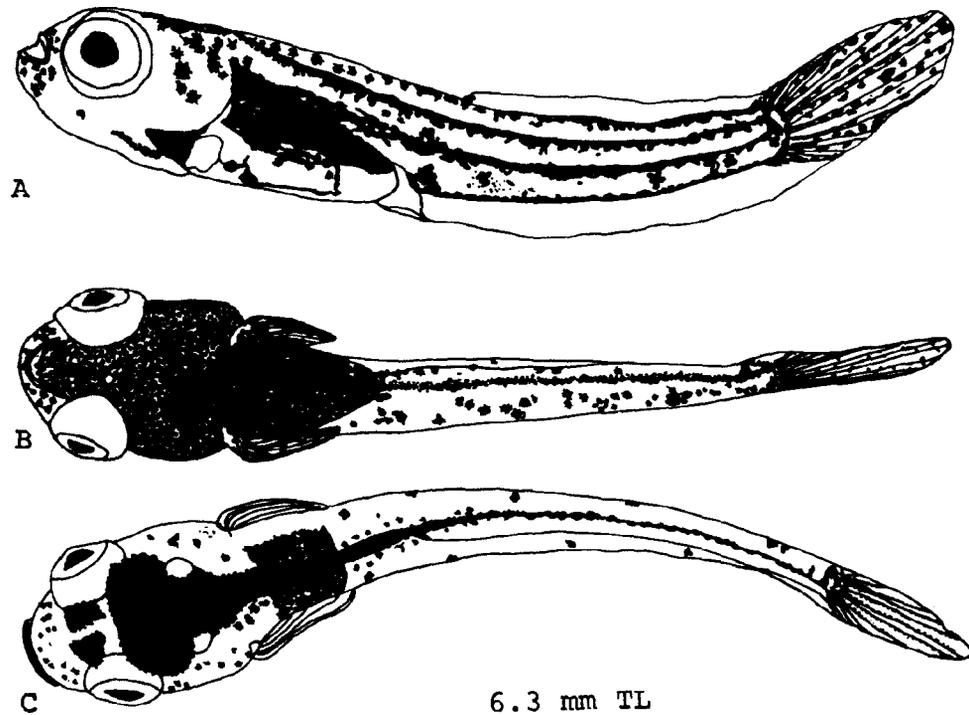


Fig. 99. *Fundulus heteroclitus*, Mummichog. A, B, C. Yolk-sac larva in life, 6.3 mm TL, lateral, ventral and dorsal views. (A-C, Original drawings, Linda L. Hudson.)

series is not this well-developed¹⁴⁴); melanophores of yolk sac densely aggregated over vitelline vessels. At one day 1-26 (average 8) melanophores in mid-lateral series.^{25,56} Gas bladder pigmented before complete absorption of yolk.⁶⁶ At 6.3 mm (in life) dark pigment on head, in relatively thin bands on dorsal and ventral surfaces of body, above and below notochord, and along developing caudal and pectoral rays; a series of widely spaced stellate white chromatophores on ventrolateral aspects of body just over ventral edge of notochord; a cluster of large white chromatophores on caudal base; white pigment in throat region and in dense masses on bases of pectoral fins; scattered orange chromatophores on yolk sac and yellow pigment in small area on ventral part of body just behind yolk.¹⁵⁴ A 7.3 mm specimen has a distinct triangle of chromatophores on head behind eye and stellate chromatophores scattered over dorsum.³³ In specimens with yolk nearly absorbed, yolk chromatophores arranged in a compact mass, especially in region of falciform ligament of liver and Cuvierian ducts, compact mass of pigment cells over pericardium, along aorta to branchial arteries, and surrounding ventral vein to cloaca.²⁵

LARVAE

Size range described, 7.0 to 25.4 mm (but also includes some juveniles).⁶⁹ Specimens may hatch as larvae (lacking yolk).⁷¹

Branchiostegals 5 (rarely 6).⁶⁹

Proportions expressed as times in TL at lengths of 7.1-25.4 mm: Head length 3.7-4.6, depth 5.0-7.6, caudal peduncle width 8.9-16.2. Proportions expressed as times in head length at 7.1-25.4 mm: Interorbital width 1.7-3.3, snout length 3.2-5.4, eye diameter 2.8-4.2.

Head blunt, straight; branchiostegals evenly spaced. Dorsal and ventral finfold no longer continuous anteriorly at 11.8 mm, finfold obliterated at 14.0 mm. Dorsal and anal rays evident at 9.0 mm,⁶⁷ ray counts apparently complete at 11.0 mm. Pectoral with⁸⁷ or without⁶⁹ rays at beginning of stage, although specimens of 7.0 mm have pectorals rayed.¹³² Pelvic buds evident at 11.0 mm,⁵⁷ rays not fully formed at 22.6 mm. Scales first evident above pectoral fin at 12.4-12.7 mm,⁶⁹ well-developed at ca. 20.0 mm.¹³²

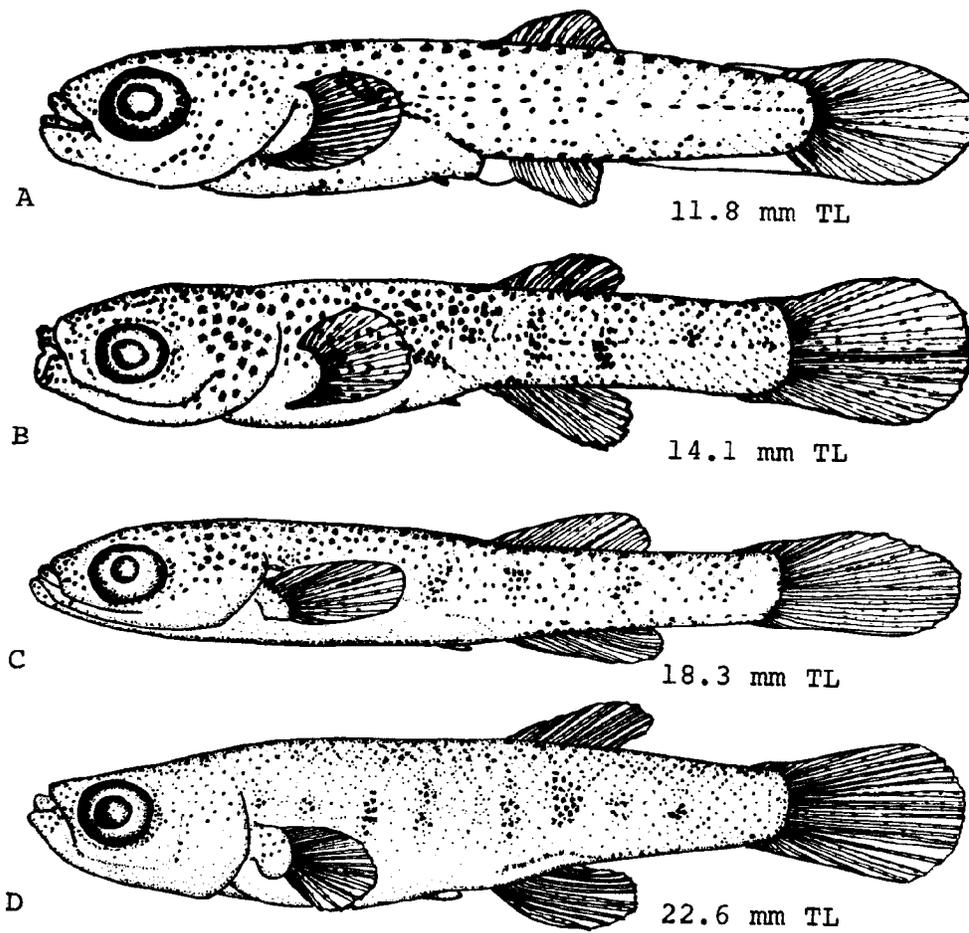


Fig. 100. *Fundulus heteroclitus*, Mummichog. A. Larva, 11.8 mm TL, pelvic fins just forming. B. Larva, 14.1 mm TL, pigment increased on body. C. Larva, 18.3 mm TL, pectoral fin elongate. D. Larva, 22.6 mm TL, pelvic fins still poorly developed. (A-D, Richards, S. W., and A. M. McBean, 1966: fig. 1.)

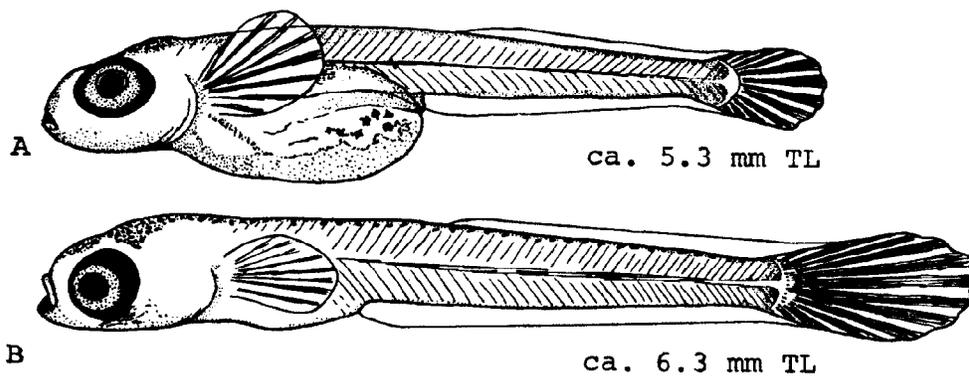


Fig. 101. *Fundulus heteroclitus*, Mummichog. Effects of developing eggs out of water. A. Yolk-sac larva, ca. 5.3 mm TL, from water-reared egg hatched 12 days after fertilization. B. Yolk-sac larva, ca. 6.3 mm TL, from egg reared out of water and made to hatch by submergence in water 18 days after fertilization. (A, B, Stockard, C. R., 1907: figs. 1-2.)

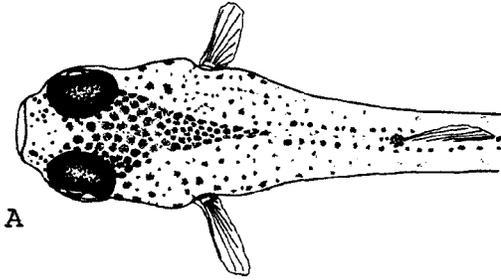


Fig. 102. *Fundulus heteroclitus*, Mummichog. A. Larva, detail of anteriodorsal pigment pattern. For comparison to *Fundulus luciae* see fig. 109. (A, Byrne, D. M., 1976: fig. 5.)

Pigmentation: At 7.13 mm a dense row of pigment mid-ventrally behind isthmus. At less than 10 mm large dorsal chromatophores from snout to tail, few chromatophores in opercular region, a line of spots from vent to tail, scattered patches of pigment on thorax, venter, flanks, head, and operculum. At 15–16 mm chromatophores more concentrated, 5 short vertical bars on flanks. At larger than 20 mm chromatophores along margins of dorsal scales, 6–10 relatively short vertical pigment bars on flanks.⁶⁹ At 8 days (size unknown) a triangle of chromatophores on head and chromatophores scattered along mid-dorsal ridge.³⁴ A larva of unknown size and age (but with incipient dorsal and anal fins barely evident) showed pigment in the pectoral and caudal fins.⁷³ Agassiz pointed out a gradual transition from a linear arrangement of pigment in early larval stages to a pattern of vertical bars in later larval stages.¹³²



Fig. 103. *Fundulus heteroclitus*, Mummichog. A. Larva, ventral view of head. For comparison to *Fundulus majalis* see fig. 119. (A, Richards, S. W., and A. M. McBean, 1966: fig. 1.)

JUVENILES

Minimum size described, ca. 25.0 mm.¹¹³

“Juveniles” with a head scale pattern consisting of a circular or slightly transverse elliptical central scale surrounded by a rosette of 7 scales.¹³⁷ Anal much deeper than dorsal in “young.”¹³⁸

Pigmentation: Young males light olive above, yellow below; immature females paler. Both sexes with a series of alternate dark and silvery lateral bands. At

ca. 25.0–26.0 mm, 9–17 (average 12) dark bands, these more narrow than the interspaces in females, wider and more numerous in males. Young males with prominent ocellus on last rays of dorsal. The ocellus is black, margined above and anteriorly by white and may be subdivided into 2 spots.^{8,17,18,31,69,99,104,113,138} “Young” typically lighter in pigmentation than adults.¹⁵⁶

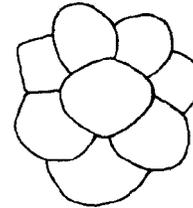


Fig. 104. *Fundulus heteroclitus*, Mummichog. A. Head scale pattern of juvenile. Note that the central scale is transversely elliptical. For comparison to head scales of *Fundulus majalis* see fig. 120. (A, Cooke, P. H., 1965: fig. 1, J. D. Hardy, Jr., delineator.)

AGE AND SIZE AT MATURITY

“Yearlings” may possibly spawn in late August;¹⁷ otherwise probably mature during 2nd year.²⁷

Females mature at 28.0 mm SL;¹²⁴ males ca. 32 mm TL.³¹

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Fundulus luciae (Baird), Spotfin killifish**ADULTS**

D. 7-9; A. 9-11; ¹⁹ P. 15 ^{15,22}-17; ³³ V. 6; ^{15,22} C. 31-34 (based on juveniles); ³⁵ scales along body 31⁹-36; oblique scale rows between upper angle of gill opening and dorsal origin 15-16; vertebrae 31-33.³⁵

Proportions as times in SL: Depth 3.0-4.4; head 3.1-3.6.²³

Body rather elongate, compressed; caudal peduncle strongly compressed; head depressed, snout short; mouth slightly superior, largely transverse.²³ Dorsal fin over anal in males, behind anal in females; ⁹ anal base longer than dorsal base; ^{10,23} pelvics small, reaching anus.^{7,22} Males with contact organs on sides, head, and median fins.³⁵

Pigmentation: Chin, cheeks, and opercles coarsely speckled with dark spots; ^{7,24,33} a very distinct dark predorsal stripe.^{16,23,33} Males olive green above, orange-white or golden below; ^{10,23} sides with 8³³-14²³ sharply defined rich black bars having bluish reflections,²⁵ the bars equal to the interspaces ^{7,33} and failing to reach mid-dorsal and mid-ventral lines by distance equal to one-half width of eye; ²⁸ dorsal fin usually bright orange to reddish,²⁵ with dark base,^{7,25} pale edge,²⁴ and a large, black posterior ocellus involving one-half of fin and bordered anteriorly and below by white; ^{7,22,23,25,29} other fins orange, pinkish, or light brown.²³ During reproductive activity vertical

bars and ocellus intensified and belly, pelvics, anal, lower caudal peduncle and caudal yellowish orange.³⁵ Females uniform grayish green above, pale below,^{9,10,23} and usually lacking lateral bars; ¹⁹ all fins plain yellowish brown; eye dark with narrow golden band.²³ Colors variable with light intensity and temperature.³⁰

Maximum length: 56 mm.²

DISTRIBUTION AND ECOLOGY

Range: New Haven, Connecticut ^{26,39} to Georgia.³⁴

Area distribution: Atlantic coast of New Jersey,^{3,5,20,21} Maryland,^{2,26} Delaware,¹¹ and Virginia;^{19,32} in Chesapeake Bay ^{4,6,8,30} north to Crisfield and Annapolis, Maryland; also reported from Indian River, Delaware,²⁷ Nanticoke River, Maryland,¹² and lower portions of Potomac River.^{19,25}

Habitat and movements: Adults—Byrne has studied the habitat of a large population of *luciae* in Fox Creek Marsh, Virginia. In this area he found the species restricted to high intertidal areas over mud-detritus bottoms of shallow ditches, mudholes, and tidal rivulets, usually among dense stands of *Spartina alterniflora*; in this environment fish sometimes partially emerge, wriggling from puddle to puddle, also sometimes hide in cave-like

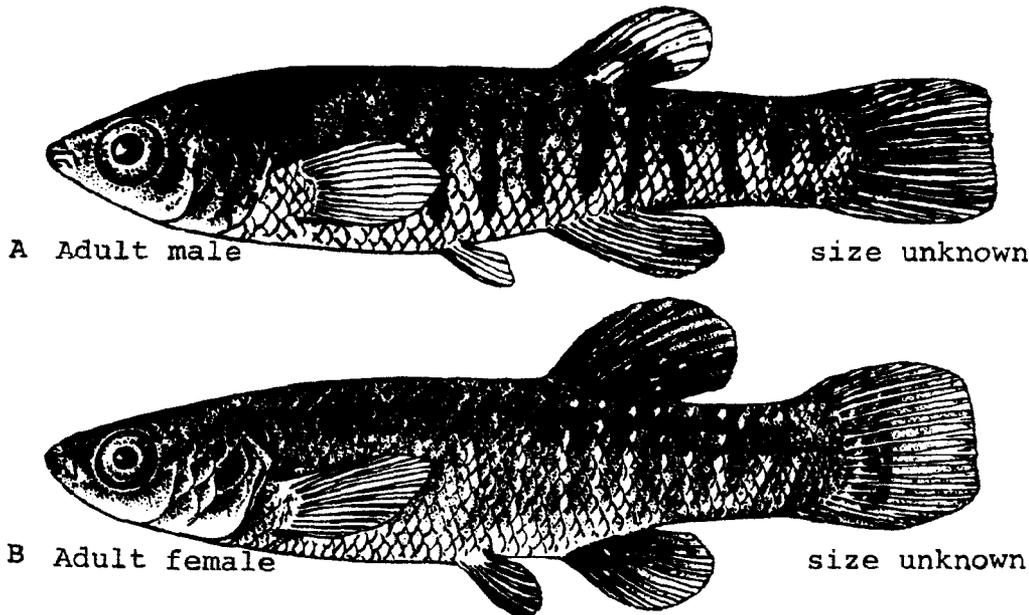


Fig. 105. *Fundulus luciae*, Spotfin killifish. A. Adult male, size unknown. B. Adult female, size unknown. (A, B, Hildebrand, S. F., and W. C. Schroeder, 1928: figs. 76-77.)

indentations or submerged wads of decaying vegetation, frequently move in small groups except during cold, overcast weather.³⁵ Other authors have described *luciae* as a schooling, shallow water species^{6,18,23} found in open ocean and estuarine habitats^{7,17,34} over sand or mud bottoms;^{5,12,19} where sometimes associated with aquatic vegetation.³⁰ Reported from ditches;^{16,26} fresh and tidal pools;^{2,11,19,21} shallow, muddy ponds;^{14,18} salt ponds;²¹ marshes;^{14,31} and mouths of creeks;¹⁹ it has been observed to burrow in mud.³⁰ Depth range less than 10 mm to seldom deeper than 0.5 m except during high spring and storm tides.³⁵ Salinity range 0.20 ppt³⁵–41.0 ppt under natural conditions,¹¹ although able to survive at 100 ppt under experimental conditions;³⁶ temperature range 4.0–36.0 C; dissolved oxygen range (natural environment) less than 1.0 to 6.8 mg/liter.³⁵

Larvae—no information.

Juveniles—specimens 12.0–22.3 mm long in salinities of 14.85–41.0 ppt in tidal creeks and pools.^{11,34}

SPAWNING

Location: Specifically unknown, although mature gonads have been found in specimens from mouths of creeks, over soft mud bottoms,¹³ under aquarium conditions; eggs deposited on spawning mops.^{35,37}

Salinity: In aquaria at 0.1, 3.9, and 16.9 ppt; during natural spawning period at Fox Creek, Virginia, salinities varied from 0.2–9.1 ppt.³⁵

Season: April to October at Beaufort, North Carolina;²³ at Fox Creek Marsh, Virginia spawning mid-April to mid-August, males with contact organs March through August;³⁵ “mature gonads” observed from May through July at Wachapreague, Virginia;¹⁹ gravid females April

and May in Chesapeake Bay; late May on Long Island.¹³ At Fox Creek Marsh, Virginia, spawning was sporadic and perhaps synchronous when it occurred, but did not correspond with lunar or tidal phases.³⁵

Time: Under laboratory conditions specifically observed between 1000 and 1400 hours (JDH).

Temperature: 20 C³⁵–30.6 C (JDH) under experimental conditions; in field during natural spawning season temperatures varied from 19–36 C.³⁵

Fecundity: Byrne reported a maximum of 16 mature or incipient mature eggs (1.6 mm in diameter),³⁵ and a range of 4–23 eggs over 0.32 mm in diameter.¹⁴ Richards and Bailey noted 9 late stage ova and 40 “smaller ones” in a single female.¹⁹

EGGS

Location: Demersal. Location in nature unknown, but in laboratory experiments deposited individually or in clusters of 2–4 on spawning mops, mostly at the base of the mop where strands are most dense.^{35,37}

Ovarian and ovulated eggs: Size range 0.32³⁵ to ca. 2.0 mm.²³ Twenty “late stage ova” described as clear and with multiple oil droplets (average diameter, 1.77 mm); “less mature” ova opaque yellow.¹⁹ “Mature eggs” (ca. 2.0 mm diameter), spherical.²³

Fertilized eggs: Spherical (JDH), diameter 1.76–2.18 mm, average 1.96 mm; chorion with papillary ornamentations³⁵ or chorionic bristles (but these conspicuously less abundant than in the very similar egg of *Fundulus confluentus*)³⁷ and usually with long adhesive gelatinous threads; 5–58 oil globules, average 21.8.³⁵

EGG DEVELOPMENT

Incubation period: At 20–25 C; at 0.1 and 3.9 ppt salinity usually 12–16 days; at 16.9 ppt salinity, incubation period longer, 13 eggs hatched in 33 days and 1 in 43 days.³⁵

YOLK-SAC LARVAE

Minimum hatching length, 4.8 mm.³⁶ Hatching length varies with length of incubation period: in early hatchlings, 5.3–6.0 mm, in delayed hatchlings 6.0–6.3 mm TL. Length at end of stage 6.0–7.0 mm.³⁶

Myomeres 8–9 + 21,³⁶ vertebrae 31, branchiostegals 5.³⁵

Morphometric variations throughout stage: As times in SL—head 3.8–4.0, depth 5.5–6.6; as times in HL—eye 2.4–2.7, snout 8.1–16.5.³⁵

In early hatchlings (5.3–6.0 mm TL) yolk sac large, in late hatchlings (6.0–6.3 mm TL) yolk sac greatly reduced. At hatching oil globules dispersed over surface of yolk

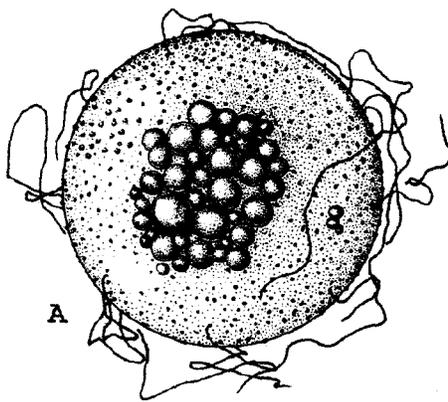


Fig. 106. *Fundulus luciae*, Spotfin killifish. A. Developing egg, showing chorionic bristles and attachment filaments. For comparison to similar egg of *Fundulus confluentus* see fig. 83. (A, Original drawing, Elizabeth Ray Peters.)

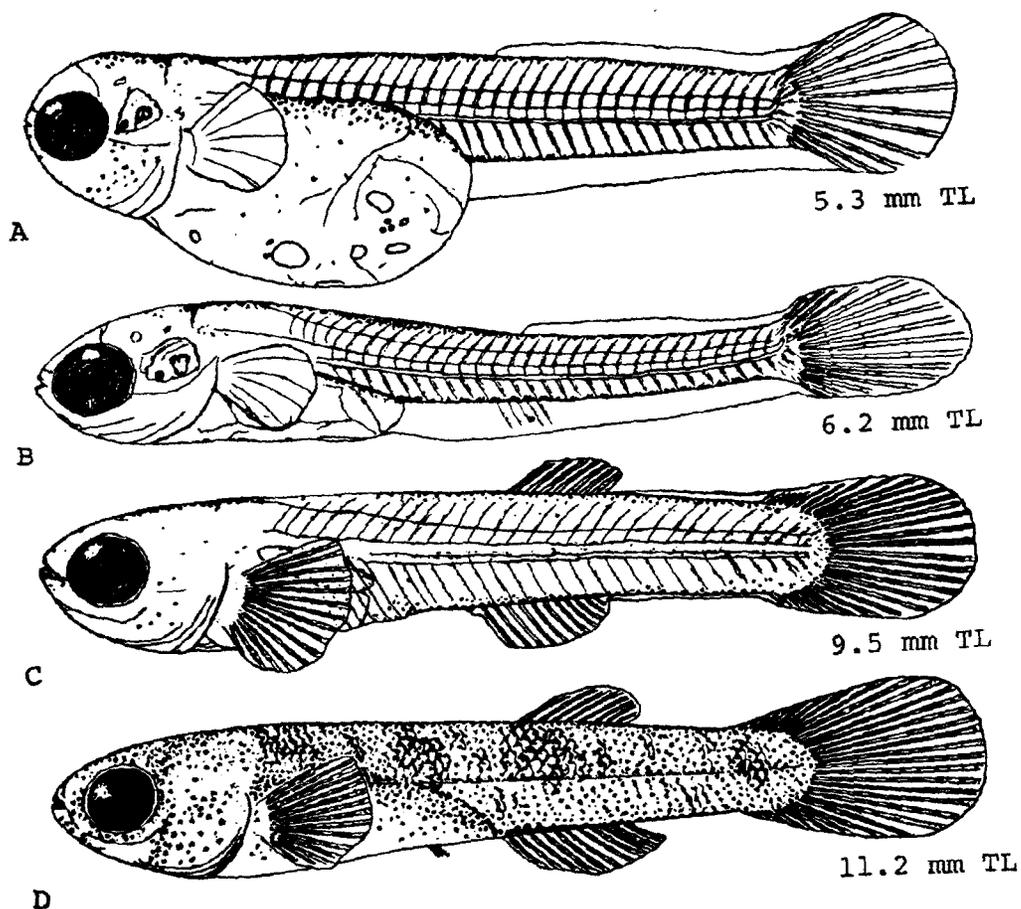


Fig. 107. *Fundulus luciae*, Spotfin killifish. A. Yolk-sac larva, 5.3 mm TL. B. Yolk-sac larva, 6.2 mm TL. C. Larva, 9.5 mm TL. D. Larva, 11.2 mm TL. (A-D, Byrne, D. M., 1976: fig. 4.)

sac; mouth terminal, nonprotractile; teeth absent; otoliths evident, the largest about 3 times as large as the smallest. Dorsal finfold forward to between 17th and 18th neural spine (counting from caudal fin). Caudal and pectoral rays evident at time of hatching. In early hatchlings (5.3–6.0 mm) ventral finfold rayless; in more advanced hatchlings (6.0–6.3 mm) anal rays partially formed. Urostyle apparently oblique at 5.3 mm.³⁵

Pigmentation: At 5.3 mm numerous small melanophores present on dorsal surface of head and back, along bases of finfolds, on yolk sac (especially dorsally) and on lateral aspects of head.³⁵ In preserved yolk-sac larvae of unspecified lengths a serrated band of pigment dorsally, pigment over dorsal edge of anterior part of notochord, dense pigment ventrally on body posterior to anus; a faint dashed line of small melanophores mid-laterally, a conspicuous bar of pigment behind eye, and scattered melanophores in developing pectoral fins. In life, hatchlings strikingly similar to those of *Fundu-*

lus confluentus, except that lateral yellow spots of *confluentus* are replaced with a solid yellow pigment bar in *luciae*.³⁸

LARVAE

Size range 6.0 or 7.0 to 13.0 mm.³⁵

Vertebrae 31–33; some larvae larger than 8.0 mm with a short, innermost 6th branchiostegal ray developed.³⁵

Morphometric variation throughout stage: As times in SL—head 3.2–3.8, depth 4.4–5.3; as times in HL—eye 2.7–3.2, snout 7.0–14.8.³⁶

At beginning of stage, villiform teeth along forward edge of each jaw; at 6.0–7.0 mm mouth protractile, slightly upturned; otoliths visible up to 9.0 mm. Vestigial finfolds evident to 11.0–12.0 mm; rays developing in dorsal finfold at 6.0–7.0 mm (but not illustrated in

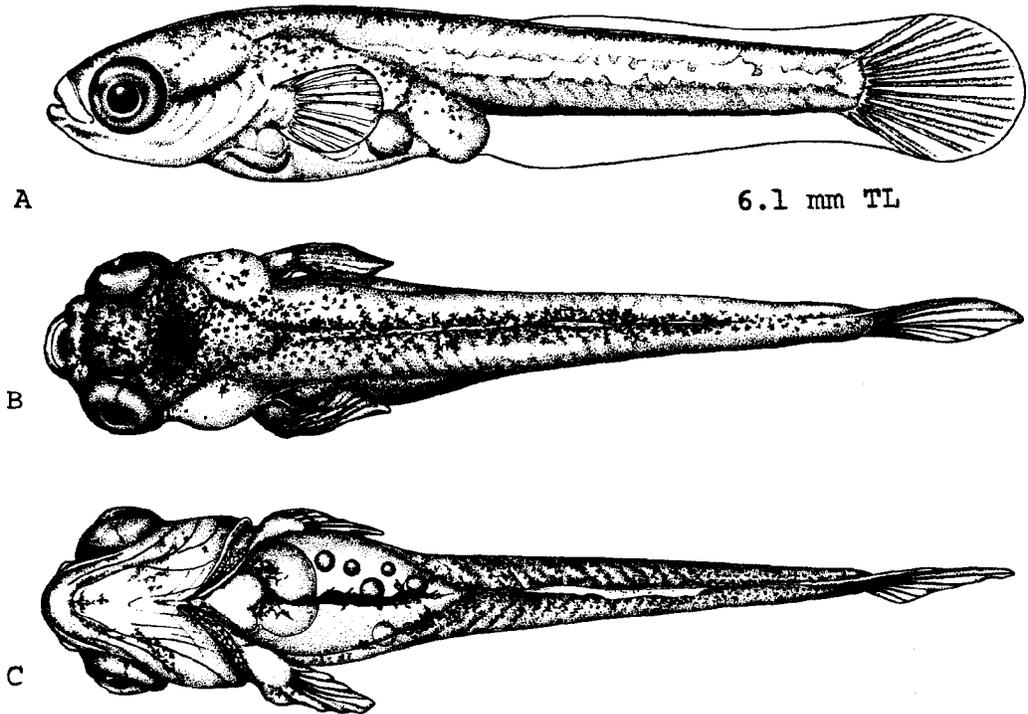


Fig. 108. *Fundulus luciae*, Spotfin killifish. A. Yolk-sac larva, 6.1 mm TL, drawn in life. B. Dorsal view of A. C. Ventral view of A. (A-C, Original illustrations, Elizabeth Ray Peters.)

specimen of this size range). Typical sequence of fin development: caudal, anal, dorsal, pectorals and pelvics. Lateral line discernible at 6.0–7.0 mm. Scales first evident on sides of body at 10.0–11.0 mm, subsequently formed on back, head, and, finally, belly; scales complete except on belly at 11.0–13.0 mm. Alimentary tract S-shaped at 6.0–7.0 mm; gas bladder well defined in a specimen 9.5 mm long.³⁵

Pigmentation: Many small, evenly spaced melanophores on head and back; melanophores near fin bases and adjacent to fin rays, also on dorsal portion of visceral

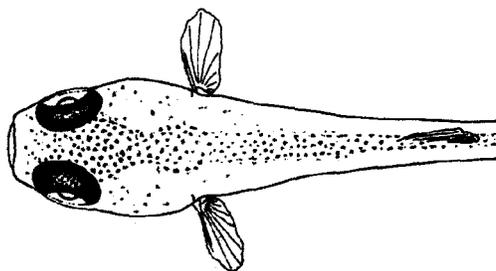


Fig. 109. *Fundulus luciae*, Spotfin killifish. A. Larva, typical anteriodorsal pigment pattern. For comparison to *Fundulus heteroclitus* see fig. 102. (A, Byrne, D. M., 1976: fig. 5A.)

cavity; sides of body and belly unpigmented; by 11.0 mm mid-dorsal stripe (typical of adult) well-developed.³⁵

JUVENILES

Minimum size described, 13.0 mm.

Morphometric variations throughout stage: As times in SL—head 3.2–3.6, depth 4.3–5.0; as times in HL—eye 3.2–3.5, snout 7.2–9.5.³⁵

Scales complete at 17.0 mm.³⁵

Pigmentation: Complete on belly at 17.0 mm. “Juveniles” grayish green, with a few possessing numerous, faint, vertical crossbars along sides.³⁵ Young (but including specimens up to “about 26 mm”) all have “female color.”²³

AGE AND SIZE AT MATURITY

Mature during first year of life (JDH), if assumption that the “life-span of the species is probably about one year” is correct; males 24–27 mm TL, females 28–30 mm TL.³⁵

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Fundulus majalis (Walbaum), Striped killifish**ADULTS**

D. 11⁵⁴-16; A. 10-12; P. 18-20;^{15,52} V. 6;¹⁹ scales in lateral series 32⁷-37,⁴¹ in transverse series 13-15,²² in oblique series 18-19;⁵⁴ vertebrae 14+20¹⁹ (although under experimental conditions averages up to 34.61³⁰); branchiostegals 6.^{19,22,36}

Proportions expressed as times in SL: Head 2.9-3.3^{7,52} (also reported as 3.75⁴⁰); depth 3.8-4.4.⁵²

Body rather slender, compressed posteriorly; head long, depressed; mouth small, terminal, oblique; lower jaw slightly in advance of upper.^{6,12} Preopercular canal with 7 pores, postorbital series not interrupted.⁴⁸ Anal fin high in males, moderate in females; pelvics longer in males than females, reaching past front of anal fin, inserted somewhat nearer base of caudal than tip of snout;^{6,8,22} caudal fin rounded.⁴⁰ Oviduct adnate to first anal ray.⁶ Males with contact organs during and shortly after spawning.³⁴

Pigmentation: Males dark olivaceous^{6,39} to bluish black above;¹⁰ sides silvery,^{4,39} salmon yellow,¹² or golden⁶

with 11⁵²⁻²⁰^{10,39} broad dark bars; lower sides and belly orange, salmon yellow, greenish yellow, or golden;^{10,12,39,47} top of head and mouth bronze-yellow;²² cheeks and opercle suffused with black;¹² dorsal fin golden,¹⁰ dusky,¹² blackish,⁴² and with a black ocellus on posterior rays; other fins yellow, sometimes partly dusky.^{6,12,22,39,42} Male color intensifies during spawning season.^{39,42,47} Females olivaceous above, white below, 1 to several prominent dark longitudinal stripes along sides and 1-2 vertical bars near base of tail.^{6,7,12,22,39,45} Egg-bearing hermaphrodites may have male pattern.²⁷

Maximum length: Ca. 200 mm,^{8,21,45} with females somewhat longer than males.^{22,51}

DISTRIBUTION AND ECOLOGY

Range: New Hampshire to Mantanzas Inlet, Florida.^{14,17,52}

Area distribution: Coastal waters of New Jersey,³ Delaware,⁹ Maryland,⁴⁰ and Virginia;⁵³ north in Chesapeake Bay to Patapsco and Chester rivers.⁴⁶

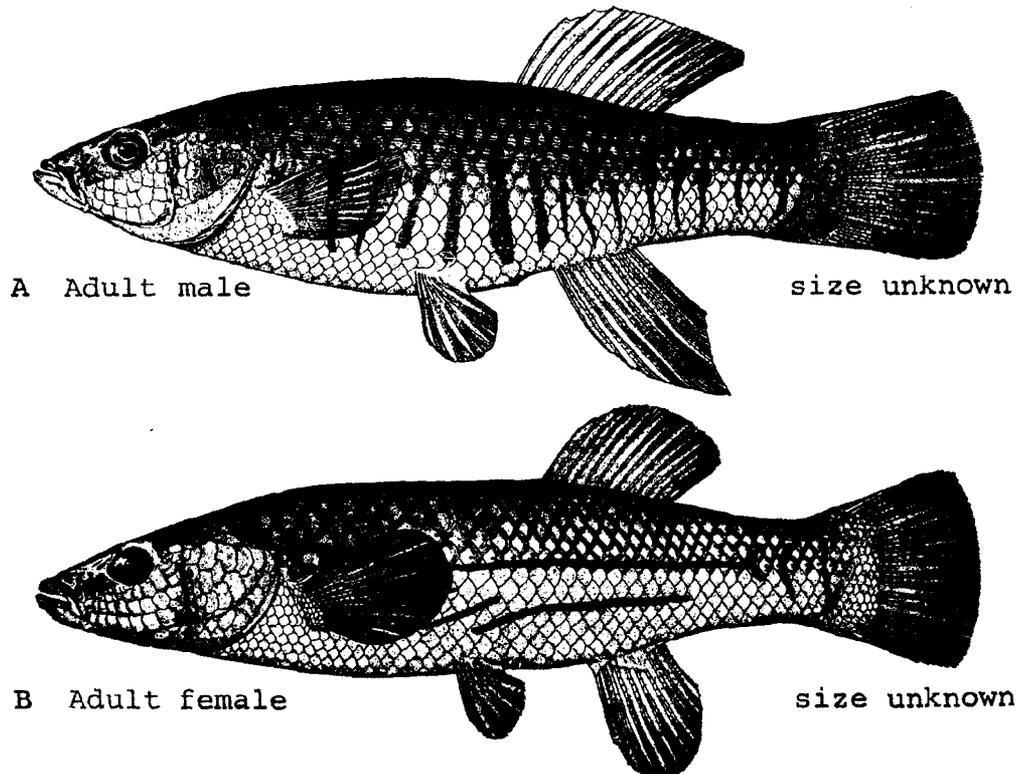


Fig. 110. *Fundulus majalis*, Striped killifish. A. Adult male, size unknown. B. Adult female, size unknown. (A. B. Bigelow, H. B., and W. C. Schroeder, 1954: fig. 77.)

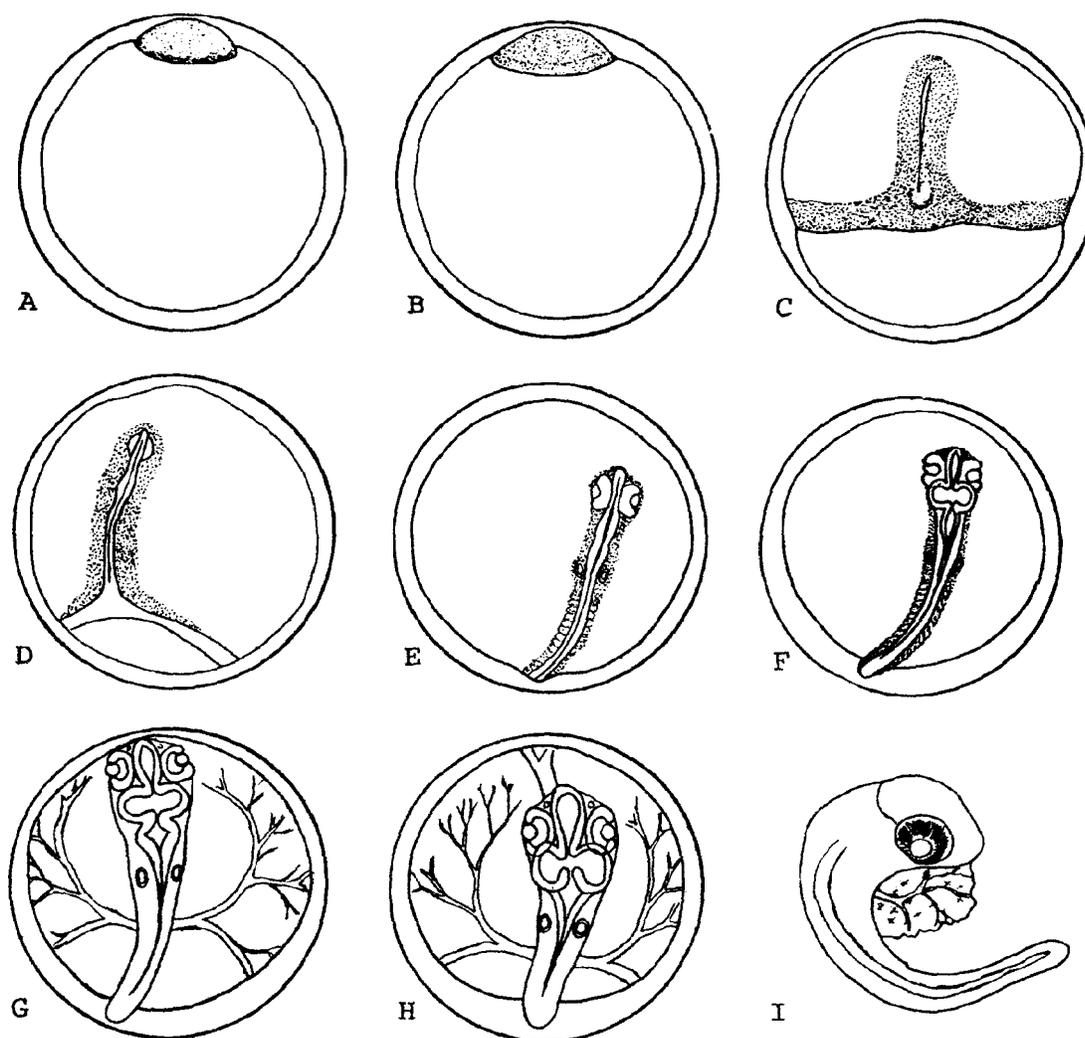


Fig. 111. *Fundulus majalis*, Striped killifish. Development of eggs. A. 18 hours, blastoderm formed. B. 24 hours, blastoderm expanding. C. 48 hours, primitive streak. D. 54 hours, anlagen of embryo. E. 72 hours, eyes, auditory vesicles, somites formed or forming. F. 80 hours, brain divisions evident. G. 96 hours, vitelline vessels evident, no pigment. H. 114 hours. I. 168 hours, pigment in eye and on yolk. (A-I, Newman, H. H., 1908: pls. 2-4.)

Habitat and movements: Adults—a schooling species^{2,32,47} found in shallow water along sandy or pebbly beaches,^{11,50} near mouths of rivers,¹ in salt marshes and fresh waters connecting with them,⁴⁰ tide pools,^{16,41} sheltered bays,^{32,50} bayous,^{22,45} creeks,^{12,45} guts, and ditches,⁴¹ and around wharves⁶ and rubbish piles.⁴⁷ Solitary individuals sometimes in muddy water and beds of eelgrass or other aquatic vegetation.^{32,47} Move in and out with tide and never found far from shore;^{16,38,39,57} capable of moving overland when stranded by receding tide,^{12,13} and sometimes in water shallower than their bodies.⁵⁸ Overwinter in mud near mouths of creeks.^{32,46}

Apparently enter freshwater^{20,33,40} and able to withstand freshwater in aquaria.⁴⁴ Inshore from April or May until fall in Rhode Island.¹¹ Maximum salinity 37.8 ppt.⁵⁷

Larvae and juveniles—specimens 9.4–51.0 mm long in salinities of 20.4–30.4 ppt;³⁰ “young” in shallow water among eelgrass and other aquatic vegetation.²¹

SPAWNING

Location: Spawning schools in still shallow water close

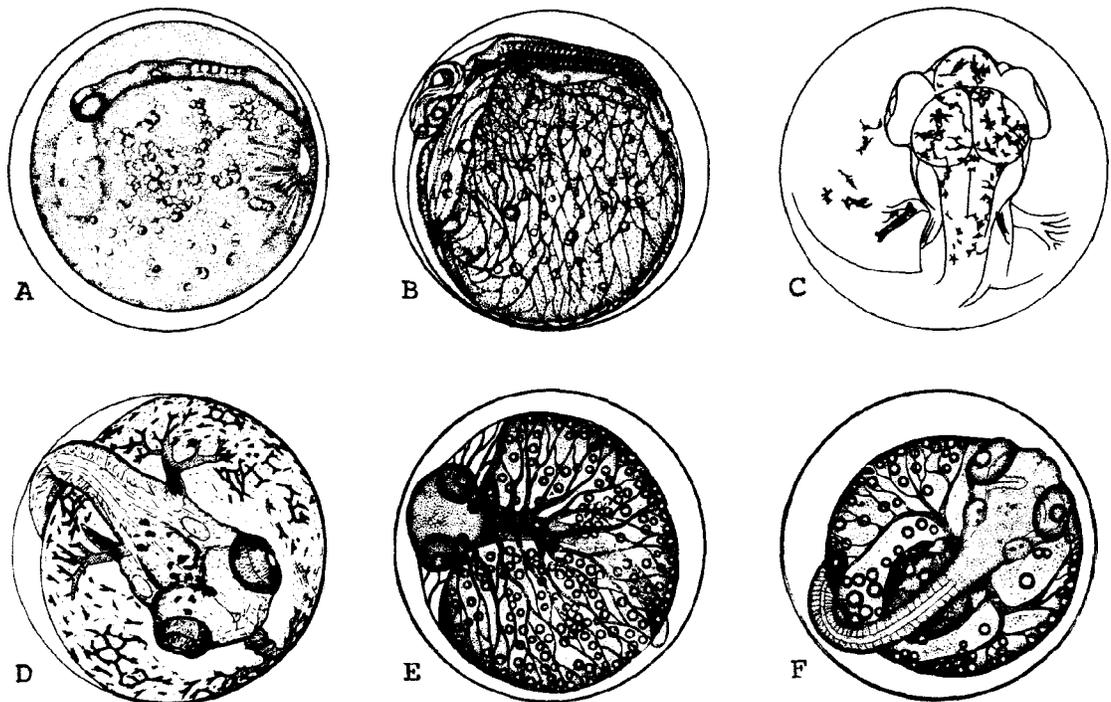


Fig. 112. *Fundulus majalis*, Striped killifish. A. 3-6 somite stage. B. 29-32 somite stage. C. Advanced embryo, age unknown, pigment developing on head, body, and yolk sac. D. 192-hour egg, otoliths formed, heart S-shaped. E. Pre-hatching stage, dorsal view. F. Pre-hatching stage, ventral view. (A, B, Fahay, W. E., 1976: fig. 1. C, Bancroft, F. W., 1912: fig. 10. D, Stockard, C. R., 1915: fig. 11. E, F, Ryder, J. A., 1885: pl. XI.)

to shore; ^{28,33} also, presumably, in small ponds.²⁶

Season: April to September in Chesapeake Bay; ¹² June, July and August from New Jersey northward; ^{32,35,37} apparently reaches peak of spawning activity 2 weeks earlier than *Fundulus heteroclitus*.¹³

Frequency: One female produces several batches of eggs per season.¹²

Fecundity: 200-800 ²⁸ with large fish generally producing more eggs than small fish.¹²

Note: Functional hermaphroditism occurs in this species.^{57,60}

EGGS

Location: Deposited close inshore during low tides; sometimes associated with *Limulus* eggs; ^{28,47} often buried ca. 75-100 mm in sand ^{32,59} (but this may result from shifting of sand in spawning area; ⁴³ however, active burying of eggs by females during oviposition has been noted, GED, JDH).

Fertilized eggs: Spherical; ^{12,32} diameter ca. 2.0 mm ¹² to at least 3.0 mm ²⁵ (averages reported at 2.16 mm,³²

2.7 mm,¹³ and 3.0 mm²⁵); deep amber or yellowish, opaque; ^{13,23,25,32,47} egg membrane tough,¹⁸ slightly adhesive,^{29,32,47} smooth (JDH), not fibrous.²⁵

EGG DEVELOPMENT

Development at unspecified temperature (second Newman series): ²³

- 3 hours—2- and 4-cell stages.
- 6 hours—16- and 32-cell stages.
- 22 hours—faint germ ring.
- 48 hours—germ ring halfway around yolk, triangular embryonic shield formed, embryonic axis evident as thin line.
- 72 hours—germ ring nearly around yolk; optic vesicles flat, lacking optic cups; no lenses; no somites.
- 96 hours—somites formed, brain vesicles well differentiated, no pigment.
- 120 hours—heartbeat, circulation established.
- 168 hours—few slender melanophores on sides of mid- and hindbrain and on yolk.
- 216 hours—stellate chromatophores on head and body, melanophores and red chromatophores on yolk.

432–480 hours (18–20 days)—hatching.²³

Development at unspecified temperature (first Newman series):¹³

- 72 hours—average of ca. 9 somites, no pigment.
- 80 hours—somites too numerous to count.
- 96 hours—heart rate slow, beat feeble.
- 114 hours—vitelline circulation complete.
- 168 hours—few melanophores on yolk.
- 288 hours—body with large grayish melanophores, yolk lightly pigmented with black.
- 528–552 (22–23 days)—hatching.¹³

Incubation period:

At 18.3 C	Ca. 58 days. ³²
At 16–20 C	First hatch 34 days, 50% hatch 41 days.
At 22–26 C	First hatch 14 days, 50% hatch 17 days.
At 28–32 C	First hatch 10 days, 50% hatch 12 days.
At 22–26 C transferred to 16–20 C	At 3–6 somite stage, first hatch 40 days, 50% hatch 40 days.
	At 9–12 somite stage, first hatch 35 days, 50% hatch 39 days.
	At 15–23 somite stage, first hatch 31 days, 50% hatch 31 days.
	At 24–28 somite stage, first hatch 27

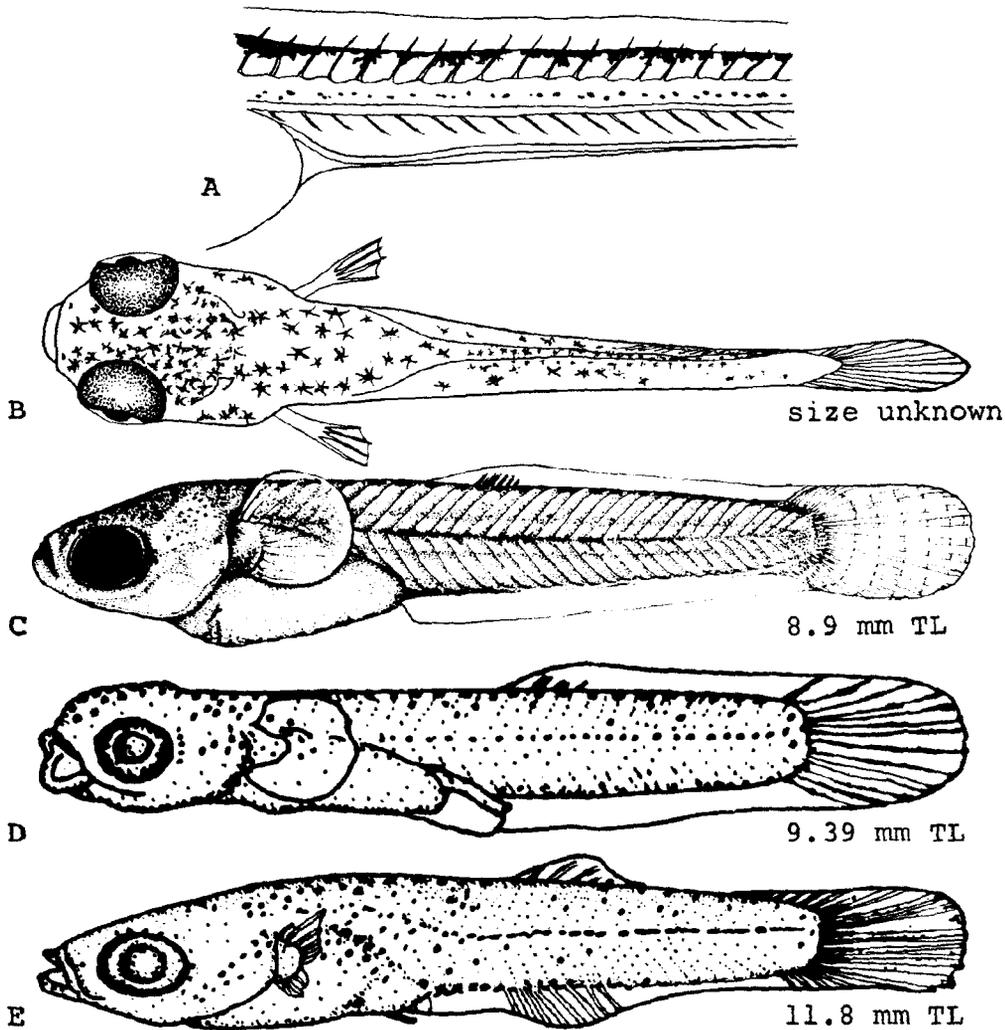


Fig. 113. *Fundulus majalis*, Striped killifish. A. Yolk-sac larva, just hatched, showing details of postanal pigmentation. B. Yolk-sac larva, dorsal view, size unknown. C. Yolk-sac larva, 8.9 mm TL, dorsal fin rays developing. D. Yolk-sac larva, 9.39 mm TL. E. Larva, 11.8 mm TL. (A, Bancroft, F. W., 1912: fig. 26. B, Newman, H. H., 1908: pl. 5. C, Foster, N., 1974: 138, photographed with permission from the original drawing by R. Lynn Moran. D, E, Richards, S. W., and A. M. McBean, 1966: fig. 1.)

	days, 50% hatch 30 days. At 29–32 somite stage, first hatch 24 days, 50% hatch 24 days.
At 22–26 C transferred to 28–32 C	At 3–6 somite stage, first hatch 10 days, 50% hatch 13 days. At 9–12 somite stage, first hatch 11 days, 50% hatch 13 days. At 15–23 somite stage, first hatch 11 days, 50% hatch 13 days. At 24–28 somite stage, first hatch 13 days, 50% hatch 14 days. At 29–32 somite stage, first hatch 11 days, 50% hatch 14 days. ⁵⁵

Note on development: In laboratory experiments agitation facilitated hatching; otherwise, hatching was delayed for excessively long periods.⁵⁷

YOLK-SAC LARVAE

Hatching length 7.0⁵⁶–11.0 mm.¹³

Total myomeres 10+24.⁵⁶

At 8.9 mm head large, elongate;⁵⁴ at 9.39 mm mouth open, yolk greatly reduced.³⁰ Hatchlings (stage and length at time of hatching uncertain) may have "full

complement of fins."⁴⁷ Caudal rays developing at hatching (JDH), segmented by 8.9 mm; dorsal rays first evident at 8.9⁵⁴–9.0 mm,³⁰ anal rays at 10.0 mm.⁵⁴

Pigmentation: Various described. Generally much paler than in hatchlings of *Fundulus heteroclitus*.¹³ In specimens of unspecified size, lateral line without red chromatophores, but with a series of 40–60 melanophores, usually 2 per segment.²⁴

In an 8.9 mm specimen little or no pigment on perivertebral vessels on ventral surface of yolk; light peppering of well-developed melanophores on head and along upper margin of tail; melanophores forming patchy lateral stripe almost to caudal fin; overall body pigment light to silvery.⁵⁴

In a living specimen 9.0 mm long, dark pigment on head; in a narrow, poorly defined double line along dorsal ridge; along ventral ridge; above and below notochord; along mid-lateral line (as series of tiny dots); and in central region of yolk sac. Ventral pigment splits at posterior margin of yolk sac forming a distinctive "Y" pattern. Sides of yolk sac milky white with silvery reflections, this pigment sharply delineated in ventrolateral region of yolk sac. A few gold chromatophores along mid-lateral line. Widely spaced white chromato-

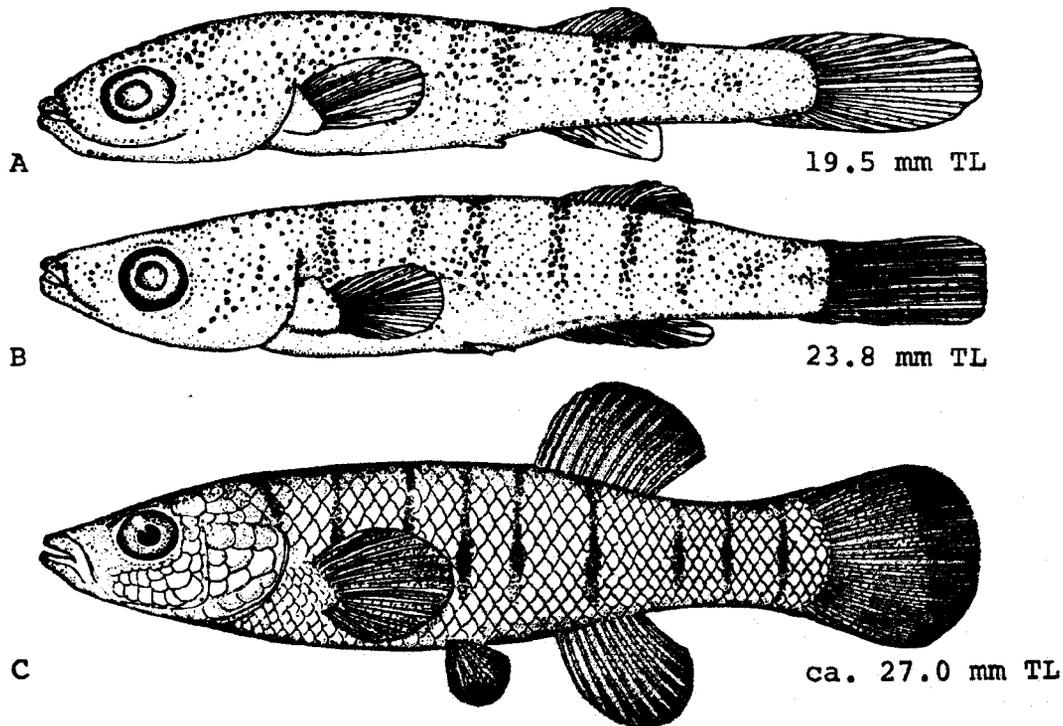


Fig. 114. *Fundulus majalis*, Striped killifish. A. Larva, 19.5 mm, ventral fin buds forming. B. Larva, 23.8 mm TL. C. Juvenile, ca. 27.0 mm TL. (A, B, Richards, S. W., and A. M. McBean, 1966: fig. 1. C, Smith, H. M., 1892: pl. 19.)

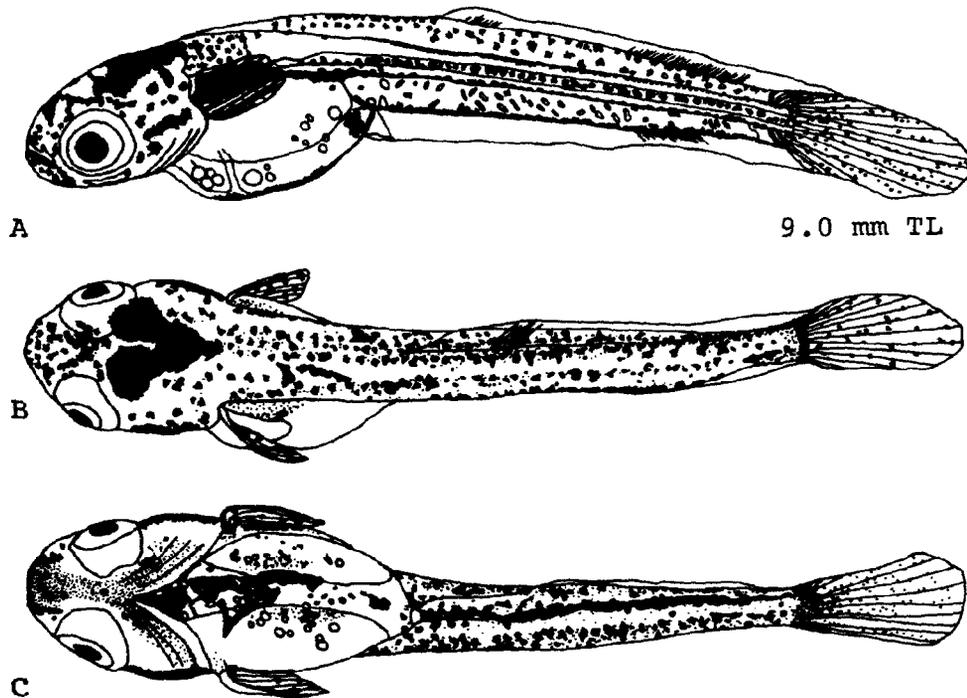


Fig. 115. *Fundulus majalis*, Striped killifish. A. Yolk-sac larva illustrated in life, 9.0 mm. B. Dorsal view of A. C. Ventral view of A. (A-C, Original drawings, Linda L. Hudson.)

phores on upper parts of body, very small white chromatophores (mixed with black) in mid-lateral line, and additional white pigment on pectoral fins, throat, and cheeks. Eye black and yellow. In preserved specimens from this same series, no pigment in pectoral fins, body pigment limited to area above and below notochord.⁵⁶

In another series, a specimen 9.0 mm long was described as having a large yellow chromatophore on finfold just behind vent, and a 10.0 mm specimen had large dorsal chromatophores from snout to tail, a few in opercular area, and a series ventrally from anus to tip of tail.⁵⁰

LARVAE

Size range 11.8–23.8 mm.

Six branchiostegals formed, the two anteriormost close together, the remainder evenly spaced.⁵⁰

Proportions as times in TL (in specimens 9.4–14.6 mm long, thus including some yolk-sac larvae): Head 3.7–4.5, depth 6.2–7.5, caudal peduncle width 10.6–13.4. As times in HL: Interorbital width 2.0–2.3, snout 3.5–5.1, eye 2.4–3.6.⁵⁰

In larvae up to 15.0 mm long, head more compressed than in *Fundulus heteroclitus*, sloping abruptly down-

ward between eyes and end of snout;⁵⁰ gape relatively large.⁵¹ Dorsal finfold no longer evident at 11.8 mm; preanal finfold vestigial at 14.6 mm, obliterated at 19.5 mm; pelvics evident at 11.8 mm.⁵⁰

Pigmentation: At 10.0–15.0 mm chromatophores larger on dorsum, venter, flanks, head and operculum; lateral stripe darker than in *Fundulus heteroclitus*. At 14.0 mm, 3–5 dark vertical bars forming on sides; at 16.0–20.0 mm, 5–7.⁵⁰

JUVENILES

Minimum length described, 26.0 mm.

Proportions as times in TL (in specimens 27.1–51.0 mm long): Head length 3.0–3.6, depth 4.6–5.8, caudal peduncle width 8.6–11.3. As times in HL: Interorbital width 2.4–2.8, snout length 2.4–3.5, eye diameter 3.6–4.7.⁵⁰ Proportions as times in SL (at 55–70 mm SL): Depth 4.0–4.5, length of caudal peduncle ca. 6.8–7.7. At 71–84 mm SL, caudal peduncle depth ca. 6.4–7.3 times in SL.⁵²

Pigmentation: “Young” of both sexes with 7^{8,10–12} 12,39 vertical black bars. Females originally like young males, but pattern of vertical bars gradually replaced by longi-

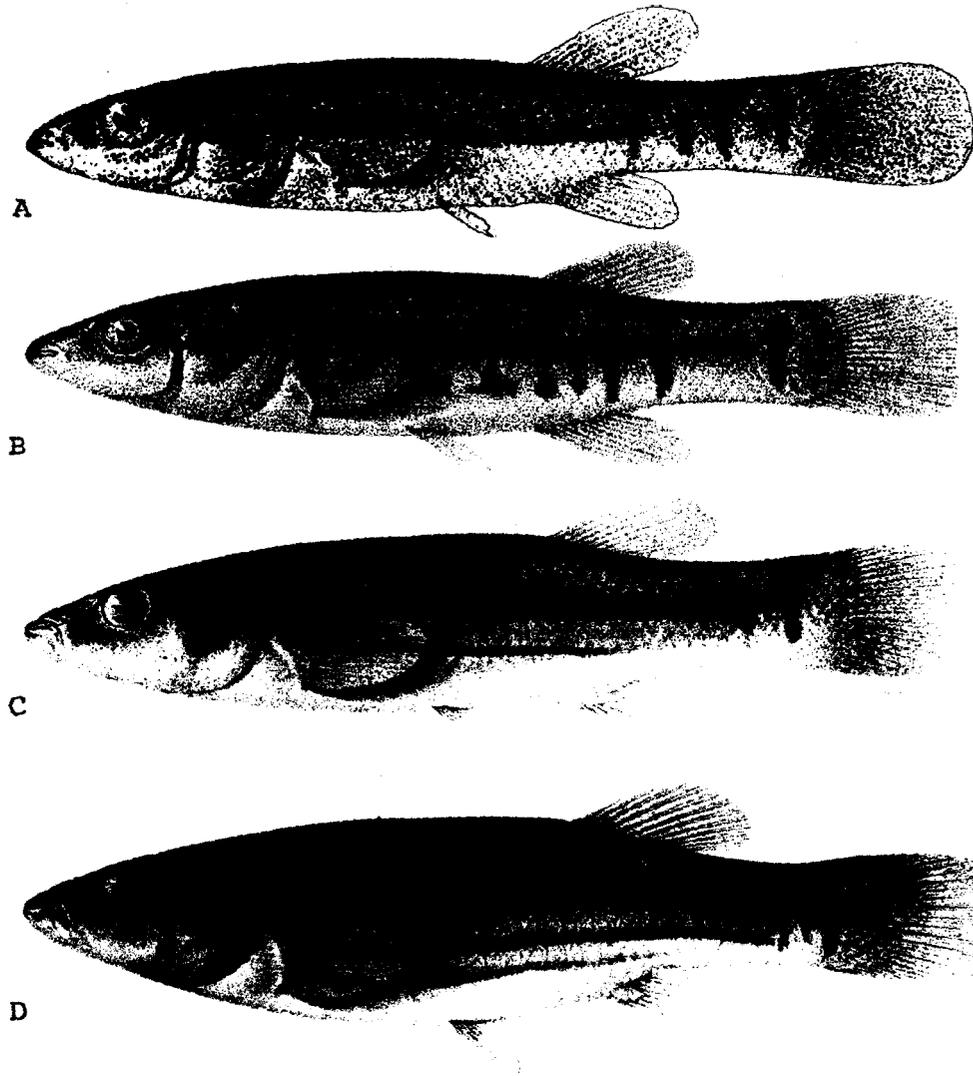


Fig. 116. *Fundulus majalis*, Striped killifish. A-D. Ontogeny of color pattern in females, sizes not stated. (A-D, Garman, S., 1895: pl. 5.)

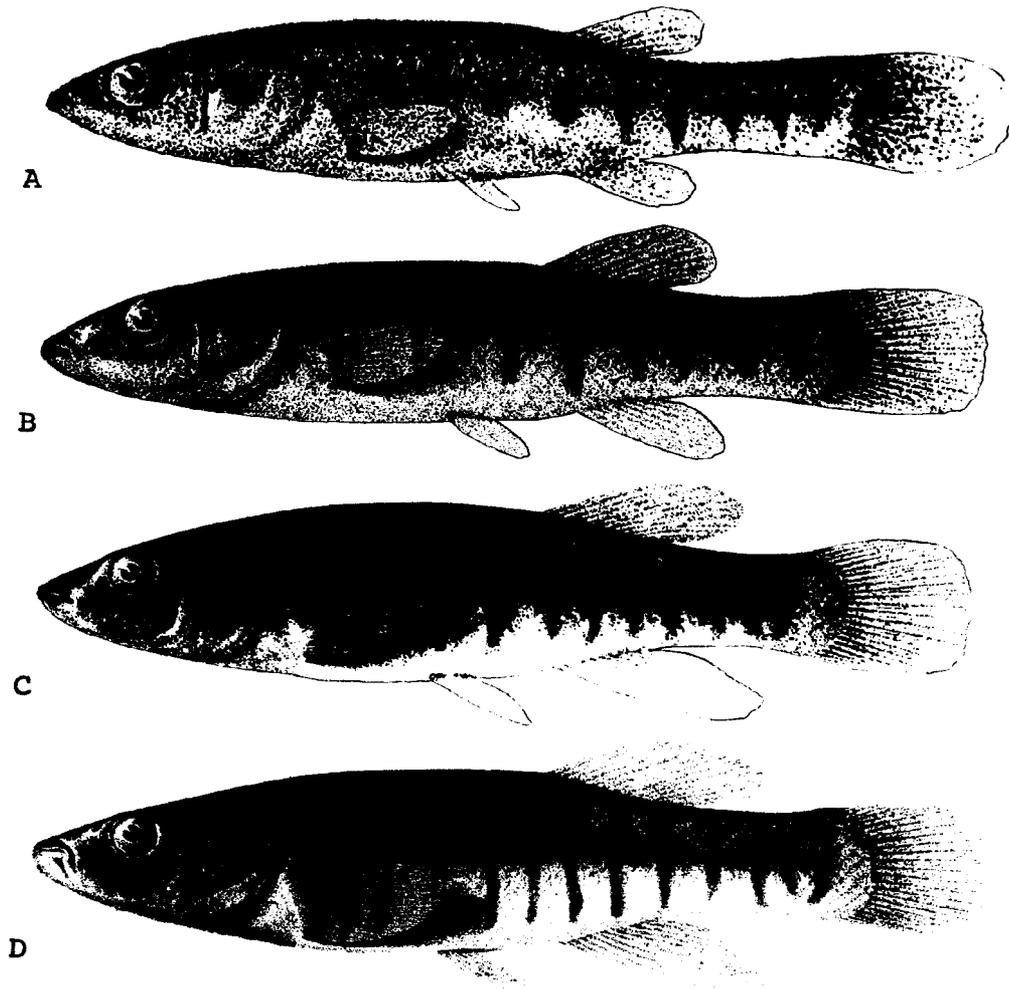


Fig. 117. *Fundulus majalis*, Striped killifish. A-D. Ontogeny of color pattern in males, sizes not stated. (A-D, Carman, S., 1895: pl. 9.)

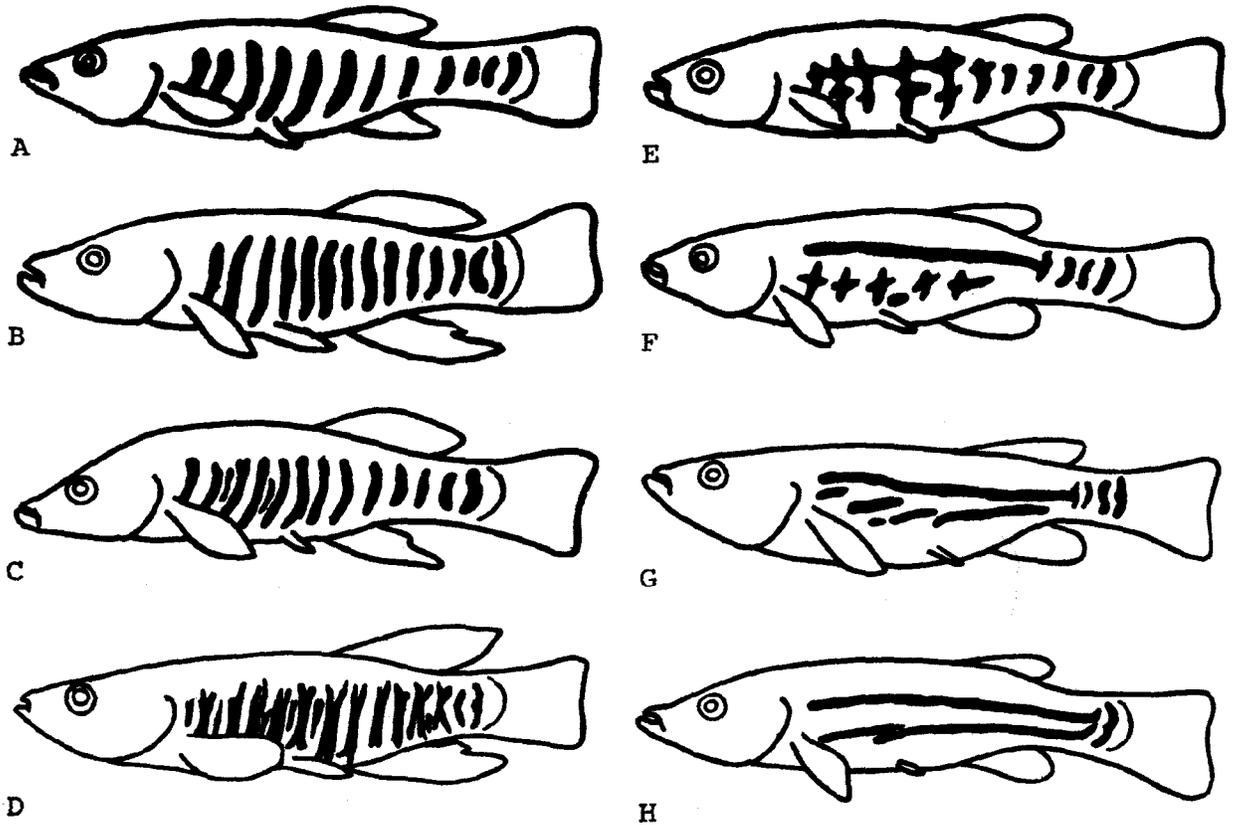


Fig. 118. *Fundulus majalis*, Striped killifish. A-D. Variation in ontogeny of color pattern in males. D. Pattern typical of very old males. E-H. Variations in ontogeny of color pattern in females. E, F. Cross-hatch pattern. G, H. Fragmentation of horizontal stripes. (A-H, Newman, H. H., 1907: pl. 5.)

tudinal stripes;¹⁰ stripes first evident at ca. 31.7 mm. Dorsal ocellus of males developed at ca. 50.0 mm.²²

AGE AND SIZE AT MATURITY

Probably mature in 2nd year.¹¹ Females ca. 76 mm, males ca. 63 mm.¹²

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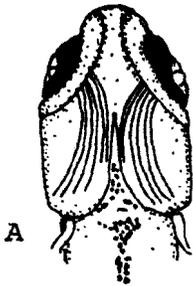


Fig. 119. *Fundulus majalis*, Striped killifish. A. Larva, size unknown, ventral view of head. Five branchiostegals are present (for comparison to *Fundulus heteroclitus* see fig. 103). (A, Richards, S. W., and A. M. McBean, 1966: fig. 1.)

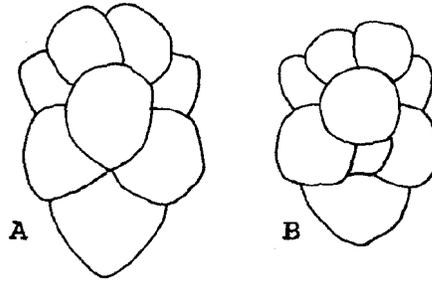


Fig. 120. *Fundulus majalis*, Striped killifish. A, B. Juvenile head scale patterns. Note that the central scale is either round or longitudinally elliptical. (For comparison to head scales of *Fundulus heteroclitus* see fig. 104.) (A, B, Cooke, P. H., 1965: figs. 2-3, Jerry D. Hardy, Jr., delineator.)

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Lucania parva (Baird), Rainwater killifish**ADULTS**

D. 9–14, mean 10.96, unbranched 1–4, branched 7–11; A. 8–13, mean 9.49, unbranched 1–4, branched 5–10; C. 12–18 principal rays, mean 15.68; P. 10–15, mean 13.31; V. 4–7; lateral line scales 23⁵–31,⁴¹ mean 26.83; scales between origin of dorsal and anal 8–11, mean 9.3, scales around body 18–25, mean 21.92, scales around caudal peduncle 10–16, mean 14.97,⁵ scales in oblique series between upper angle of gill opening and dorsal origin 6–7;⁴³ vertebrae 14 + 14,³⁰ but total vertebrae vary from 25–30, overall mean 27.73, mode geographically variable, stated as 26, 28, and 29; branchiostegals 5–6; preopercular pores usually 7; supraorbital canal complete to incomplete, typically with 7 pores; lachrymal pores 0–5; mandibular pores 0–5.⁵

Depth as times in SL ca. 2.6–4.5, mean 3.56;⁵ head in TL 3.25³³–3.70. Proportions expressed as percent SL: Predorsal length 47–59; anal origin to caudal base 33–46.⁵

Body rather deep, compressed; head flattened above, tapering to vertically rounded, blunt snout; mouth small, slightly superior; mandible vertical, projected.^{22,24,30,37} Teeth hooked;⁴⁰ premaxillary teeth uniserial or irregular; inner teeth, if present, few and strong; mandibular teeth uniserial.^{5,32} Dorsal fin higher in males than females, its origin midway between snout and base of caudal²⁴ and slightly in advance of anal. Caudal straight³⁰ to broadly rounded.³⁷ Breeding males with tubercles on top and sides of head, and sides of body between dorsal and anal fins.^{13,39,43}

Pigmentation: Pale green,⁴¹ olive,²⁴ or brown above,¹⁸ shading to pearly gray⁴¹ or silvery below;⁴⁰ anterior part of sides with bluish reflections;^{18,30} a faint stippled line along body, ending abruptly at hypural plate; a definite stripe from occiput to dorsal; scales on top of head with light centers; subocular bar present;⁷ scales black-edged, making dark crosshatches on back and sides of some individuals;⁴¹ iris brownish; pupil black, surrounded by narrow circle of gold.²⁶

Females dark olive above, pale below; dorsal and caudal fins greenish or olivaceous³⁰ and lacking black spots or edges,^{18,33} pectoral usually greenish or olivaceous,³⁰ rarely black;³⁹ other fins plain;³⁰ some specimens with dorsal and caudal fins and subopercle faintly washed with silver;⁴¹ in aquaria usually a series of 7 faintly visible broad, dark, vertical blotches on sides.⁴³

Males more brightly marked than females;³⁰ olive tan or green to pale brown above;¹⁸ dorsal fin with yellow or yellow-orange base⁴¹ or dusky orange throughout, usually with a large black spot, ocellated with yellow, at anterior base;^{18,33} entire dorsal fin sometimes bordered

with black;³⁹ anal and pelvics pale orange³⁵ to orange-red,^{18,33} or pinkish,⁴¹ their edges bordered with dusky^{18,33} to jet black;²¹ anal sometimes faintly washed with gold;⁴¹ pelvics also described as yellow with maroon-orange or dusky edges, anal as green or maroon with black edge;³⁸ caudal fin orange-yellow¹⁸ or dusky, edged with clear,³⁹ dusky,²¹ or black;³³ pectorals translucent,^{18,33} or rarely, black.⁴¹ Breeding males usually with “crosshatched” pattern on sides of body.⁴¹

Maximum length: 62.0 mm,³⁵ the females larger than males.³³

DISTRIBUTION AND ECOLOGY

Range: Cape Cod, Massachusetts, to lower Rio Panuco system, Tamaulipas, Mexico; primarily coastal, but with inland populations in Florida and the Pecos River, New Mexico; apparently introduced in California, Oregon, and Utah.^{5,25}

Area distribution: Chesapeake Bay, north to Love Point, Maryland;³⁶ the Delaware River estuary;²⁷ New Jersey;²⁸ Virginia.¹²

Habitat and movements: Adults—a schooling species³⁰ typically found along open shores or among aquatic vegetation^{3,10,15,23} in coves, bays, and creeks, and over flats;^{14,17,30} usually found at mid-depth³⁹ in shallow water;²³ variously reported from tidal streams,² brackish ponds, marshes, and ditches,^{4,6,20,26} barrier beach ponds,³⁴ pools,³³ muddy ponds,²¹ bayous,¹⁵ swamps,¹⁸ sloughs,⁴³ lakes, and the boil regions of large springs;³⁸ occasionally in harbors;² sometimes offshore in strictly marine water. Maximum distance from shore 11 km.²⁹ Salinity range 0.0⁸–48.2 ppt,¹⁵ with southern populations apparently entering undiluted seawater more frequently than northern populations.³⁶

A mass downriver migration involving thousands of fish was noted in York River, Virginia, in mid-October;¹² inshore in Florida Keys only during October, November, and February;¹ the species may be anadromous, migrating to fresher water to breed, and returning to saltier water after breeding.⁴³

Larvae—newly hatched rest on bottom; after yolk absorption, larvae swim just above bottom.⁴⁹

Juveniles—no information.

SPAWNING

Location: Male courtship behavior observed near clumps of *Najas* and *Vallisneria*;³⁹ spawned in aquaria in water 15 cm deep.¹⁰

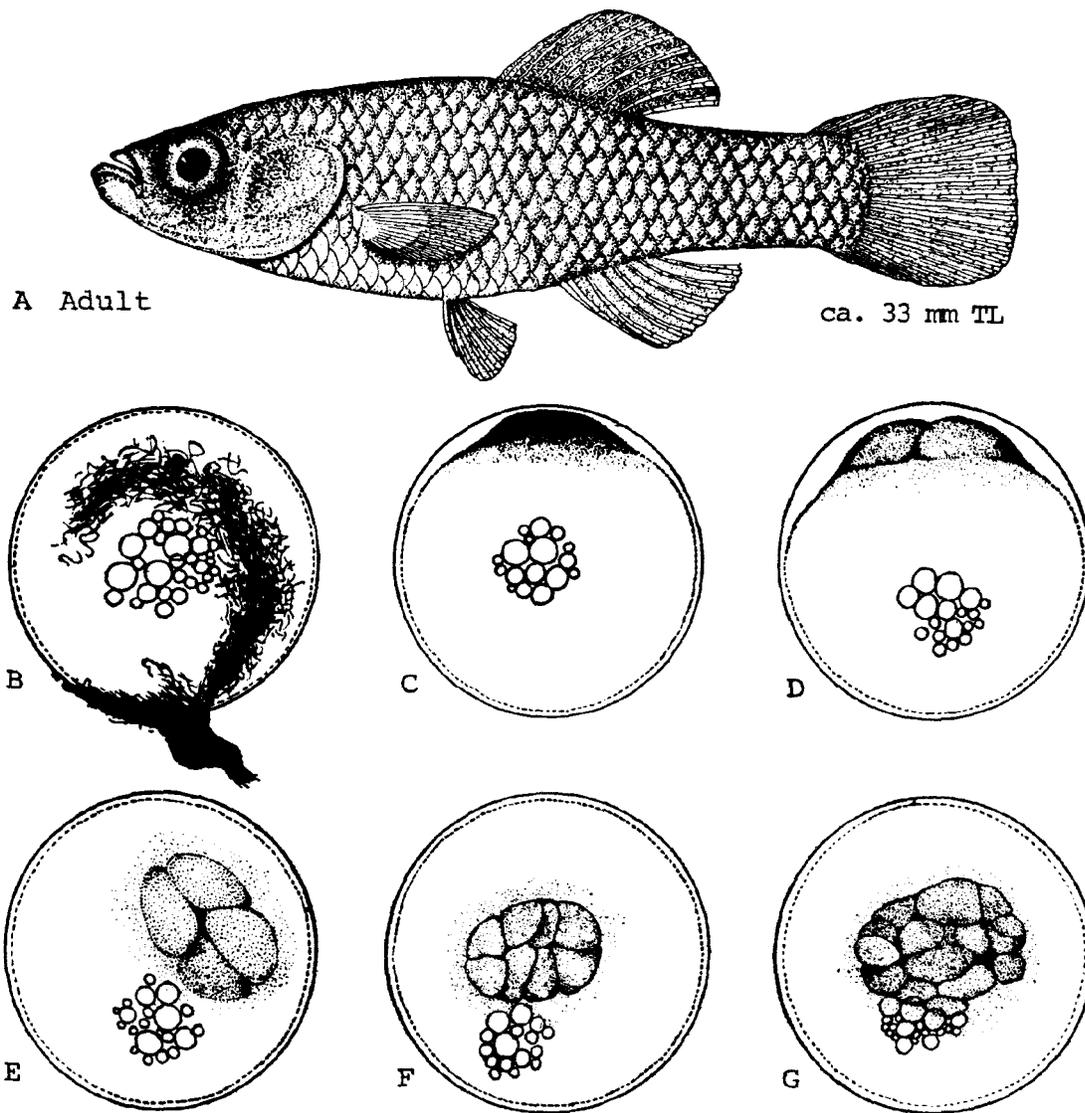


Fig. 121. *Lucania parva*, Rainwater killifish. A. Adult, ca. 33 mm TL. B. Mature unfertilized egg showing attachment filaments, diameter 1.1-1.3 mm. C. Blastodisc. D. 2-cell stage. E. 4-cell stage. F. 8-cell stage. G. 16-cell stage. (A, Bean, T. H., 1888: pl. 2. B-G, Kuntz, A., 1916: figs. 16-21.)

Season: In Chesapeake Bay ripe or nearly ripe fish early April to end of July;³⁰ in North Carolina, mid-April to late August;¹⁶ in Texas ripe individuals from late January to July, peak activity May and June;^{35,41} in Florida February to October;³⁹ or more or less continuous throughout year.¹¹ More than one brood may be produced per year by a single female.^{16,30}

Temperature: Ca. 17.8 C in aquaria.^{10,28}

Fecundity: 7-46 ripe ova (mean 24.5 per fish) plus "many smaller ova";³⁹ maximum reported count 104.³⁰

EGGS

Location: Demersal, deposited on fibrous substrate near surface or on bottom in shallow water;⁴² in aquarium experiments on floating spawning mops, always near top.⁴⁴

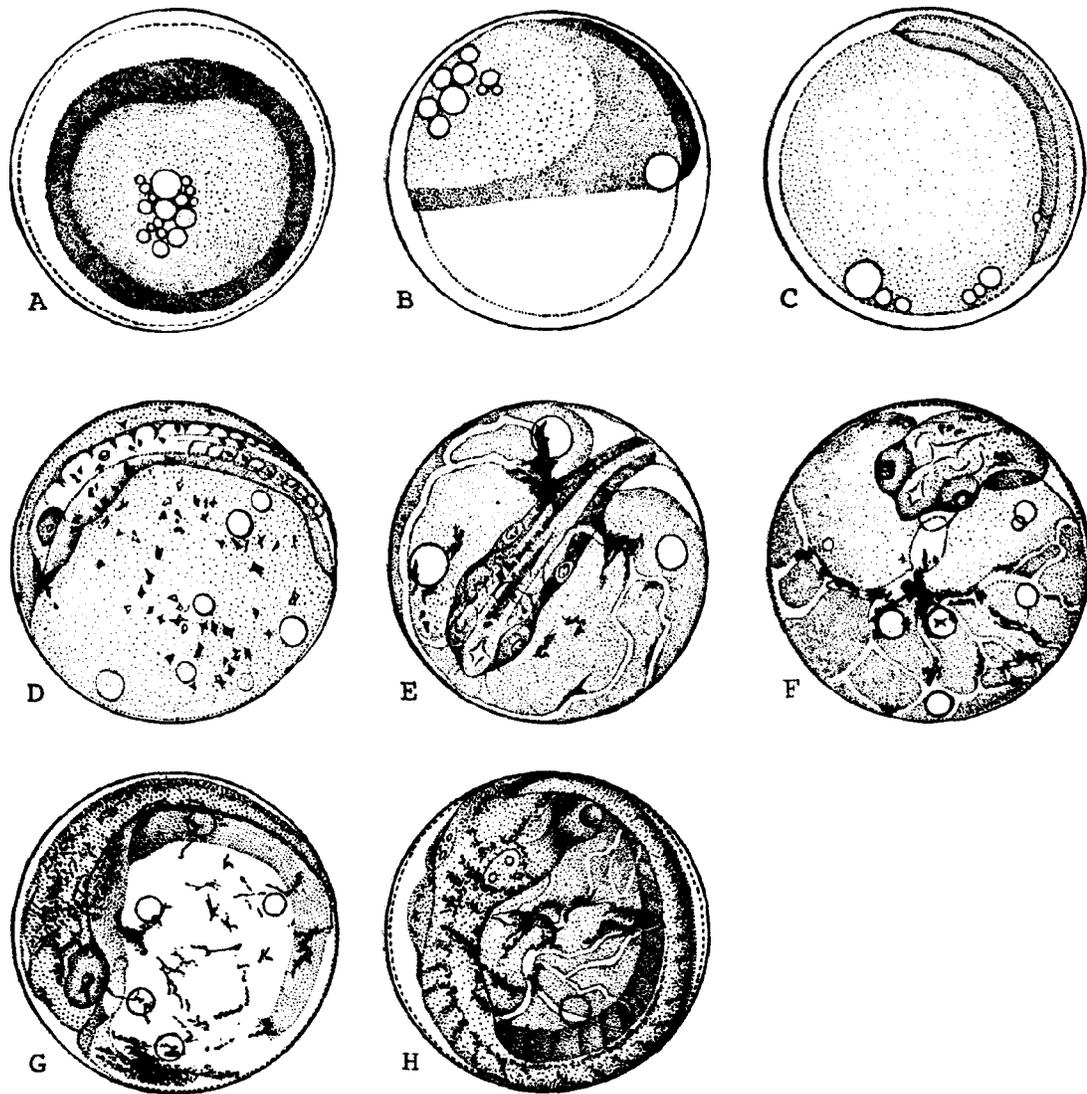


Fig. 122. *Lucania parva*, Rainwater killifish. A. Blastoderm showing germ ring. B. Germ ring and embryonic shield. C. Kupffer's vesicle, 24 hours. D. Early pigmentation, somites evident, 48 hours. E, F. Yolk circulation established, chromatophores along yolk vessels, otoliths formed, 68 hours. G. Advanced embryo, 90 hours. H. Pre-hatching stage, tail completely around yolk, pigmentation heavy. (A-H, Kuntz, A., 1916: figs. 22-29.)

Unfertilized eggs: Spherical; 1.0-1.3 mm in diameter; slightly yellowish, transparent; micropyle small; oil globules unequal, normally 12-20 at animal pole; egg membrane equipped with tangle of coarse adhesive threads which hold eggs loosely in clumps; perivitelline space narrow.^{9,16,30,31,39}

Fertilized eggs: Diameter 1.0-1.3 mm,⁴⁴ average 1.23;⁴³ outer membrane relatively thick, horny;⁴² attachment filaments typically most abundant in one area of egg surface;⁴⁴ perivitelline space very narrow.⁴²

EGG DEVELOPMENT

Development at laboratory temperature:¹⁶

1 hour—blastodisc formed.

1 hour, 15 minutes—first cleavage.

13 hours—germ ring differentiated.

24 hours—blastopore closed, Kupffer's vesicle formed, embryo less than 1/2 yolk circumference.

"Soon after closure of blastopore"—melanin granules in cells.

44-48 hours—embryo segmented throughout, auditory

vesicles evident, circulation established, melanophores and yellow chromatophores developed on yolk sac and body.

68 hours—otoliths evident, yolk with heavy vascular network, chromatophores concentrated along extra-embryonic blood vessels.

“At late stage of development”—tail completely around yolk, yolk reduced.¹⁶

Incubation period:

At 23.9 C—6 days.⁴³

At unspecified temperature—7¹⁶–14 days.^{16,36}

YOLK-SAC LARVAE

Hatching length 4.0⁴²–5.0 mm; ¹⁶ yolk absorbed at 6.0 mm⁴² or in 7 days.⁴³

Total myomeres, 8 + 18.⁴⁶

At time of hatching head large,⁴² not deflected over yolk; ¹⁶ margin of operculum more than half distance from snout to vent,⁴² yolk sac large; origin of dorsal finfold near midpoint of SL; rays evident in pectorals and caudal.¹⁶

Pigmentation: At hatching uniform light yellow.¹⁶ In a specimen 4.0 mm long (and presumably just hatched) pigmentation on perivitelline vessels moderately dark, light peppering of small melanophores over most of body, and small melanophores on distal end of mandible.⁴² At 4.7 mm (in life) head and dorsal aspects of body washed with golden yellow; orange or brownish orange pigment on head and body; developing caudal rays darkly pigmented; well defined rows of orange chro-

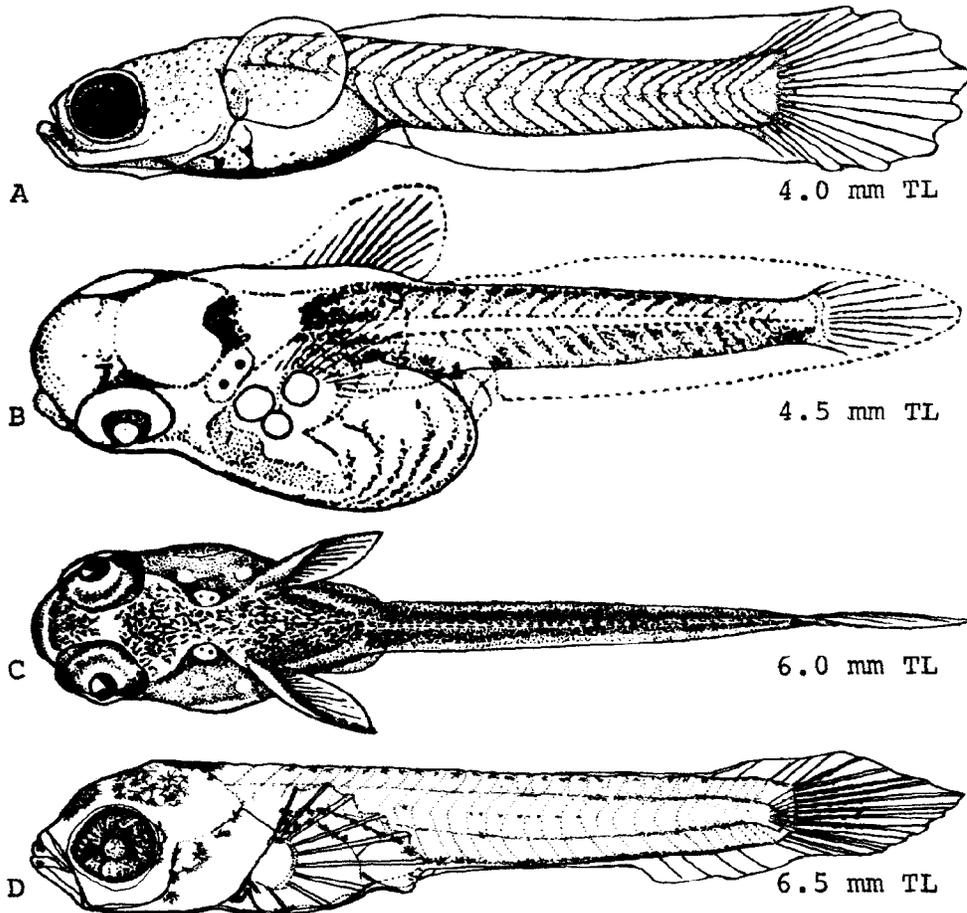


Fig. 123. *Lucania parva*, Rainwater killifish. A. Yolk-sac larva, 4.0 mm TL. B. Yolk-sac larva, 4.5 mm TL, just hatched. C. Larva, 6.0 mm TL, 7 days old. D. Larva, 6.5 mm TL, finfold greatly reduced, pigment forming in caudal membrane. (A, Foster, N., 1974: 140, photographed, with permission, from the original drawing by R. Lynn Moran. B, C, Kuntz, A., 1916: figs. 30–31. D, Original drawing, Nancy Schenk Smith.)

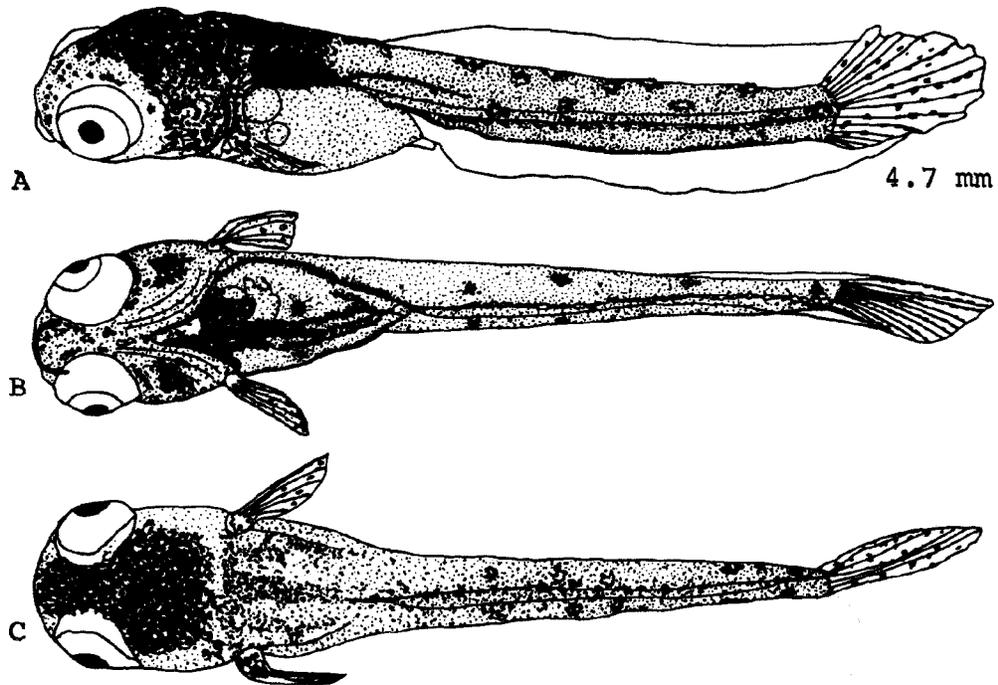


Fig. 124. *Lucania parva*, Rainwater killifish. A. Yolk-sac larva illustrated in life, 4.7 mm TL. B. Ventral view of A. C. Dorsal view of A. (A-C, Original drawings, Linda L. Hudson.)

matophores along mid-ventral line and beneath notochord; exceptionally large white chromatophores on body, cheeks, throat, yolk sac, and bases of pectoral fins. In preserved specimens of this size, body pigment more or less evenly distributed.⁴⁶

LARVAE

Specimens described, ca. 6.0¹⁶-6.5 mm.⁴⁵

At 6.0 mm body depth somewhat greater than in previous stage, head slightly depressed, otoliths still visible.¹⁶ At ca. 6.3 mm proportionately more slender than adults, caudal fin relatively longer.^{10,28} At 6.5 mm pectoral fins large, well-developed.⁴⁵

Pigmentation: At ca. 6.0 mm light yellow.¹⁶ At 6.5 mm a row of chromatophores developing mid-laterally, a well-developed row mid-dorsally, and a third ventrally over gut and along body to tail; chromatophores also developed along basal halves of caudal rays, on opercle, and on top of head.⁴⁵

JUVENILES

Minimum size described, 20.0 mm.

Specimens 20.0 mm long show "many of the diagnostic characters of the species."¹⁶

Pigmentation: "Small specimens" less dark than adults and with more silvery bands on flanks;⁴⁰ ca. 42 days after hatching, black markings develop in dorsal fin of male.⁴²

AGE AND SIZE AT MATURITY

At about 25 mm TL (corresponding with color differentiation of the sexes).³⁰

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Gambusia affinis

livebearers
Poeciliidae

FAMILY POECILIIDAE

The family Poeciliidae contains 21 genera and 138 species and was originally limited to tropical and subtropical waters of North, Central, and South America. Certain of its members have now been introduced, either accidentally or as potential mosquito control organisms, into other parts of the world. *Gambusia affinis*, the only regional member of the family, now occurs, for example, on all of the continents and a number of oceanic islands. Some species are remarkably ubiquitous, occurring in a wide variety of habitats including saltwater.

Poeciliid fishes may be characterized as follows: females are either viviparous or, rarely, ovoviviparous; males have a well-developed intromittent organ, the gonopodium, and produce spermatophores; fertilization is usually internal; the mouth is terminal and directed upward; the caudal fin is rounded; and there is a single dorsal fin which lacks spines. Sexual dimorphism is common within the group and may involve fins, mouth parts, ribs, and cranial structure, in addition to pigment.

In all poeciliids except the South American *Tomeurus*, spermatophores are introduced directly into the gonoduct of the female by the male gonopodium. In *Tomeurus*, spermatophores are applied externally to the area around the genital opening. Once introduced into the female gonoduct, the spermatophores immediately disintegrate, releasing individual sperm. Sperm can be stored for long periods of time and fertilize several successive batches of eggs.

Some of the species within this family, such as *Poecilia formosa*, are comprised entirely of females. In these, sperm is derived through matings with males of other species. In other species, two kinds of females occur: Those which produce only female offspring, and those which produce a normal ratio of male and female offspring. Hermaphroditism has been suggested in several species, but apparently has not been well documented.

In all members of the family except *Tomeurus* the eggs lack a chorion. Development occurs primarily in the ovaries, and ovulation (follicular rupture) does not take place until long after fertilization. Developing embryos are nourished both by yolk and, at least in part, directly by the female, and the extent of direct nourishment appears to vary from species to species. In *Tomeurus* the eggs have a chorion and well-developed long attachment filaments. Development begins internally, but the eggs are subsequently released and attached to plants and sand grains.

Young may be born with or without yolk, and, except in *Tomeurus*, development of the fins and scales is remarkably precocious.

Gambusia affinis (Baird and Girard), Mosquitofish**ADULTS**

D. 5¹⁵-10;¹¹⁷ A. 8-11;^{21,95} C. ca. 24;²² P. 12-14;^{115,117} V. 6;^{73,115} scales in lateral series 26⁹⁵⁻³⁴; 197 scales in transverse series 7-10;⁴⁰ scales from front of dorsal to front of anal 6-10;²² trunk vertebrae 13-14; caudal vertebrae 17-20;^{98,117} gill rakers 5 + 12.⁷³

Proportions expressed as times in TL: Depth 3.0³²-4.7,⁹⁵ head length 3.0²²-4.4.⁹⁵ Proportions expressed as times in SL: Depth, males 4.0-4.5, females 3.8-4.5; head length, males 3.7-4.0, females 3.3-4.0.¹²¹

Body plump,⁴⁰ rather robust, compressed,⁴⁴ with females deeper-bodied than males³¹ and relative depth of both sexes increasing with age;⁹⁹ head greatly depressed, broadened above;^{22,73} mouth small,¹³ terminal⁴⁴ or dor-

sal, with lower jaw projecting beyond upper.²² Teeth small, pointed, in a single villiform band in each jaw.^{22,95}

Dorsal fin origin well behind anal fin origin;^{26,40} anal fin of male modified into intromittent organ⁹⁵ and with rays 3, 4 and 5 greatly elongated.⁷³

Pigmentation: Light olive,^{40,93} olivaceous tan,²² dark greenish brown,²⁷ dark green, silvery,³¹ yellowish silvery, or yellow⁸⁷ above; grayish on sides; usually pale below,^{22,95} but sometimes violet or pearly,⁸⁷ or with vivid yellowish gold sheen on breast and belly.¹²⁰ Scales of upper body with dusky punctulations, often concentrated on scale margins.^{40,93,95} Sometimes with a thin, dark lateral streak,^{22,31,40,93} a black, bluish black, or purple triangular bar below eye,^{40,93,118} and/or a dark vertebral streak in front of dorsal fin.⁹⁵ Iris dusky brown, paler

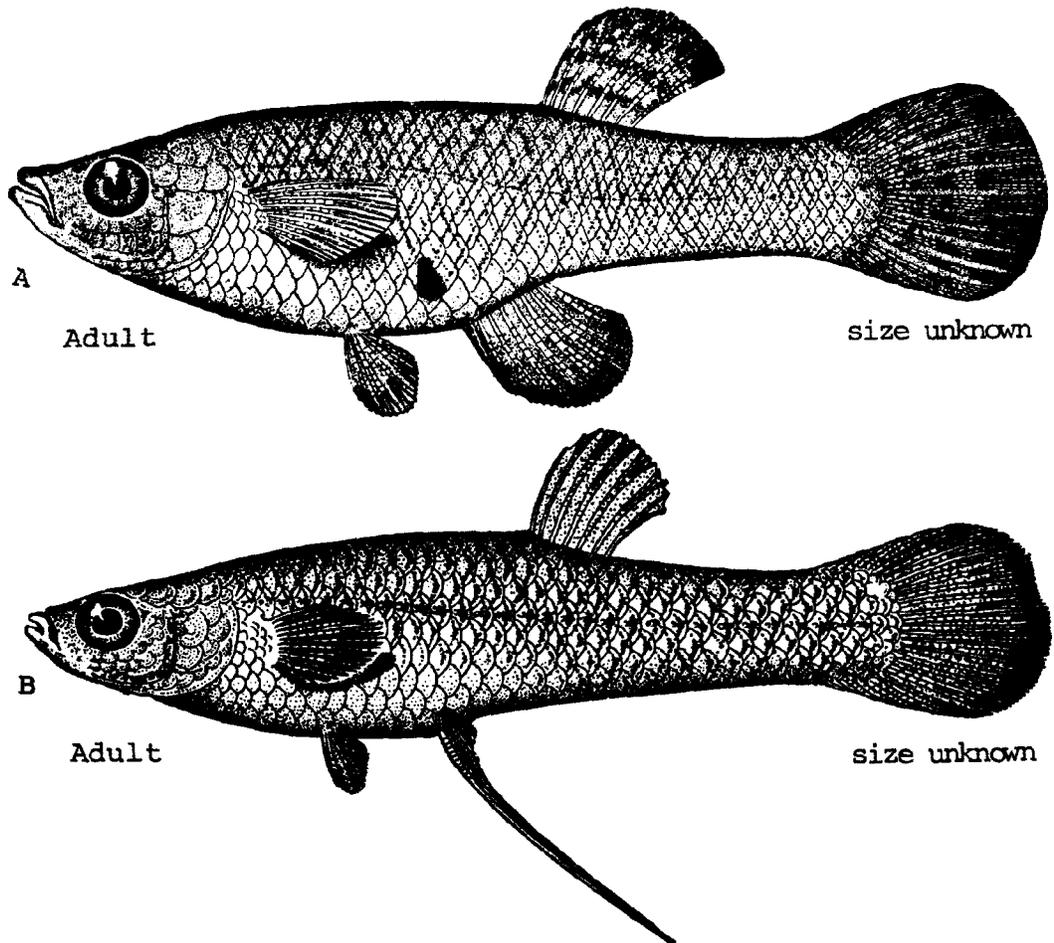


Fig. 125. *Gambusia affinis*, Mosquitofish. A. Adult female, size unknown. B. Adult male, size unknown. (A, B, Hildebrand, S. F., 1919a: figs. 1-2.)

below; pupil blackish. Dorsal fin pale translucent⁷³ or slightly greenish⁹⁵ and with 2–3 transverse rows of fine black dots; ^{31,40} pectoral and pelvic fins dusky.^{31,73} Females with gravid spot on body which becomes conspicuously black or purplish during reproductive period.^{10,68,72} Melanism occurs in both sexes, and individuals may be spotted with black or entirely black.^{43,87,120}

Maximum length: Females 80 mm,⁹⁶ males 52 mm.²³

DISTRIBUTION AND ECOLOGY

Range: Originally from southern New Jersey along Atlantic and Gulf coast to Rio Panuco basin, northern Veracruz State, Mexico; ¹³³ in the Mississippi drainage as far north as central Illinois ^{31,60} and southern Indiana.¹³³ Widely introduced in the United States,⁴¹ and now established in the Great Lakes region,³⁰ Rocky Mountain National Park,⁶² Utah,³⁵ and Nevada.²² Also established in Alberta and Manitoba provinces of Canada.^{51,56} Through world-wide introduction, *Gambusia affinis* probably now has a wider range than any other freshwater fish.⁶⁰ In North America it has been introduced from Alaska⁶⁰ to Mexico; ^{8,61,105} in Central America, in Panama; ⁸ in South America, in Ecuador; ⁶¹ in the West Indies, in Puerto Rico,^{1,2} Cuba,¹²² the Bahamas¹¹² and other islands; ³¹ in Europe, throughout most of western continental Europe,^{31,41,60,64,92} and the Mediterranean islands of Corsica,^{38,70} Rodhos (Rhodes), Sardinia, and Sicily; in the Near East in Turkey, Syria,⁶⁰ Israel, and Jordan; ^{5,31,34} in Africa along the Mediterranean, in the Sahara,^{49,60,65} and in South Africa; ^{31,88} in Asia as far west as Turkestan,⁶⁰ and as far north as China ^{4,31} and Japan; ^{31,122} Burma,⁶⁰ Thailand,^{4,31,41} Malaysia,⁶⁰ India and Sri Lanka (Ceylon); Australia; ⁶¹ New Zealand; ⁶⁰ in the Pacific, Hawaii,^{13,31} the Bonin Islands, Borneo, Caroline Islands, the Celebes, Guadalcanal, Cook Island, Fiji,⁶⁰ New Ireland, New Guinea, Samoa, Tahiti,⁶⁰ Formosa,¹²² the Philippines.^{13,31}

Area distribution: Coastal waters of New Jersey¹¹ and Delaware; ^{25,47,89} Chincoteague Bay; ¹¹⁶ Virginia; ¹²³ tributaries of Chesapeake Bay as far north as Annapolis.¹¹⁶

Habitat and movements: Adults—an essentially ubiquitous species (JDH) often congregating in large schools²² and found in brackish and fresh, running and still, clear and muddy, deep and shallow, acid and alkaline, and warm and cold water,^{6,13,31,73} and up to elevations of 427 m.¹⁵² In Chesapeake Bay region, recorded from restricted areas in brackish and freshwater arms and disconnected pools and marshes along the bay in quiet, more or less stagnant water.⁹⁵ Otherwise recorded from both open and shallow waters of rivers; ^{40,118} streams; ^{22,113} rocky brooks; ⁹⁴ creeks (in moderate current); ³⁷ ditches ^{27,58} (including semipermanent drainage ditches); ¹³¹ canals; ⁸² pools; ^{17,66} ponds; ^{46,122} tarns; ⁹² lakes; ^{20,22} oases; ⁶⁵ warm springs, sulphur springs, and the boil regions of large

springs; ^{22,62,118} bogs; ⁸² cypress, tupelo-oak, and mangrove swamps; ^{27,94,111} bayous; woodpools; flooded pine flatwoods; ^{14,59,118} lagoons; ⁸² coves; and backwaters ^{7,9} over muddy, sandy, or rocky bottoms ^{66,73} and sometimes associated with dense aquatic vegetation ^{17,20} such as red and green algae.⁸⁹ Also adapted to a wide variety of man-made habitats such as rice fields,⁷⁵ cisterns,⁶¹ water tanks,⁵⁴ septic tanks,^{31,61} cattle ponds, barrels⁵⁴ and wells,^{53,67,74,80} Recorded from extremely polluted water,^{17,52} anerobic water (at O₂ concentrations of 0–1 ppm),¹¹⁸ and sulphurous water;⁶⁹ capable of remaining out of water in wet grass for up to 3 1/2 hours.⁹¹ Apparently move offshore at night.¹²⁴ Sometimes found in water up to 3.6 m deep.¹¹⁸ Gravid females nearshore over light-colored sand, nongravid females 0.3–1.0 m from shore over dark mud bottom.¹²⁴

During drought conditions may concentrate in pot-holes.¹¹¹ Feed at surface⁵⁰ and frequently congregate in sunny spots at waters edge during day.⁵⁵ The species easily invades new areas, and has been observed swimming on roads in both small rivulets and thin sheets of rainwater.¹¹⁸ At 10 C hibernate by digging into mud; ^{82,91} hibernation has also been recorded at bottom of ice-covered ponds.⁴¹ Maximum recorded salinity 29 ppt,¹³⁰ although also reported in “pure sea water.”¹¹³ In one series of observations, mean salinity 3.4 ppt.¹²⁹ The species is extremely temperature tolerant, adapting to temperatures of 0.0³⁵–38.9 C¹⁹ (10 C, however, is considered critical minimum).⁸⁰ Salt marsh specimens are apparently more heat resistant than freshwater specimens.^{10,22}

Larvae—begin to swim immediately after birth,^{10,72} and may seek refuge in very shallow, warm water.⁴⁰ “Fry” (including newborn) in schools.⁹⁶ From birth to about one week remain where born, during night settle to bottom and remain till sunrise; typically over sand bottom.¹²⁴

Juveniles—“fry” in schools; ⁹⁶ have “very high” thermal tolerance (presumably of adaptive significance).⁴⁰ At 2–3 weeks move into deeper water at night and return to shallow water by day; at about 4 weeks begin moving with adults.¹²⁴

SPAWNING

Location: Apparently ubiquitous within both the normal and artificial (man-made) environment (JDH). Specifically noted in streams in Japan.¹²²

Season: Length of reproductive activity varies with latitude and to some extent weather conditions; ⁵⁴ in Long Island, early May to sometime in October,¹²⁴ in Chesapeake Bay region May to September; ^{46,110,116} in North Carolina, April to late October; ¹¹³ in Georgia, May 1 to late October; ^{50,54,63} in Florida, throughout the year, but

with longer periods between broods in winter,^{17,54,63,131} and apparently with peak activity from March to October in some areas; ¹¹⁸ in Louisiana, March 15 to October 1 or slightly later; ⁵⁹ in Mississippi, gravid females in "practically all months"; ¹³⁰ in Texas, peak activity in April; ^{72,81} in Oklahoma, March to late September and again in November; ²⁴ in Montana, March through October; ¹³² at Winnipeg, Canada, gravid females as late as October; ⁵¹ in Russia, late May and early June; ⁸² in Portugal, reproductive activity as early as January, breeding April to September; ^{57,76,108} in Italy, all months except October; ¹⁰⁷ in Egypt, April to September; ⁴⁹ in India, throughout year, but with peak activity in October and November; ^{23,66,84} in Japan, March to October, with peak activity from May to September.¹²² Under laboratory conditions young have been produced from early December to late June and in November and January; ^{13,71} in laboratory specimens from Maryland, January to June.¹²⁹ Length of reproductive period varies with individual fish: in Illinois 8–10 month old females are reproductively active for 10–15 weeks; those which begin reproducing during summer of birth are active for 4–10 weeks.⁶⁰

Brood frequency: 2 ^{10,45} to 8 broods ¹⁰² per reproductive season. Interval between broods varies from 19 ¹⁰⁷ to 85 days, although, following the birth of young, the next batch of eggs may be ready for fertilization within 10 days.³⁹ Average times between broods have been recorded as 20.5 ¹⁰⁷ and 35 days.¹²⁷

Reproductive temperature: Ca. 15.5 C ^{72–30} C.¹²² A critical temperature of ca. 15.5 C has been established ⁷² although in other experiments a temperature of 20 C was needed to induce breeding ³⁶ and breeding ceased if the temperature dropped below 18 C.⁶⁴

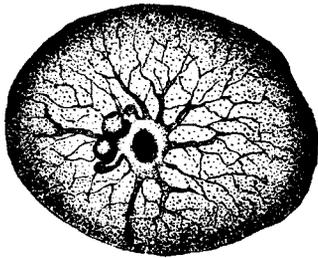


Fig. 126. *Gambusia affinis*, Mosquitofish. A. An ovarian follicle containing an embryo and showing the follicular pore. Two immature eggs are attached near the pore. (A. Ryder, J. A., 1885a: fig. 11.)

Fecundity: Apparently highly variable. Number of young from a single brood varies from 1 to 315,^{22,132} although only 345–428 young may be produced by one female in a single season which may include up to 5 broods.^{54,82} Published average brood sizes: 11.3,¹¹⁸ 24,¹⁰

33 (in 50–60 mm fish),¹¹⁴ ca. 40,⁵⁴ 41.5, 43,¹⁰⁷ ca. 50,^{63,124} and 100.¹⁰ Six investigators give total fecundities of less than 50; ^{3,13,119,36,40,85} nine give totals between 50 and 100; ^{50,59,64,84,86,87,113,114,118} one gives up to 200; ⁶³ two give figures in excess of 200; ^{59,105} and two give figures higher than 300.^{22,44} Ovarian egg counts (as opposed to counts of ripe eggs or embryos) vary from 20 ^{110–240}.²³ Fecundity apparently increases with increasing size of female.^{50,59,60} Broods become smaller as season progresses,⁴⁵ although the 4th brood for an individual female is usually the largest; ¹⁰⁷ one author found that broods varied from 84–135 in June with a mean of 100, to 18–30 in August with a mean of 24.¹⁰

EGGS

Location: Developed entirely within the ovaries; each ovum enclosed in a Graefian follicle, ovisac, or ovarian capsule, surrounded by fluid, and having independent blood supply.^{3,12,116}

Immature ovarian eggs—diameter 0.3–0.7 mm at time that earlier embryos are ready to be born; still immature at 1.7 mm diameter; ^{39,110} egg membrane absent; ^{3,12,116} micropyle apparently replaced by "follicular pore."¹¹⁰

Ripe ovarian eggs (although description probably contains some information based on fertilized eggs)—diameter 1.6 ^{59–2.1} or, possibly, ca. 3.0 mm; ⁴² golden yellow ¹¹⁴ and transparent ⁴² or with orange, opaque yolk: a thin vitelline membrane; ¹¹⁴ each egg attached to central nucleus of ovary by thread or membrane; ⁴² entire surface of egg with many small refringent oil globules of various sizes.^{3,110,114}

Fertilized eggs—at segmentation diameter 1.6–1.9 mm. at late embryo stages diameter 1.5–2.4 mm.¹⁰³

EGG DEVELOPMENT

Development at unspecified temperature (the Medlan series): ⁷²

3.0 mm embryo—buccal cavity wide; esophagus curved to right side; intestine with single coil; swim bladder, liver, spleen, and pancreas formed; heart pulsating; sinus venosus, auricle, and ventricle established; mesonephric kidneys formed; Wolffian ducts open directly to outside posterior to anal opening; gonads visible as paired structures on each side.

4.0 mm embryo—essentially like 3.0 mm embryo, except that sexes can now be differentiated.

5.0 mm embryo—esophagus constricted, liver markedly increased in size.

6.0 mm embryo—yolk mass noticeably decreased; lateral body wall extends over yolk; snout protrudes through respiratory portal system; chromatophores scattered on upper surface of embryo and concentrated on

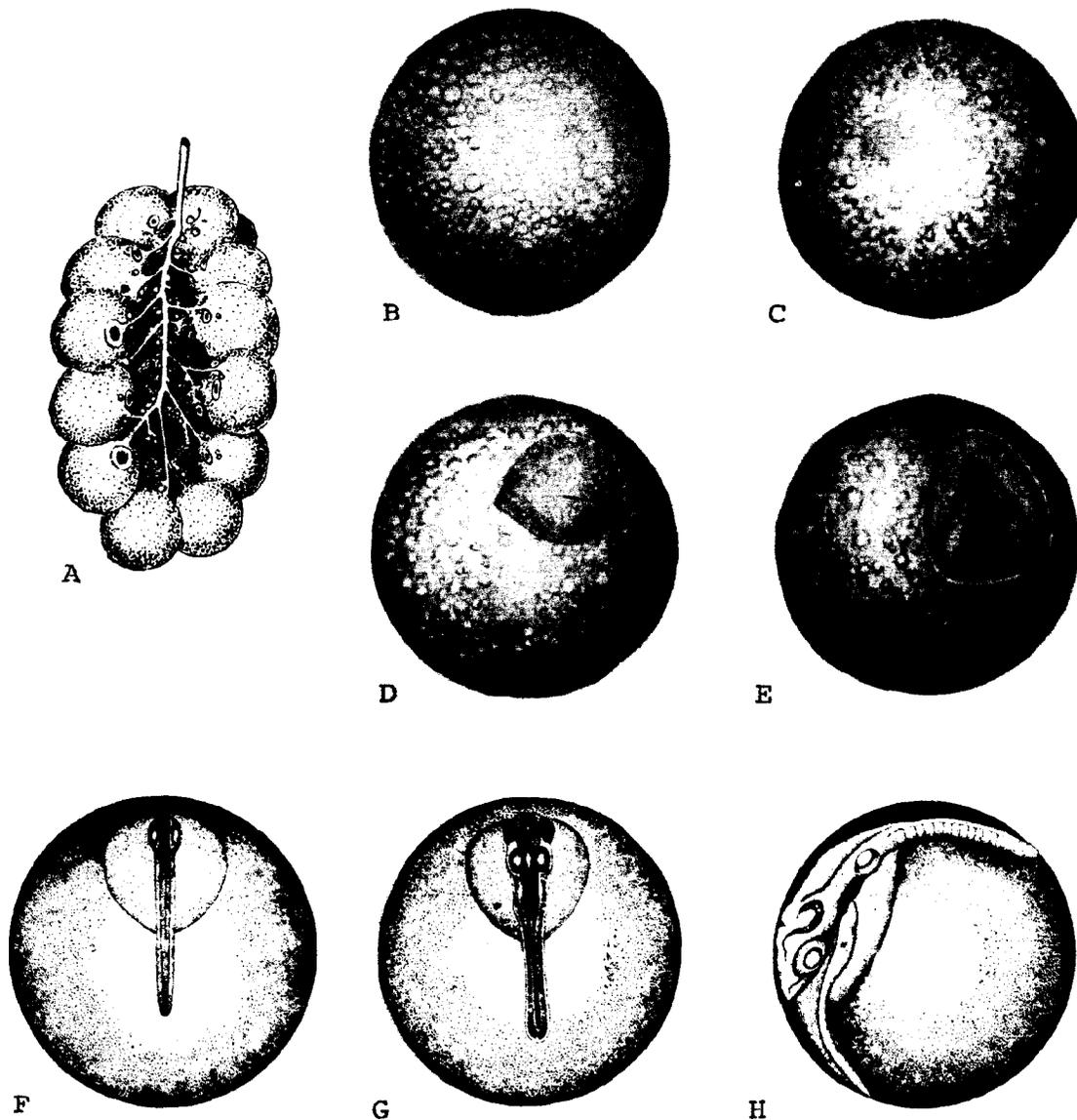


Fig. 127. *Gambusia affinis*, Mosquitofish. A. Ovary, showing attachment of ripe ova to median vesicle. B. Mature ova, ca. 1.8 mm in diameter. C. Early blastoderm. D. Blastoderm spreading over yolk, blastocoel formed. E. Embryonic shield. F. 3-4 somite stage, optic vesicles well formed. G. 12-14 somite stage, brain divisions developing, auditory vesicles evident. H. Advanced embryo with ca. 12 somites, lateral view. (A, Ryder, J. A., 1885a: fig. 10. B-H, Kuntz, A., 1914: figs. 1-7.)

dorsal surface immediately behind eyes; eyes pigmented.

7.0 mm embryo—operculum well-developed, simulating respiratory movements; mucosa of esophagus cuboidal in appearance due to presence of numerous globular cells which may be related to hatching enzyme; gas bladder somewhat flattened dorsoventrally; lateral body wall almost encloses remaining yolk sac; chromatophores concentrated near mid-dorsal line, gradually

becoming less numerous on sides.

Just before hatching—pneumatic duct open.⁷²

Development at unspecified temperature (the Self series):⁹⁰

At time of incipient embryonic axis—embryo consists of large, flat embryonic shield covering only small part of yolk, thickened on its posterior margin, exceedingly flat anteriorly, and with longitudinal axis of animal

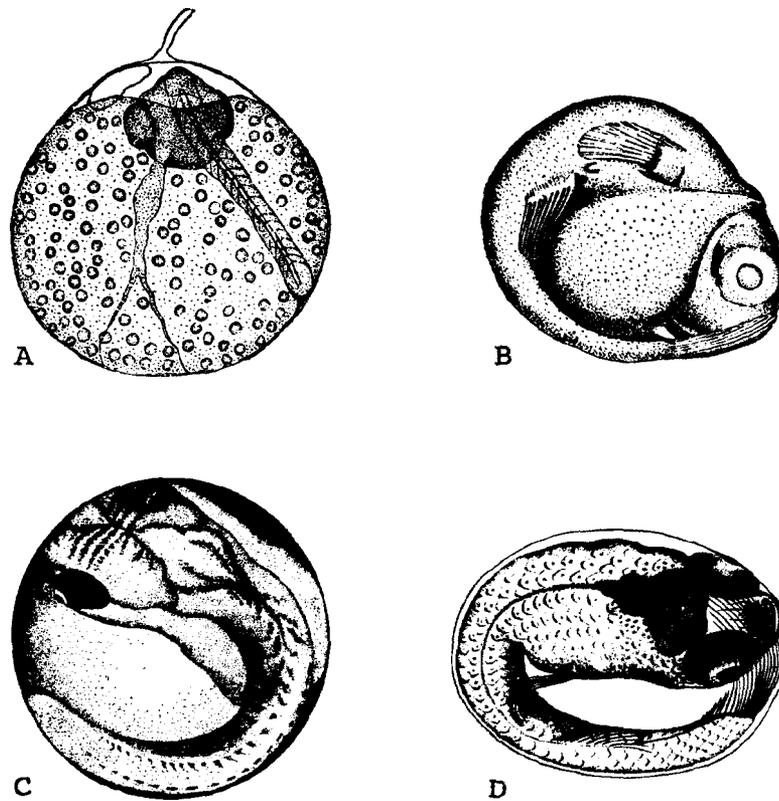


Fig. 128. *Gambusia affinis*, Mosquitofish. A. An embryo within a follicle showing mode of attachment of egg. B. Embryo showing upward prolongation of yolk over body. Note well-developed anal fin, lack of dorsal fin. C. Advanced embryo, showing pigmentation in eye and on body. D. Advanced embryo, scales and dorsal fin forming. (A, B, Ryder, J. A., 1885a: figs. 4, 13. C, D, Kuntz, A., 1914: figs. 8-9.)

indicated by marked median thickening.

0.31 mm embryo—shield decreased in size, embryonic axis markedly increased in length, anlagen of neural tube established.

3-somite stage—embryo and extra-embryonic region more narrow and more elongate.

7-somite stage—continued lengthening and thickening of notochord, eye primordia evident.

11-somite stage—eye vesicle completely separated from forebrain; optic cup, lens forming; optic lobes enlarging; auditory vesicles present; cells of notochord with large vacuoles.

30-somite stage—pectoral buds well formed; foregut, pharynx, esophagus, stomach, liver, intestine, blood formed or forming.⁹⁰

Development at unspecified temperature (the Ryder series):¹¹⁰

Earliest stages described (size not stated)—body in groove in yolk; tail “about to bud out”; somites well-developed; heart, brain, intestine, and sense organs established.

About 4.3 mm stage—mouth not completely open; air bladder evident; liver large, located on left side; intestine more or less straight; otoliths present; lateral line organs developed; incipient anal, dorsal, and pectoral fins evident; rays developing in caudal fin; eye and top of head pigmented.

About 6.3 mm stage—a conspicuous prolongation of tissue upward from yolk sac toward opercle (author states that in some specimens yolk extends up and over body eventually forming a collar of yolk); incipient pelvic fins present, rays formed or forming in all other fins.

About 7.1 mm stage—five branchial arches formed, the posterior of which supports clusters of teeth; venous end of heart still directed downward; chondocranium with incomplete roof; vertebrae differentiated, more so anteriorly than posteriorly; ribs developed in cartilage; scales forming.¹¹⁰

Development at unspecified temperature (the Kuntz series):¹¹⁴

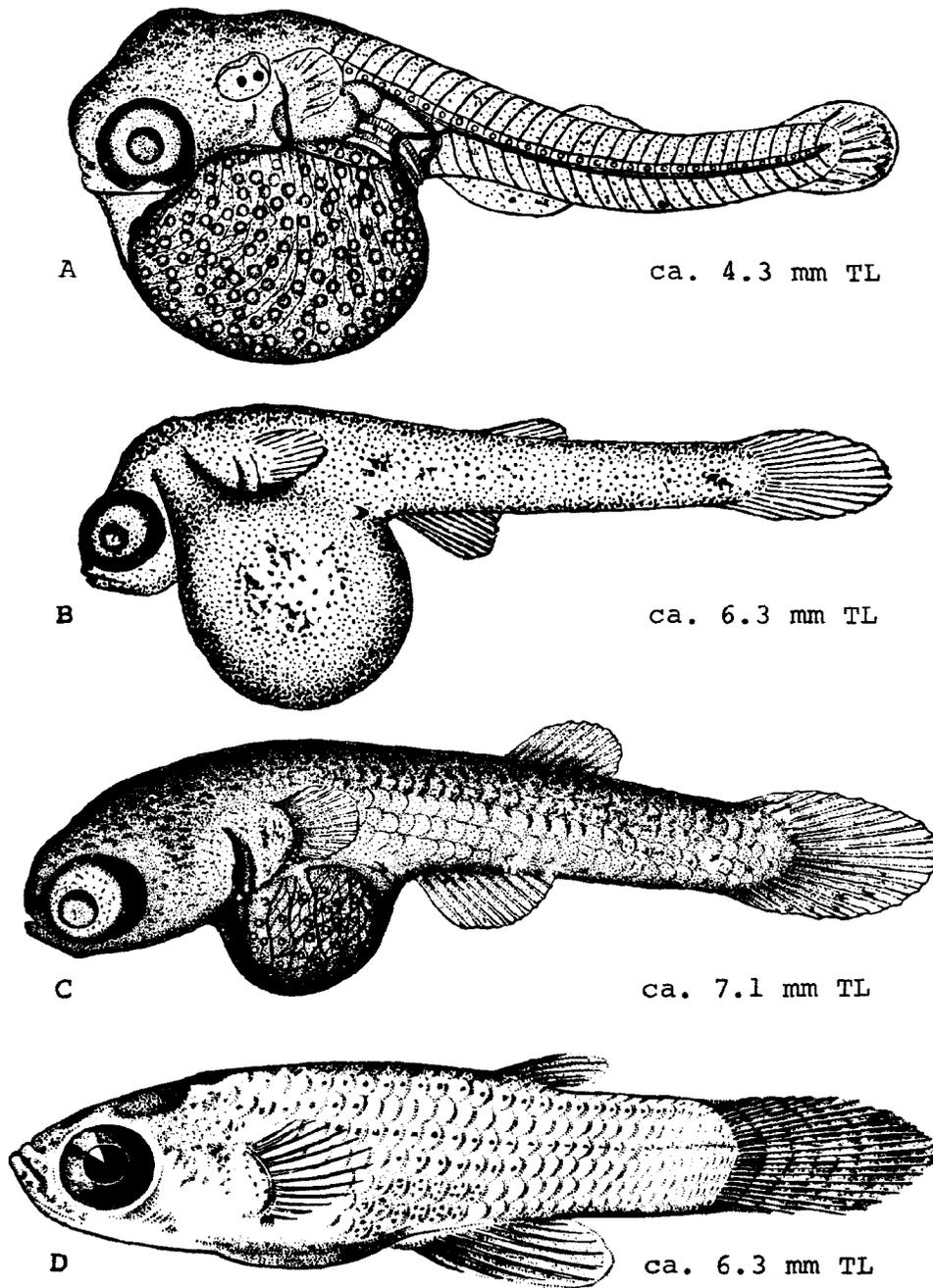


Fig. 129. *Gambusia affinis*, Mosquitofish. A. Embryo, ca. 4.3 mm TL, otoliths formed. Note lack of continuous finfold. B. Embryo, ca. 6.3 mm TL, yolk extended upward in region of head, dorsal and anal fins formed. A small projection at the posterior upper margin of the yolk sac may represent incipient ventral fins. C. Embryo, ca. 7.1 mm TL, scales forming, ventral buds definitely identified. D. Embryo, ca. 6.3 mm TL, but more advanced than previous stage, yolk nearly absorbed, pigmentation in definite linear pattern, mouth and head well-developed. (A-B, C, Ryder, J. A., 1885a: figs. 1-3. D, Kuntz, A., 1914: fig. 10.)

Early stages—multicellular blastoderm developed as small almost circular cap slightly elevated above surface of yolk; as blastoderm increases cleavage cavity becomes visible; germ ring never well defined, developed as thickening at edge of blastoderm; cleavage cavity becomes somewhat triangular; blastoderm elongates somewhat prior to formation of embryonic shield.

3-4 somite stage—anlage of neural axis apparent throughout, optic vesicles well formed; tail bud evident.

12-14 somite stage—auditory vesicles present, heart differentiated as single curved tube.

Pigmentation (all stages)—scattered chromatophores first appear on dorsal surface, and are more closely aggregated on posterior region of head and along mid-dorsal line of body; chromatophores more numerous and more closely aggregated until, at birth, pigmentation is nearly complete.¹¹⁴

Development of anal fin at unspecified temperature (the Turner series):⁷⁹

10 days after fertilization—9th anal ray divided, all other rays single.

16 days after fertilization (length 5.8 mm)—rays 3, 4 and 5 slightly longer than other rays (the largest ca. 0.8 mm long) and segmented.

Just before birth (length ca. 6.0 mm)—longest rays 1.0 mm, all rays but first segmented, segmentation formula for 10 anal rays 1,3,5,6,6,6,6,5,3,2.⁷⁹

Development of axial skeleton at unspecified temperature (the Kamel series):⁴⁷

2.0 mm stage—notochord a rounded, continuous rod mainly composed of vacuolated cells.

4.0 mm stage—vertebral centra formed, distinct up to 24th vertebra; indications of vertebral and intervertebral portions of notochord evident.

6.0-7.0 mm stage—vertebral column definitely differentiated into vertebral and intervertebral parts.⁴⁷

Miscellaneous comments on development:

Eyes may be evident in embryos as small as 1.0 mm.¹¹⁸

Primary germ cells first develop in the mesoendodermal layer in the early gastrula; ¹²⁶ definitive sex cells have been observed beneath the gas bladder in embryos 1.58-2.05 mm long.⁹⁷

Pseudobranchiae are evident in embryos of 5.0 mm.¹⁰⁹

Just before birth yolk greatly reduced; bones of skull cartilaginous³ (although in unborn embryos 9.0 mm long the chondrocranium is "fully formed"¹⁰⁰); intermaxillary elements with teeth; branchiostegals developed in cartilage; opercles completely formed and covering gills; neural and haemal arches developed in cartilage; scales developing in dermal pockets on sides and back; all fin rays developed except pelvics; yolk nearly absorbed; ³ eyes movable.⁴²

Gestation period: 21-28 days, average 23.9 days.^{31,60} Young are usually expelled head first¹³ or as tightly rolled balls 2.0-3.0 mm in diameter if without yolk,¹¹⁴ and in lots of 1-5 over a period of 1 1/2 to 3 hours.¹⁰

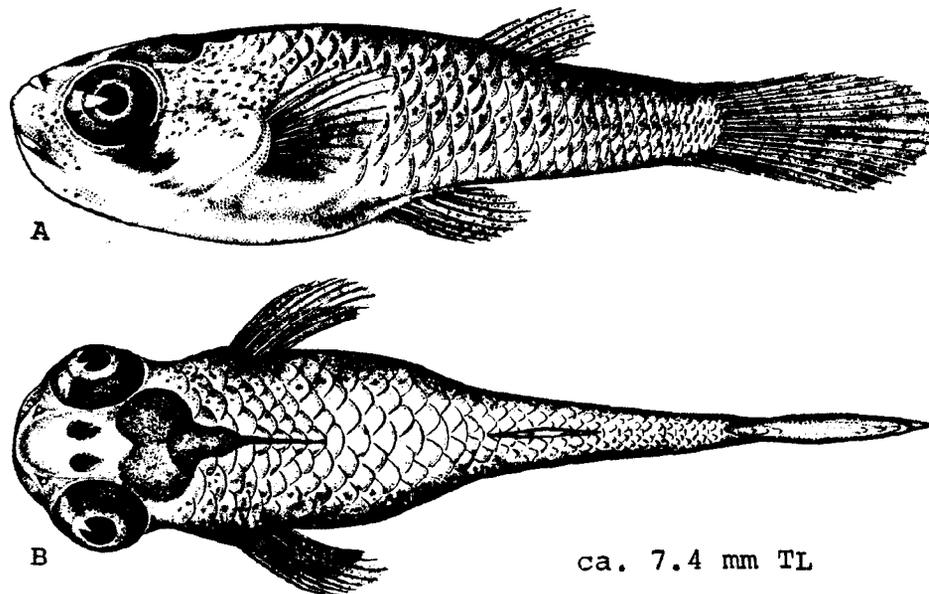


Fig. 130. *Gambusia affinis*, Mosquitofish. A, B. Larva, ca. 7.4 mm TL, lateral and dorsal views. (A, B, Kuntz, A., 1914: figs. 11-12.)

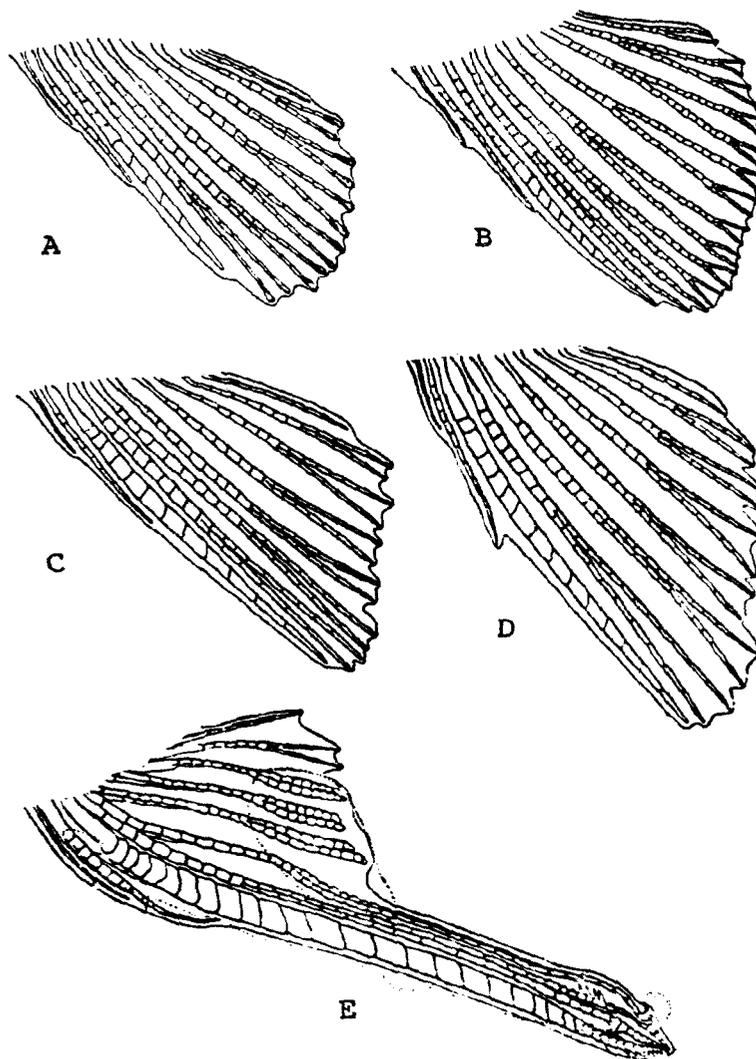


Fig. 131. *Gambusia affinis*, Mosquitofish. Development of the anal fin and gonopodium. A. Female, 15 mm TL. B. Female, 30 mm TL. C. Male, 12-segment stage. D. Male, 15-segment stage. E. Male, mature gonopodium. (A-E, Turner, C. L., 1941b: figs. 7-11.)

although one author states that 10-300 young are expelled "at one time."⁴⁴

YOLK-SAC LARVAE

Length apparently just after birth, 5.1-6.2, \bar{x} 5.5 mm.¹⁰³
Length at birth 7.0^{43,72}-ca. 12.7 mm.⁴² At least some specimens ca. 7.4 mm or longer are born without yolk,¹¹⁴ while others up to at least 8.0 mm retain yolk.²³

Trunk vertebra 11, caudal vertebrae 21 at birth (there is a subsequent shift of trunk features into anterior part of original tail region).¹⁶

Body initially curved, but straightened after birth;⁴² yolk mass visible at birth, but completely enclosed by

lateral body wall;^{72,99} teeth functional at birth;⁹⁶ during "early development" testes separated except at posterior ends;¹¹⁹ posterior part of gas bladder thin-walled and expanded, pneumatic duct a solid ligament at birth.⁷²

Anal fin of male and female (stage uncertain) with 10 rays and identical.²³

Pigmentation: Sometimes transparent and with black eyes,²³ and sometimes well pigmented.⁴²

LARVAE

Size range described: 7.4¹¹⁴-15.0 mm.⁷⁷

In specimens born without yolk the adult number of

lateral line and transverse scales is established. At ca. 7.4 mm dorsal, anal, caudal, and pectoral fins are free and fully rayed.¹¹⁴ At ca. 8.0 mm anal fin of female shows beginning of ankylosis of certain basal segments of all rays (this feature can be used to distinguish sexes in specimens of this size).⁷⁸ At 8.2 mm (11 days after birth) anal fin presents the following segmentation formula: 2,4,5,8,8,8,8,6,4,2.⁷⁹ At 13.0–15.0 mm pectoral fins of both sexes with 13 bony rays, each segmented except for basal third.⁷⁷

Pigmentation: Often uniformly yellowish, with dusky fins and cross series of dots in caudal fin.³¹ At ca. 7.4 mm a prominent blotch of pigment, elongated posteriorly, on back of head; chromatophores on head and upper sides, and in discrete row in mid-lateral region; also on membrane of some fins. At 9.0–10.0 mm light olive, darker above than below; a fine line along side; 2–3 transverse rows of dark spots on dorsal; dark margin on anal fin; 3–4 rows of dark spots (characteristic of female) differentiating on caudal fin.¹¹⁴

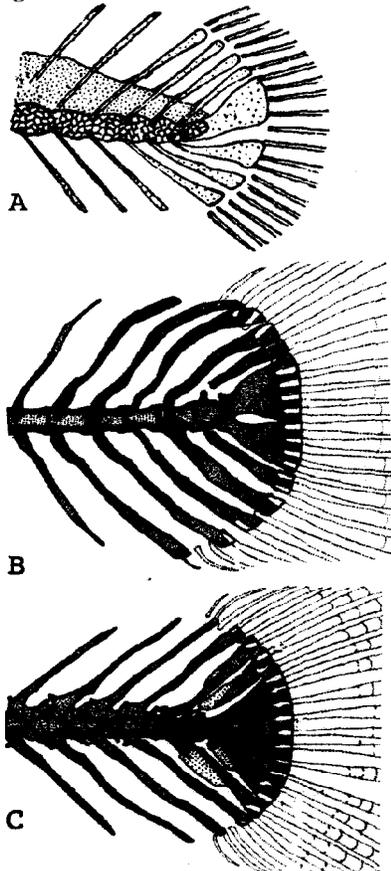


Fig. 132. *Cambusia affinis*, Mosquitofish. Development of caudal skeleton. A. Tail of advanced embryo showing hyaline notochord. B. Embryo, 5.0 mm TL. C. Adult female, 23 mm TL. (A, Ryder, J. A., 1885a: fig. 18. B, C, Hollister, G., 1940: figs. 12–13.)

JUVENILES

Minimum size described 13.0 mm.¹¹³

Anal fin tends to be more pointed in immature males than immature females.⁷⁴ Anal fin of male begins to differentiate in contour from that of female at sizes varying from 13.0–17.0 mm;¹¹³ up to 10-segment stage (counting segments in 3rd ray) contour of fin is same in both sexes; at 9-segment stage rays 4 to 9 divide at ends and new terminal segments are added to the branches, ankylosis of joints of the rays begins basally and proceeds apically (in the male this process ends after eradication of a single intersegmental space, in the female it continues throughout life); at 9- to 10-segment stage 3–5 intersegmental spaces disappear or persist only faintly in female so that basal solid segment is longer than that in male.⁷⁹

Sexual differentiation evident at 14 mm, complete by 21st day.¹²⁴ At 2–3 months testes fused more or less completely along median line.¹¹⁹

Pigmentation: No information.

AGE AND SIZE AT MATURITY

Age at maturity, 28 days³¹ to second summer of life;⁶⁰ size at maturity, for males 18.0²⁹–28 mm⁷⁷ (possibly as small as 13.0 mm⁴³), females 22^{101,132}–34.0 mm.¹³

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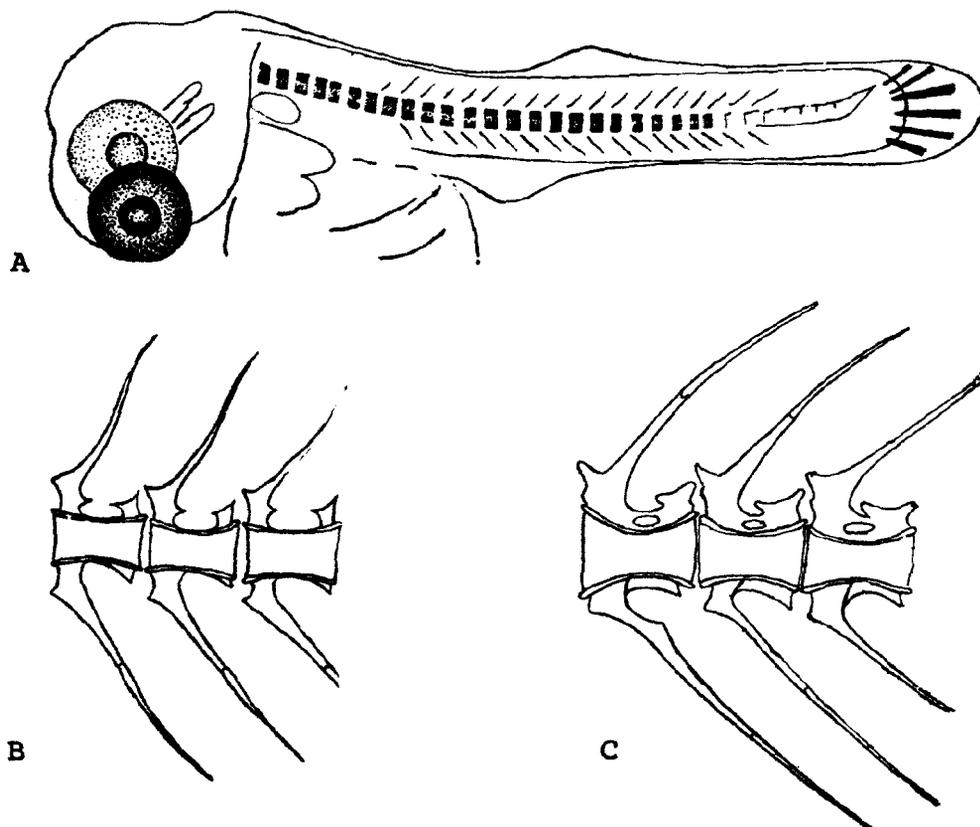


Fig. 133. *Gambusia affinis*, Mosquitofish. A. Embryo, 4.0 mm TL, stained with alizarine to show arising chordal centra. Note low continuous finfold. B. Caudal vertebrae in a 14.0 mm TL specimen. C. Caudal vertebrae in a 20.0 mm TL specimen. (A-C, Kamel, A., 1954: figs. 3, 11, 12.)

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Enchelyopus cimbrius
Gadus morhua
Melanogrammus aeglefinus
Microgadus tomcod
Phycis chesteri
Pollachius virens
Urophycis chuss
Urophycis earlii
Urophycis regius
Urophycis tenuis

codfishes
Gadidae

FAMILY GADIDAE

Gadid fishes occur in arctic, boreal, and subtropical waters of the northern hemisphere and, sometimes, in cool waters of the southern hemisphere. The family, as herein defined, contains 21 genera and approximately 55 species.

Although primarily found in oceanic waters where they have been recorded at depths greater than 1000 meters, one species, *Lota lota*, is restricted almost entirely to freshwater. Others, such as *Microgadus tomcod* and *Gadus morhua*, sometimes enter fresh or estuarine waters.

Gadid fishes are distinguished by the following characteristics: the head of the vomer is toothed, the gas bladder is not connected to the auditory capsules, the teeth in the jaws are small and in wide bands, the scales are cycloid, and the first vertebra is attached to the skull. In the subfamily Gadinae there are three dorsal fins and two anal fins. The caudal fin is truncate or slightly forked and barbels are usually present on the chin. In the Lotinae there are one or two dorsal fins and one anal fin. The caudal fin is round and chin barbels are always present.

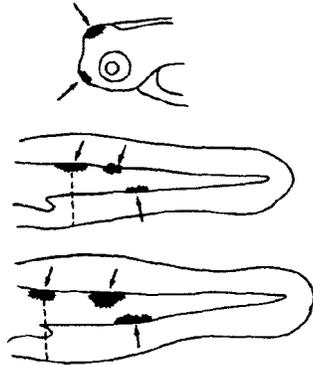
Little is known of the spawning of these fishes. Males of the Atlantic codfish defend territories on the bottom, but go through a distinctive courtship pattern which terminates with spawning at or just below the surface. In the haddock, in which spawning occurs while the male and female are swimming upward, sound production may be an important aspect of courtship behavior.

Eggs of gadid fishes are typically small, and may be either adhesive or non-adhesive, even within the same species (as in *Microgadus tomcod*, for example). A number of species, such as members of the genera *Enchelyopus*, *Phycis*, *Urophycis*, *Brosme*, *Molva*, and *Raniceps*, produce eggs having one to many oil globules. In the eggs of *Microgadus tomcod* there may be a number of very minute oil globules. Oil globules are entirely lacking in other gadid fishes such as *Gadus morhua*, *Melanogrammus aeglefinus*, and *Pollachius virens*. A few members of the family (*Microgadus* and *Lota*) produce demersal eggs, but most species have either pelagic or buoyant eggs. Pertinent data on eggs of the gadoid fishes of the Mid-Atlantic Bight are presented in table 5.

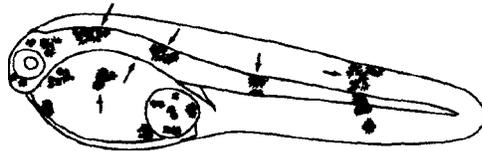
Larvae of gadid fishes may be characterized as follows: the anus is one-third to two-fifths the distance to the tip of the tail; as development proceeds, the gut becomes distinctly coiled; the anal opening is at the side, not the edge of the finfold; and pigment is developed at the time of hatching or very shortly thereafter. Among the regional gadid fishes the pelvic fins develop precociously in *Enchelyopus cimbrius*, *Urophycis chuss*, and *Urophycis regius* and probably also in *Phycis chesteri*, *Urophycis earlli*, and *Urophycis tenuis*. Gadid larvae are generally pelagic, and those of a number of species characteristically become associated with jellyfishes. In some gadid species there is a distinct prejuvenile stage characterized by remarkable changes in pigmentation associated with a descent from surface to bottom waters. The prejuveniles of some genera (*Gaidropsarus*, for example) are so different from the adults that they were originally thought to belong in different genera.

Characteristics useful in identifying yolk-sac larvae and larvae of the regional gadoid fishes are presented in the following key and in tables 5 and 6 and figure 135.

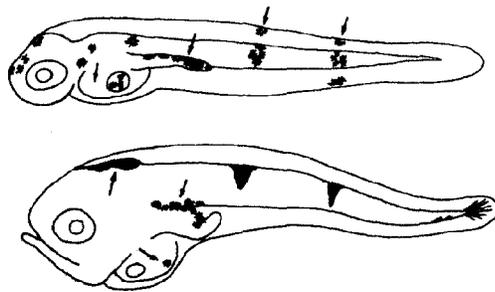
- 5B. Pigment blotches on head widely separated, one on crown and one at tip of snout; usually 2 (rarely 1) dorsal pigment spots posteriorly, 1 on tail and 1 just above or slightly posterior to anus, and 1 ventral pigment spot on tail; length 1.57–2.05 mm *Urophycis regius*



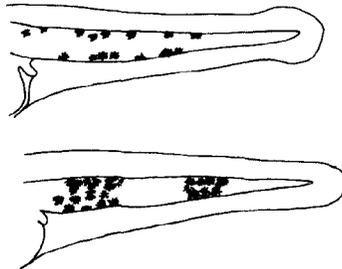
- 6A. No pigment above posterior part of gut; yolk pigmented; 2 well-developed broad bands of pigment dorsally between head and anus and 2 on tail, the posteriormost extended into the dorsal and ventral finfolds; length 3.05–3.75 mm *Merluccius albidus*



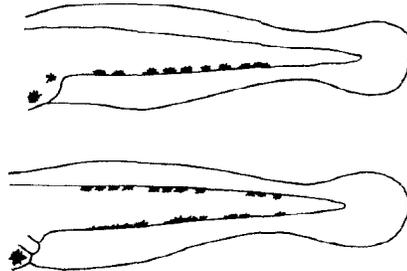
- 6B. Pigment above posterior part of gut; yolk not pigmented, or slightly so by end of stage; in early stages few pigment spots on body beyond head, these not developed into definite bands; in later stages a single pigment band dorsally on posterior part of head; 2 broad pigment blotches on tail; in early stages both caudal blotches extended into dorsal finfold, the posteriormost also into ventral finfold; length 2.64–4.42 mm *Merluccius bilinearis*



- 7A. Preanal myomeres 22 or less 8
 7B. Preanal myomeres 23-25; no pigment on yolk and little or no pigment on gut; pigment on tail initially scattered, ultimately in two bars; no pigment near tip of tail; length 3.2-5.3 mm *Pollachius virens*



- 8A. Pigment present dorsally between back of head and anus, absent on yolk 9
 8B. Pigment absent dorsally between back of head and anus, usually present on yolk; pigment in long, continuous or broken bar ventrally on tail, present or absent dorsally; preanal myomeres ca. 14-18; length 4.12-6.45 mm *Microgadus tomcod*



- 9A. Two dorsal and three ventral pigment bands on tail; the posteriormost ventral pigment band near tip of tail; length 3.0-5.19 mm *Gadus morhua*



- 9B. Dorsal surface of tail lacking pigment, ventral surface with continuous row of closely-spaced melanophores; length 2.0–5.5 mm . . . *Melanogrammus aeglefinus*

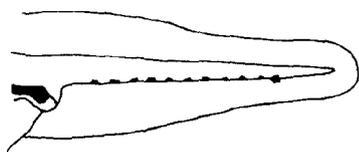


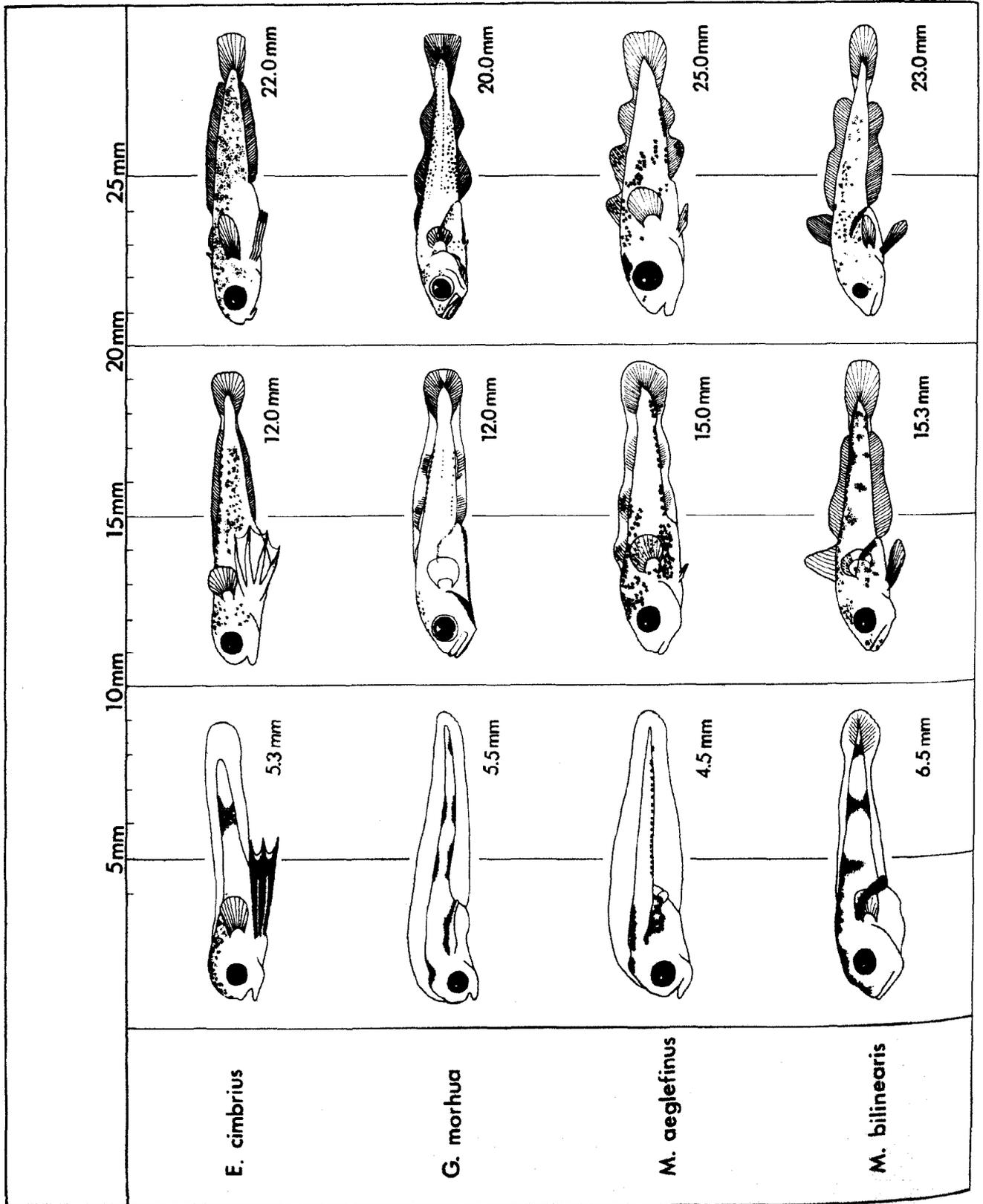
TABLE 5. Eggs of gadoid fishes of the Mid-Atlantic Bight

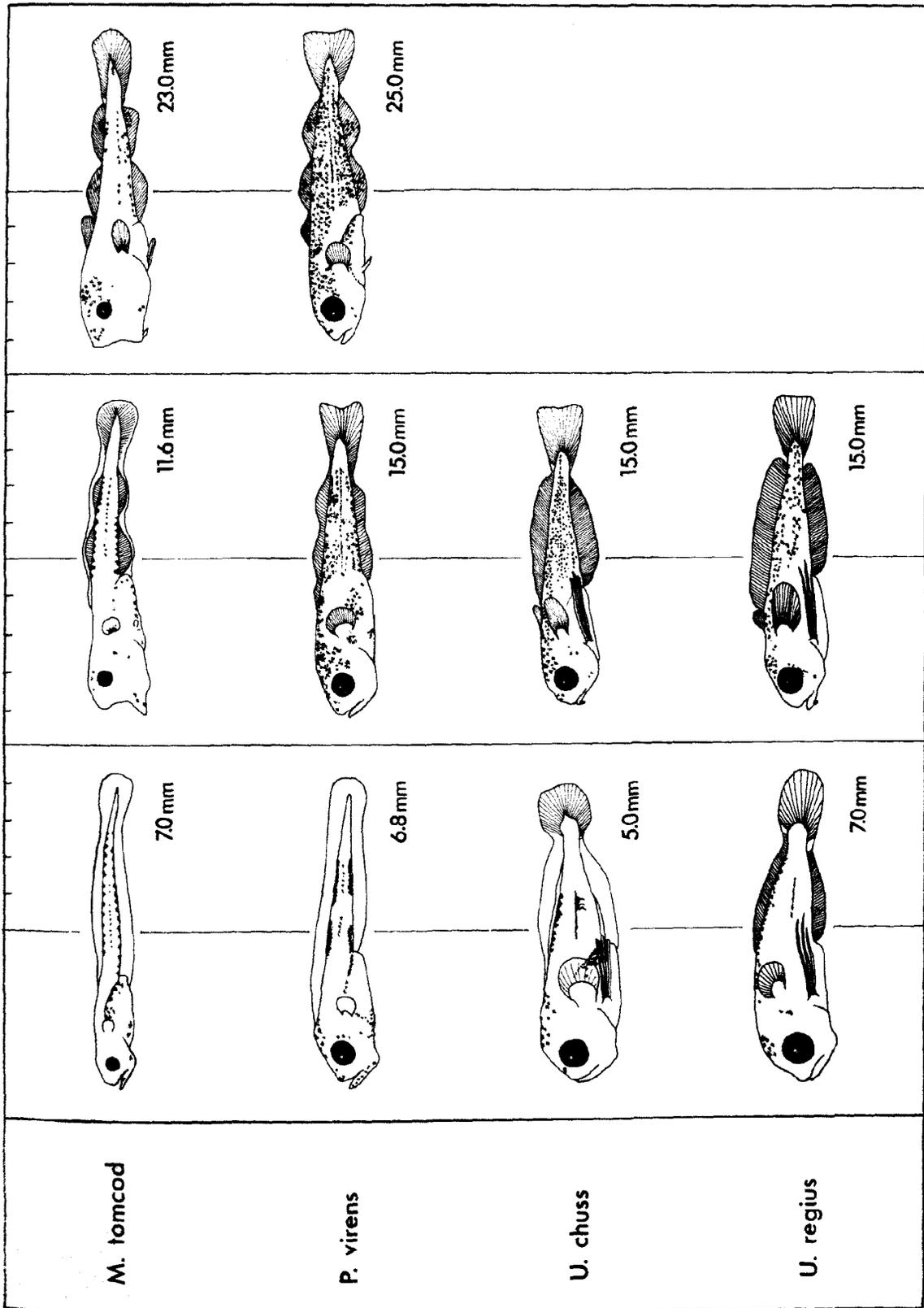
	Diameter	Oil globule(s)	Color	Ecology	Season
<i>E. cimbricus</i>	0.65–1.25	present, initially many, later coalesced	greenish, yellowish, reddish, blackish, cream, or colorless	pelagic	mid-Feb. to Sept. or Oct. (N. Amer.)
<i>G. morhua</i>	1.0–1.89	absent	cream, green, yellowish red, deep red, or clear	pelagic	year round (N. Amer.)
<i>M. aeglefinus</i>	1.1–1.72	absent	clear	pelagic	Jan. to July (N. Amer.)
<i>M. bilinearis</i>	0.70–1.11	present, single	clear	pelagic	April to Oct.
<i>M. tomcod</i>	1.39–1.7	present or absent, when present several extremely small	clear, yellowish	demersal	Nov. through Feb.
<i>P. virens</i>	1.0–1.22	absent	clear, transparent	pelagic	late Sept. to early March
<i>U. chuss</i>	0.63–0.97	present, initially up to 54, later coalesce to 2 or 3	clear	pelagic	May (or possibly April) to late Sept.
<i>U. regius</i>	0.67–0.81	present, one large and cluster of small	clear	pelagic	Sept. to Feb. or March

TABLE 6. Vertebrae counts and size ranges of larvae of gadoid fishes of the Mid-Atlantic Bight

	Prenatal vertebrae	Postnatal vertebrae	Total vertebrae	Size range
<i>E. cimbricus</i>	16	38–39	51–55	2.75–20.0 mm
<i>G. morhua</i>	18–20	32–35	44–57	5.5–30.0 mm
<i>M. aeglefinus</i>	19–22	32–35	50–57	4.0–28.0 mm
<i>M. bilinearis</i>	27–28	26–27	54–56	3.5–22.5 mm
<i>M. albidus</i>	25	26–27	50–56	–
<i>M. tomcod</i>	14–18	–	52–57	7.0–12.1 mm
<i>P. chesteri</i>	–	–	49	–
<i>P. virens</i>	23–25	29–32	53–57	4.0–23.0 mm
<i>U. chuss</i>	14–17	33	45–50	2.1–11.0 mm
<i>U. earlii</i>	14–16	31–32	46–47	–
<i>U. regius</i>	13–14	31–33	45–46	4.0–15.0 mm
<i>U. tenuis</i>	13–17	42	47–50	–
			56–57(?)	

Fig. 135 (on next page). Development of larval and early juvenile stages of gadiform fishes of the Mid-Atlantic Bight. Information is lacking for *M. albidus*, *P. chesteri*, *U. earlii*, and *U. tenuis*.





Enchelyopus cimbrius (Linnaeus), Fourbeard rockling**ADULTS**

D_1 1; ^{8,43} D_2 45-53; ¹⁰ A. 37-45 ^{8,43} (although once reported to 48 ⁴⁵), in western Atlantic 39-43; ¹⁰ C. 30-34; ⁴³ P. 15-17; ^{8,43} V. 5-7; ^{10,45} scales 54-55 (but 51-57 according to some authors); ⁴³ gill rakers 9-10; pores in lateral line, ca. 29⁸ to ca. 35 pairs; ¹⁰ total vertebrae 51-55; ³⁴ precaudal vertebrae 16; ⁴⁷ caudal vertebrae 38-39.³⁰

Proportions as percent body length: Head 16.0-17.2, interorbital space 7.9-8.9. Proportions as percent head

length: Diameter of eye 22.2-24.4.⁸ Proportions as times in TL: Depth 7-8.¹⁰ First ray of dorsal nearly equal to head length.⁴⁵

Body slender, tapering from tip of pectorals to caudal peduncle,¹⁰ rounded in front of vent, laterally compressed behind.⁴⁵ A pair of long barbels at anterior nostril, a shorter one on chin, and one at tip of snout.⁸ Upper jaw longer than lower.⁴⁵ Teeth in upper jaw small, uneven, the anteriormost 6-8 enlarged; teeth more numerous in lower jaw.¹⁰ Lateral line slightly curved

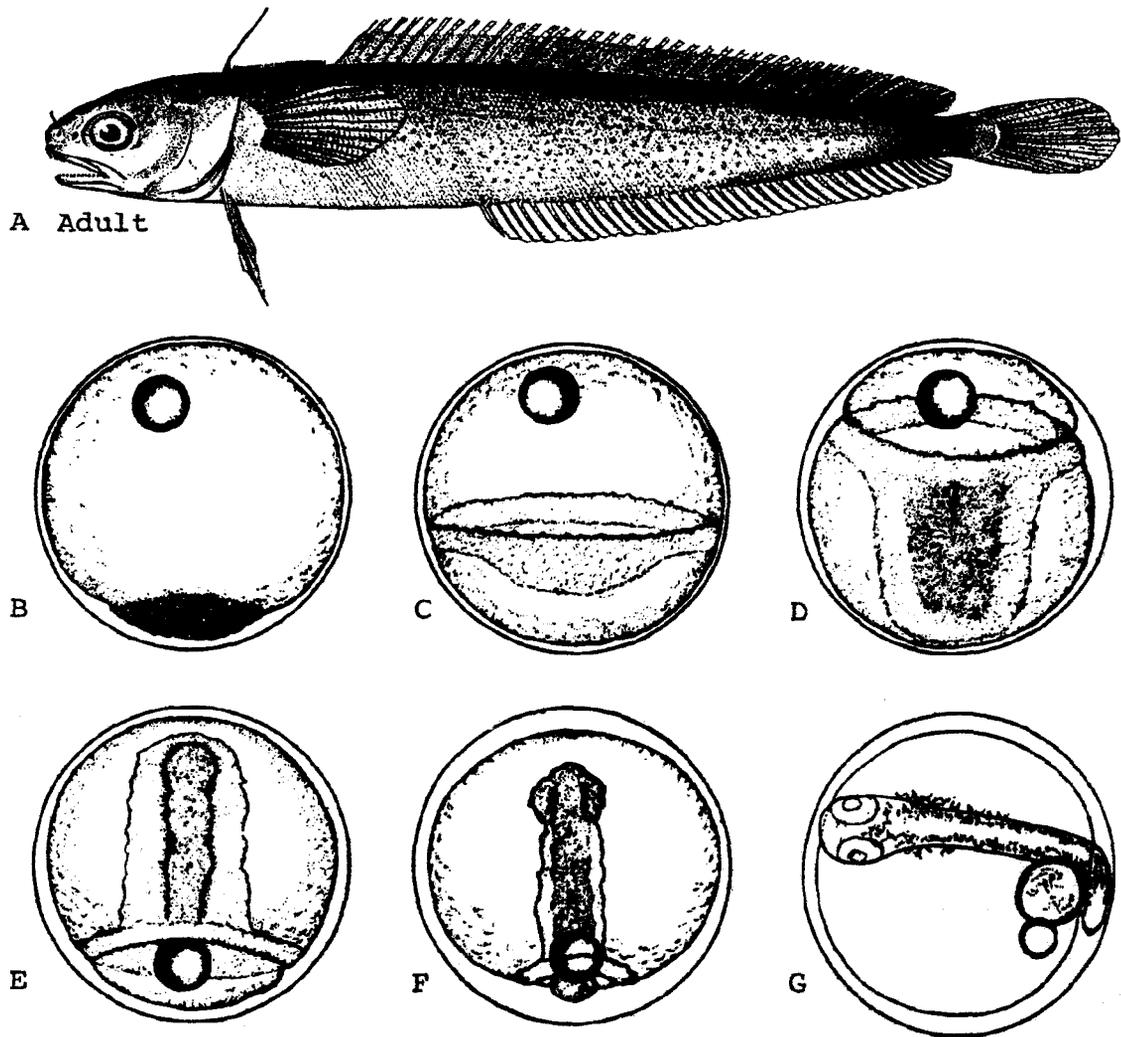


Fig. 136. *Enchelyopus cimbrius*, Fourbeard rockling. A. Adult, length unknown. B. 32- to 64-cell stage. C. Blastoderm over one-fourth of yolk. D. Blastoderm over one-half to three-fourths of yolk. E. Blastopore forming. F. Blastopore small, optic vesicles formed. G. Lens formed, tail apparently free. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 907. B-F, Batlle, H. I., 1929: fig. 2. G, Ehrenbaum, E., and S. Strodtmann, 1904: fig. 4.)

near posterior end of pectorals.^{8,43} Caudal and pectorals rounded; pelvics noticeably in front of pectorals.^{10,45}

Pigmentation: Reddish, grayish, yellowish, or dusky brown above, paler on sides, and with irregular brown spots on rear of body; sides of head silvery; belly whitish (although also reported as grayish sky blue), dotted with brown; cavity of mouth dark purplish or bluish. First dorsal blackish blue, other unpaired fins grayish blue or ashen gray edged with yellowish or reddish. Second dorsal, anal, and distal parts of caudal lobes with dark spots. Pectoral bluish black, pelvic lighter.^{8,10,22,43,45}

Maximum length: Ca. 419 mm,^{3,8,32} although this record has been questioned and total length may not exceed ca. 380 mm.⁴³

DISTRIBUTION AND ECOLOGY

Range: In the western Atlantic, coastal waters from the Gulf of St. Lawrence (or further northward) to Narragansett Bay, southward generally along the edge of the continental shelf to off Cape Fear, North Carolina.^{3,8,43} In the eastern Atlantic, along the coast of Europe northward to the western Barents Sea, eastward to the western Baltic, and occasionally, the Gulf of Finland, and southward around the British Isles to the coast of France in the Bay of Biscay. Also recorded from the Faroes and Iceland, but not known from Greenland.^{5,8,14,22,43}

Area distribution: Recorded from off New Jersey,¹⁶ from mouth of Delaware Bay,²⁹ and from off mouth of Chesapeake Bay.⁴⁰

Habitat and movements: Adults—a bottom dwelling,⁸ somewhat solitary species,²¹ usually found in relatively shallow water¹⁰ over soft bottoms^{3,23,32} of mud,^{8,10,30,38} silt,⁴² or muddy clay,¹² and, less frequently, sand, gravel, or sand-shell bottoms^{10,12} and oyster beds.^{30,34} Probably never rises far from bottom except by "accident."⁴⁵ Sometimes in great numbers in gullies at 55 m or deeper,¹⁰ also in harbors,^{18,36} rivers,²⁵ and coastal "ponds."³⁵ Depth, in water "only a few feet deep"⁴⁵ to ca. 1463 m,³¹ but "generally distributed" and "abundant" at ca. 10 to 38 m.³

No large migrations are known, but small inshore-offshore movements occur, with individuals moving inshore in fall, offshore in spring.⁸

Larvae—found at surface^{3,30} near shore⁴ and out to and beyond the 40 m depth contour;³⁰ also in schools in bays.²¹ Float upside down until yolk is absorbed.²⁶ Specimens ca. 12 mm long near wharves³⁵ and in schools mixed with sticklebacks.¹⁸

Movements undescribed, but apparently drift with current.⁴¹

Juveniles—initially pelagic,^{3,14} found inshore and at

surface at sizes up to 45 mm.^{9,11,35,45}

Apparently go to bottom after reduction in size of pelvic fins,¹⁹ at a length of 40–45 mm, and an age of "a few months"³¹ (but probably not more than three⁴⁵). Probably remain in shallow water for one or two years, then move out into deeper water.³¹

SPAWNING

Location: At bottom.¹ Eggs have been observed in the Gulf of Maine⁴ and in Narragansett Bay, but eggs in the latter area may have actually been spawned offshore.⁴⁴ In European waters spawning occurs "in shallow water near the coast."⁵

Depth: In Gulf of Maine, probably less than 137 m, but may be deeper on the slope.⁴⁵ In Europe a ripe female taken at 48 m.⁴⁰

Season: In North American waters, February 10^{12,31} to September^{8,26} or October,^{10,45} but with peak activity mid-July to mid-August.¹ In New England, February to August.^{15,35} In Long Island Sound, February 10¹² to June 11.³¹ Spawning increases with spring high tides associated with new or full moon.^{1,10} In European waters January^{5,8,26} to November.^{13,37} In the North Sea February to August, peak activity in May;⁵ in the Baltic January²⁸ to mid-October,⁴¹ peak in May;²⁸ in the Gulf of Gdansk first week of May¹³ to possibly November, peak June to August, but primarily August.^{13,31,37}

Time: Probably at all times, but peak activity during the morning.¹

Temperature: In Canadian waters normally at 13–19 C.¹⁰ In U.S. waters eggs recorded at 1.15 to 16.10 C, with peak abundance at 6–9 C;^{12,31} spawning activity peak, however, apparently at 9–10 C.^{31,45} Optimum temperature 9.64 C, with maximum spawning occurring one day after temperatures reached 9.17 C.¹

Salinity: In Canadian waters 18.6–45.0 ppt.¹⁰

Fecundity: Ca. 500,000.⁴³

EGGS

Location: Pelagic,^{1,20} but found both at or near the surface and at bottom;^{27,41} probably drift considerable distances from spawning grounds.¹²

Ripe ovarian eggs: Diameter 0.80–0.875 mm.⁴⁰

Fertilized eggs: Spherical,^{10,26} transparent. Overall size range 0.65¹⁰–1.26 mm⁴¹ with diameter varying geographically. In New England 0.74–0.89 mm,⁶ in North Sea 0.66–0.98 mm,³³ in Belts Sea 0.88–1.08 mm,²⁸ in Baltic 0.81–1.32 mm,^{5,34} near Bolholm and in Danzinger Basin 1.07–1.26 mm.⁴¹ Diameter decreases with sea-

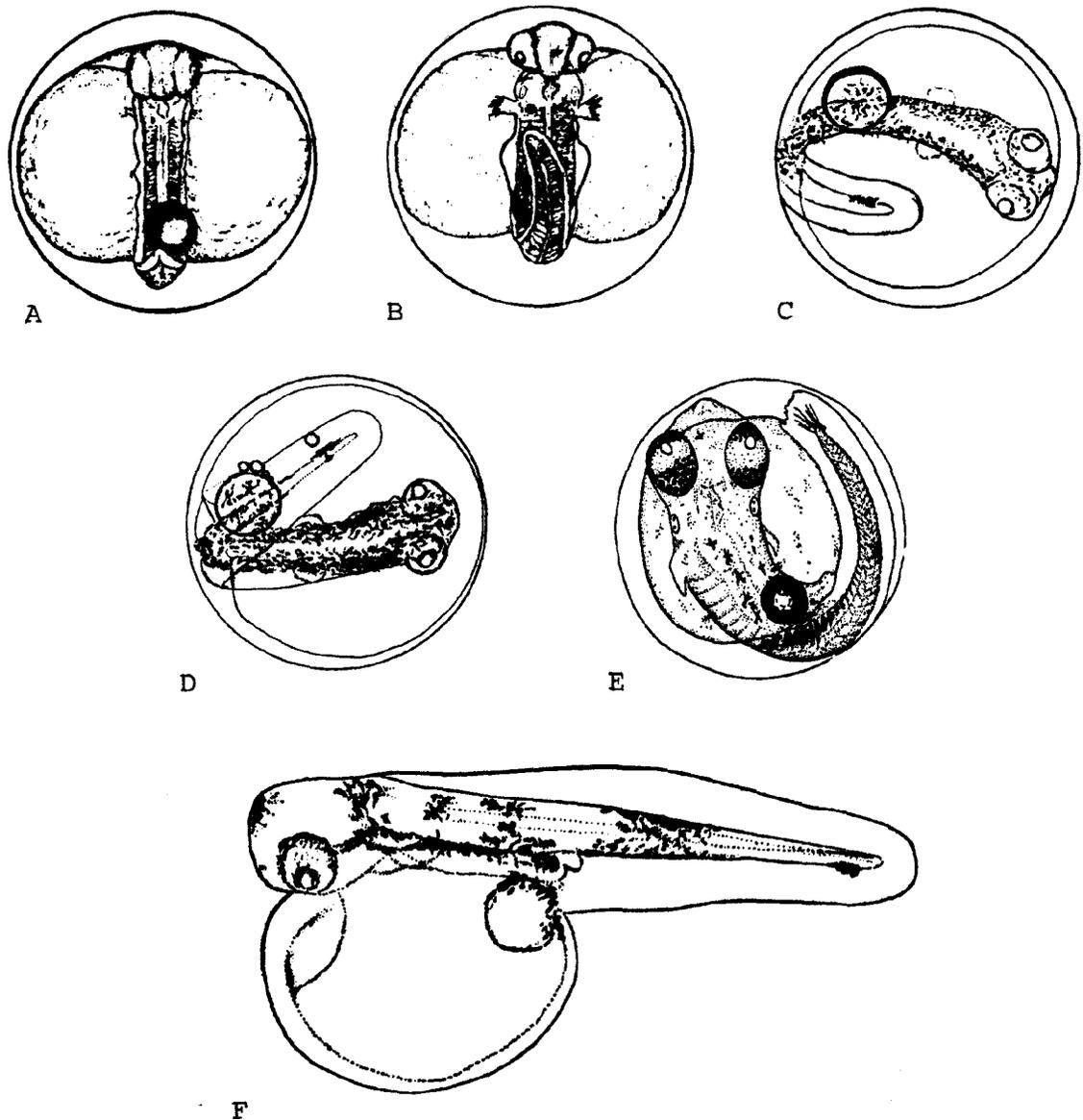


Fig. 137. *Enchelyopus cimbrius*, Fourbeard rockling. A. Blastopore closed; somites, pigment forming. B. Otoliths evident, pectoral fins forming. C. A somewhat more advanced embryo, pigment developed on head, body, and tail. D. Pigment on tail well defined. E. Body movements, heartbeat established, eye pigment well-developed. (A, B, E, *Battle, H. I.*, 1929: figs. 2, 3. C, D, *Ehrenbaum, E., and S. Strodtmann*, 1904: fig. 4.)

son.^{5,12} In North Sea average 0.90 mm in March, 0.873 mm in April, 0.834–0.827 mm in May, and 0.766–0.743 mm in June.³⁰ In Baltic 0.97–1.10 (\bar{x} 1.04 mm) in February, 0.82–1.07 (\bar{x} 0.93–0.96 mm) in May, \bar{x} 0.90 in August. Geographic and seasonal variation in egg size. Eggs larger at lower salinities.^{28,34,41} Oil globules variable, “1 to many”;¹⁵ in very young eggs oil occasionally evenly spread over yolk in many droplets which later coalesce;⁴¹ typically, however, one large

oil globule, with sometimes several smaller ones in earliest stages.⁴² Largest oil globule ca. 1/5 diameter of yolk.^{5,41} Diameter of oil globule 0.13^{10,26} (or possibly as small as 0.08¹⁵) to 0.25 mm;³⁴ average size 0.16 mm.^{6,19} Oil globule usually pigmented;^{20,42} color variable: greenish, yellowish,²¹ reddish,⁵ reddish yellow, greenish yellow,⁴¹ blackish or cream (rarely colorless).⁴¹ Pigmentation varies geographically: In Baltic blackish to yellowish,^{5,34} in Bay of Fundy light cream to golden

yellow.²⁶ Perivitelline space narrow (JDH). Ehrenbaum⁴¹ has described an air space which is frequently visible along the exterior of the egg membrane, and "appears in the form of an irregular caul."³⁴

EGG DEVELOPMENT

Development at 15 C (Battle series):²⁶

- 8 1/2 hours (Stage A) 32-64 cell stage, segmentation cavity formed.
- 11 hours (Stage B) Blastoderm over 1/4 yolk; germ ring visibly thickened; embryonic shield evident.
- 14 hours (Stage C) Blastoderm over 1/2 to 3/4 yolk, embryonic shield considerably lengthened.
- 17.5 hours (Stage D) Embryonic shield generally narrowed, more distinct and with a spatulate

- flattening extended posteriorly to margin of blastopore.
- 21 hours (Stage E) Optic vesicles formed; yolk almost surrounded by blastoderm.
- 36 hours (Stage F) Closure of blastopore; oil globule located posteriorly just under caudal prominence; optic vesicles more distinct; alar membrane, some somites formed; heart forming; scattered melanophores on ventral surface.
- 51 hours (Stage G) Body elongate, pressed into surface of yolk; tail elongate; pectoral fins outlined; heart chambers, auditory vesicles, otoliths, and lenses formed; additional melanophores on body; eye pigmented.
- 72 hours (Stage H) Yolk decreased; finfold formed; pectorals clearly defined; 2-3 branchial

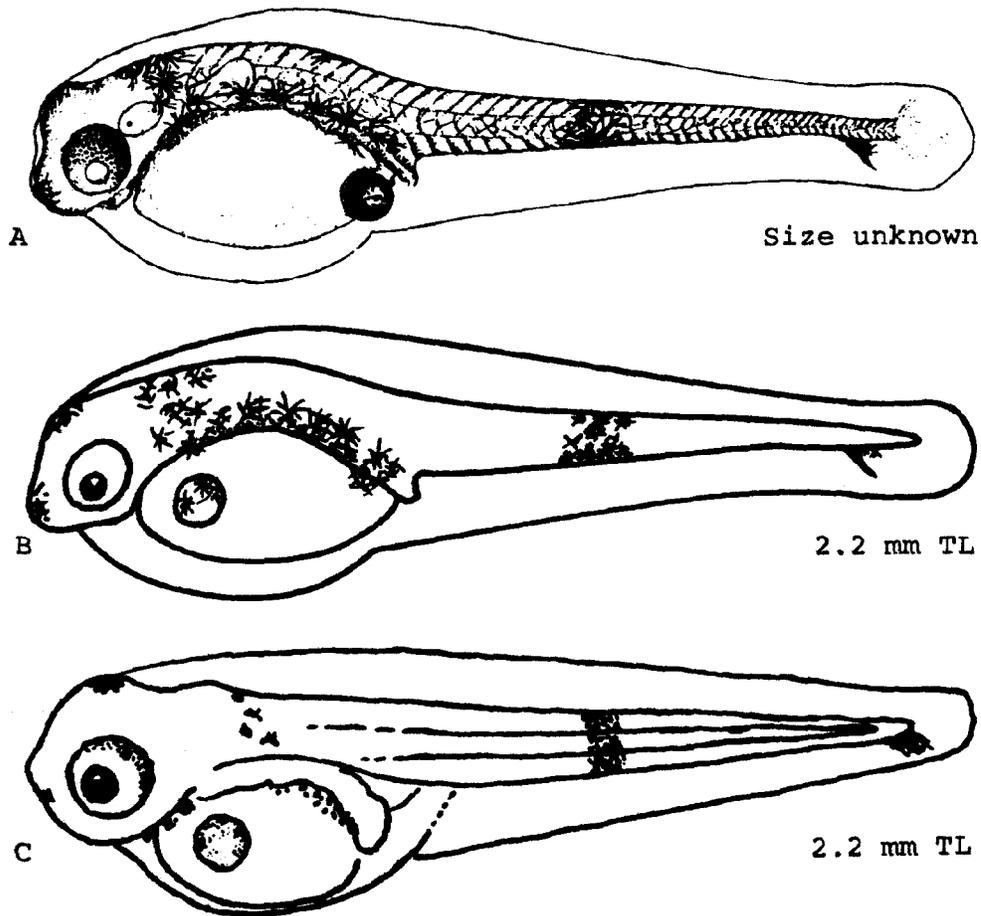


Fig. 138. *Enchelyopus cimbrius*, Fourbeard rockling. A. Yolk-sac larva, size unknown, pigment in eye well-developed. B. Yolk-sac larva, 2.2 mm TL. C. Yolk-sac larva, 2.2 mm TL. (A, Battle, H. I., 1929: fig. 3. B, Colton, J. B., Jr., and R. R. Marak, 1969: 14. C. Miller, D., 1958: unnumbered.)

clefts formed; movements evident; heart beat established, irregular. Pigment on snout and above midbrain just above eye; a vertical pigment band posterior to otocysts and above pectoral fin, extending horizontally along intestine to anus; a band of pigment at approximate midpoint of tail; a single stellate melanophore just ventral to somites at base of tail; melanophores on eye.

108 hours
(Stage I)

Hatched or hatching.^{1,26}

Development at 13 C (Battle series);¹ identical to development at 15 C, but with time sequence occurring as follows:

Stage A.	10.2 hours.
Stage B.	13.2 hours.
Stage C.	16.8 hours.
Stage D.	21.0 hours.
Stage E.	25.2 hours.
Stage F.	43.2 hours.
Stage G.	61.2 hours.
Stage H.	86.4 hours.
Stage I.	129.6 hours. ¹

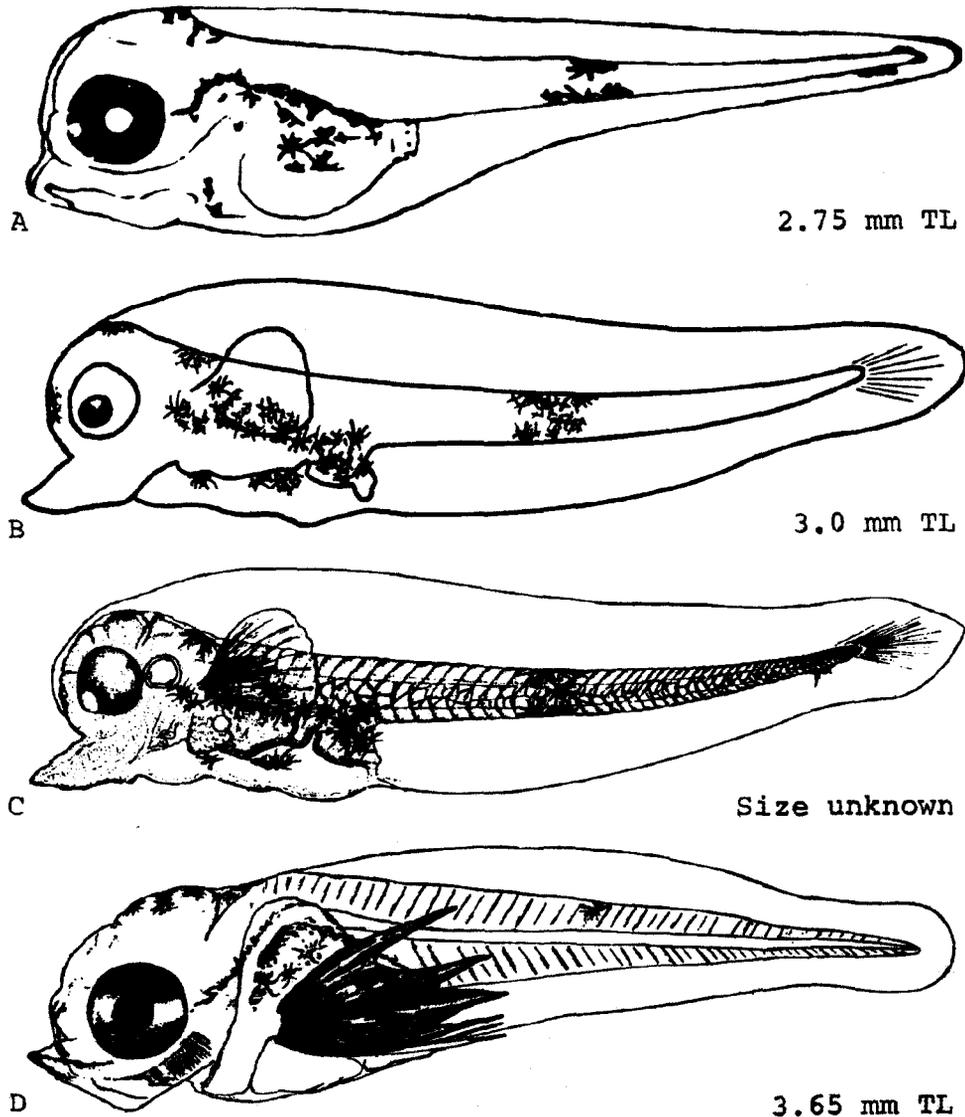


Fig. 139. *Enchelyopus cimbrius*, Fourbeard rockling. A. Larva, 2.75 mm TL. B. Larva, 3.0 mm TL, mouth well-developed, incipient rays in caudal fin. C. Larva, size unknown. D. Larva, 3.65 mm TL, pelvic fins well-developed. (A, Rass, T. S., 1949: fig. 22. B, Colton, J. B., Jr., and R. R. Marak, 1969: 14. C, Battle, H. I., 1929: fig. 3. D, Ehrenbaum, E., and S. Strodtmann, 1904: fig. 5.)

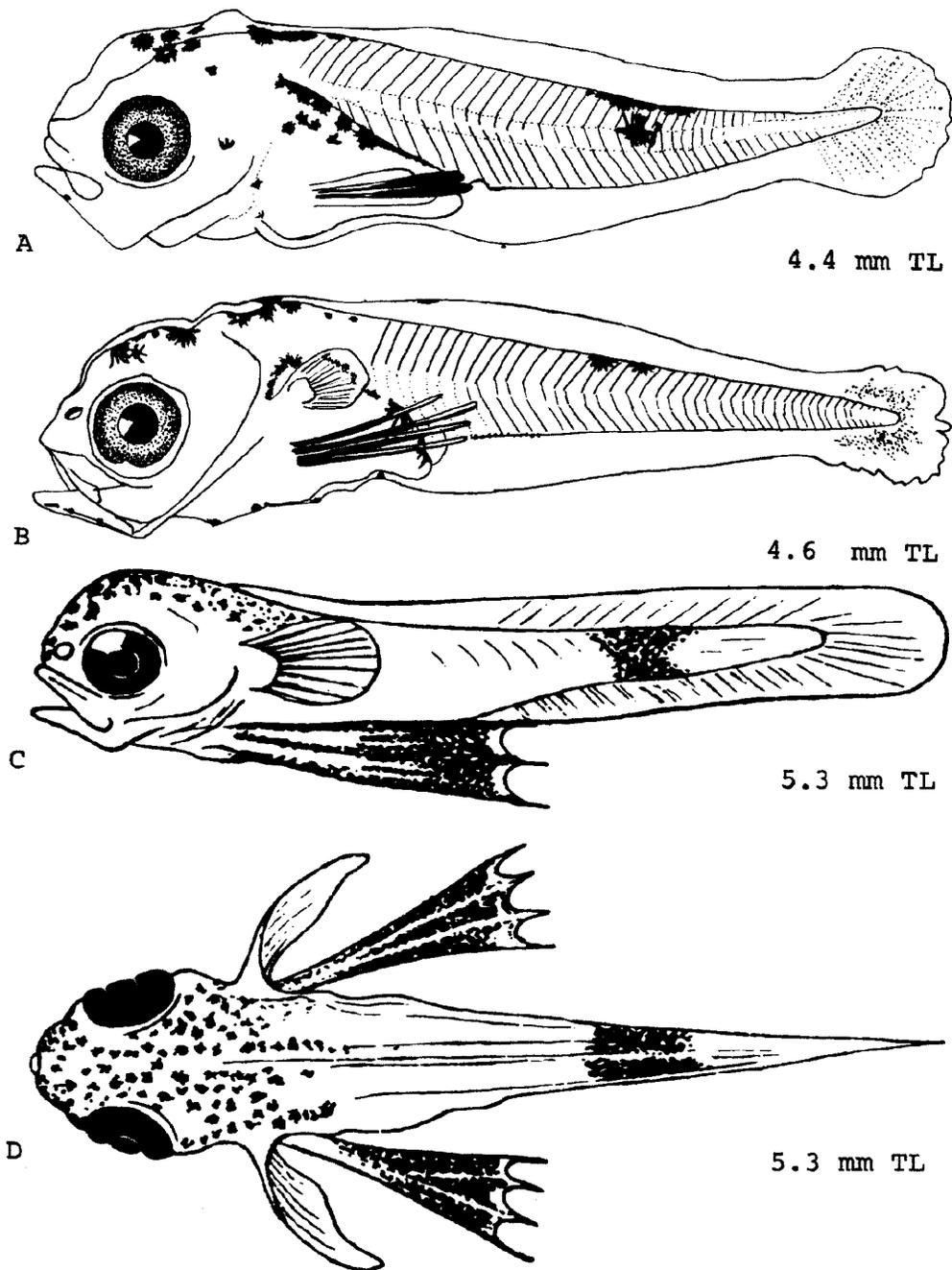


Fig. 140. *Enchelyopus cimbrius*, Fourbeard rockling. A. Larva, 4.4 mm TL. B. Larva, 4.6 mm TL. C. Larva, 5.3 mm TL. D. Dorsal view of C. (A, B, From Dannevig, A., 1919: *Taniko Karr, delineator*. C, D, Ehrenbaum, E., 1909: after Brook, G., 1891: pl. 6.)

Comments on development: Pigment appears first on oil globule;⁵ may also develop on yolk, but this is not typical of all populations.⁴² In advanced embryo two pigment patches on tail; one at midpoint, one at tip.⁴¹

Incubation period: At 13 C, average 5.4 days; at 15 C, average 4.5 days.¹

Incubation temperature: Normal development 13–19 C; ^{1,8,41} hatch abnormally at extremes of 5.0 and 24 C; ²⁶ found in nature at minimum of 0.4 C, but probably not developing.¹⁶

Incubation salinity: Normal development at 18.6–45.0 ppt, abnormal development at extremes of 5.6 and 80.0 ppt (author notes that larvae hatched at high salinity are distinctly smaller than those hatched at low salinity).²⁶

YOLK-SAC LARVAE

Minimum length reported, 1.63 mm; maximum hatching length, ca. 2.42 mm,⁶ average hatching length, 2.03 mm; ^{6,17,20} length at end of stage 2.75–3.0 mm.⁵

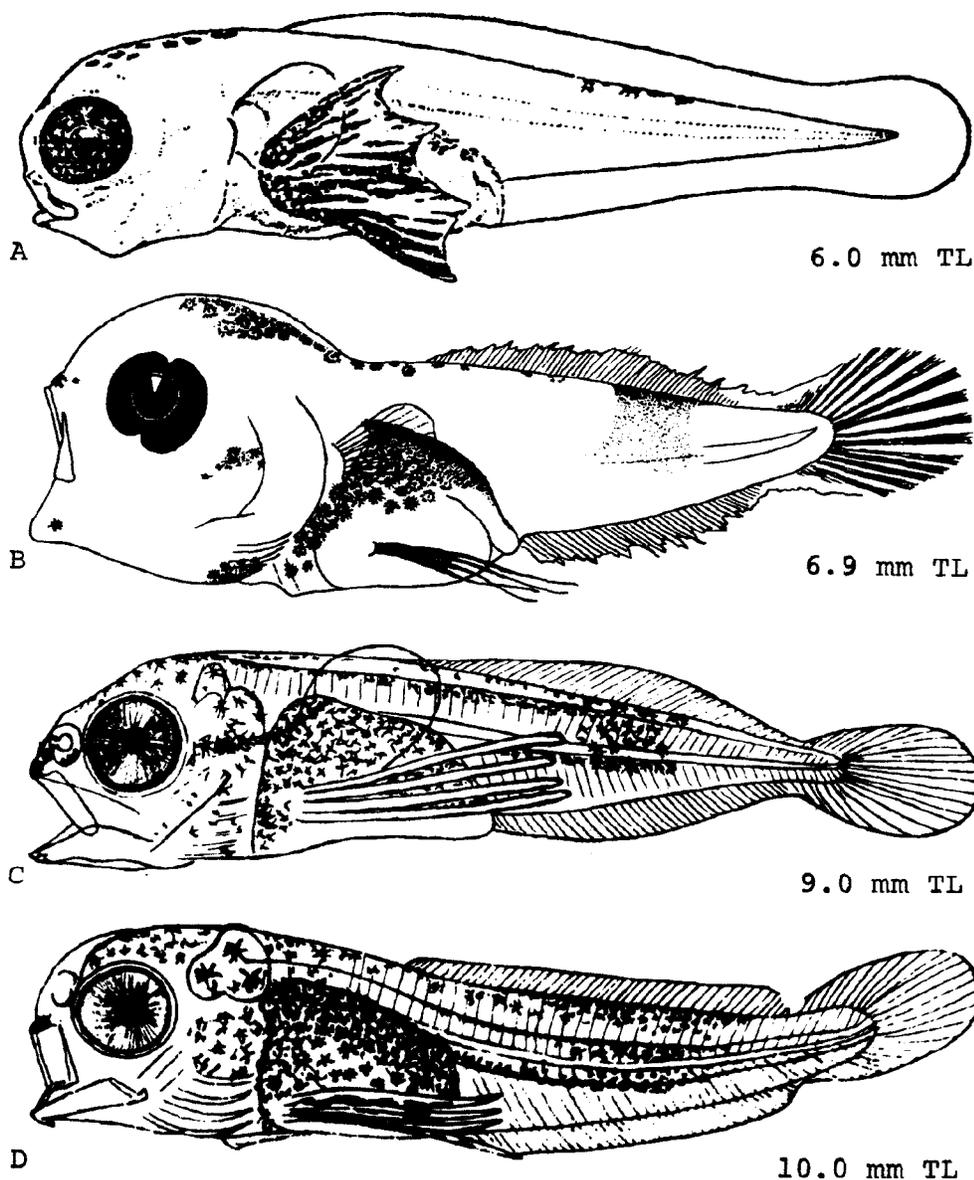


Fig. 141. *Enchelyopus cimbrius*, Fourbeard rockling. A. Larva, 6.0 mm TL. B. Larva, 6.9 mm TL. C. Larva, 9.0 mm TL. D. Larva, 10.0 mm TL, barbel evident. (A, Rass, T. S., 1949: fig. 22. B, Colton, J. B., Jr., and R. R. Marak, 1969: 14. C, D, Ehrenbaum, E., 1908: fig. 1.)

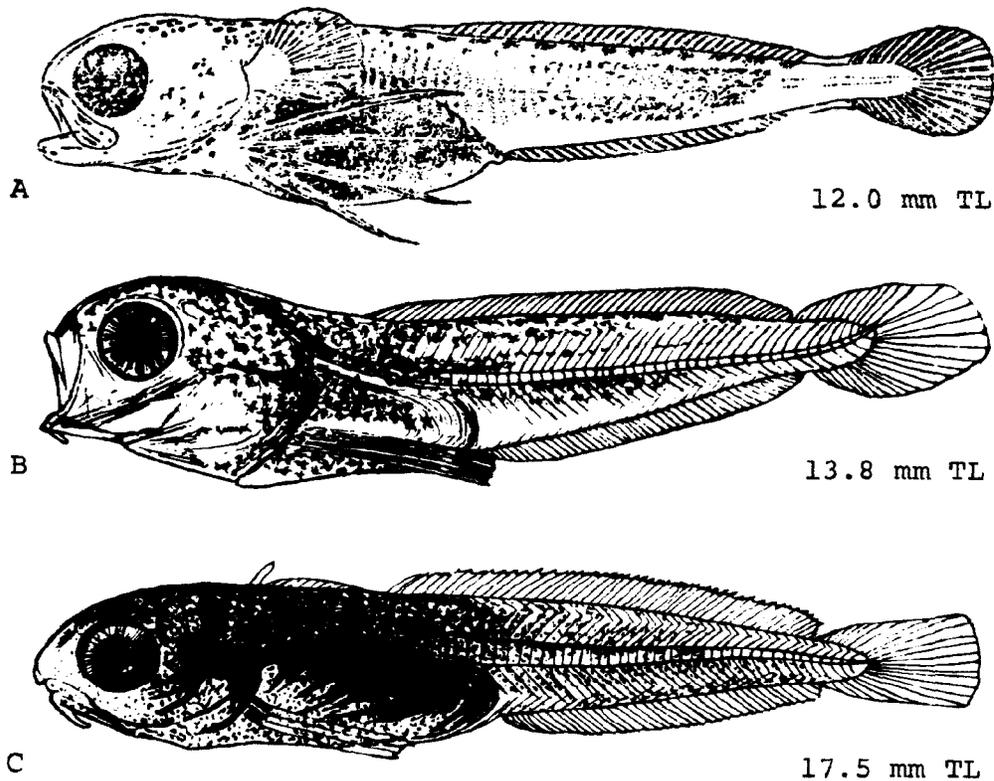


Fig. 142. *Enchelyopus cimbrius*, Fourbeard rockling. A. Larva, 12.0 mm TL. B. Larva, 13.8 mm TL. C. Pre-juvenile, 17.5 mm TL. (A, Rass, T. S., 1949: fig. 22. B, Ehrenbaum, E., 1908: fig. 1. C, Ehrenbaum, E., 1909: fig. 101, after Brook, G., 1891: pl. 6.)

At hatching head deflected over yolk, mouth not evident, yolk rounded or oval. At beginning of stage oil globules sometimes distributed throughout yolk, but usually consolidated in posterior part of yolk; oil carried progressively forward throughout stage; at end of stage one large oil globule and, often, one or two smaller ones. Dorsal finfold forward to head throughout stage; incipient rays in caudal fin of some individuals at hatching. Intestine straight;^{26,34} opening of anus lateral and at base of finfold.^{9,7}

Pigmentation: Pigment more intense than prior to hatching.²⁶ Pigment on top of head and at tip of snout; a vertical band of dendritic melanophores posterior to otocysts, and, extending from this, a heavy row of scattered melanophores along dorsal gut wall; a vertical band of pigment at midpoint of tail, and a large stellate melanophore on ventral finfold below posteriormost myomeres. Oil globules orange by end of stage.^{6,20,34}

LARVAE

Size range, ca. 2.75⁵–20.0 mm.³

Body relatively short, thick.¹⁹ At beginning of stage

mouth open, lower jaw extending considerably beyond upper; otocysts visible, somewhat elongate, and with 2 or 3 visible otoliths; olfactory pits developing; fore-brain narrow, laterally compressed; medulla somewhat elevated. Three or four branchial arches usually present; mandibular and hyoid arches composed of large elongate cartilagenous cells.²⁶ Barbel of lower jaw evident as distinct papilla at 10.0–11.0 mm; two lateral snout barbels at 12.5 mm.^{19,34} Dorsal finfold forward to head at beginning of stage;²⁶ greatly reduced by 6.9 mm;⁶ essentially obliterated by 9.0.³⁴ Incipient rays in caudal at beginning of stage;²⁶ 2nd dorsal well-developed at 6.9 mm,⁶ no longer continuous with caudal at 10.0 mm; 1st dorsal developed at 15³⁴–20 mm;³ anal well-developed at 6.9 mm⁶ no longer continuous with caudal at 13.8 mm. Pectorals with rays at beginning of stage. Pelvics first evident at minimum of 3.0 mm;²⁰ extended 1/3 their length beyond anus at 9.0 mm;³⁴ elongate, fan-like by end of stage.^{19,20} Intestine convoluted: Notochord 2–4 cells in diameter, surrounded by thin, firm sheath.²⁶

Pigmentation: At 3.65 mm body with dark yellow and green-yellow pigment; pectorals colorless, transparent; pelvics black marked with reddish.⁴¹

Postanal crossband evident up to 10 mm.^{3,20,39} At 9.0 mm pigment spot on ventral surface near tip of tail present³⁴ or absent;⁶ entire ventral outline and, usually, tip of tail free of pigment; gut and eyes with bluish sheen. At 8.0 to 10.0 mm silvery pigment developing on gut and gill covers. At 10 mm dorsal and mediolateral postanal pigment greatly increased.^{30,34} Eyes brilliant iridescent blue-black.²⁶

PREJUVENILES

Size range, ca. 16 (but evidence based on color)⁴¹—ca. 32 mm.

Snout barbel evident as faint tubercle at 20 mm^{19–22} mm,³⁴ well-developed at 30 mm.¹⁹

At 22 mm pelvic decreased in relative size, not quite reaching anus.³⁴

Pigmentation: At 16–18 mm green and silvery;⁴¹ at 17–22 mm shiny silvery;^{3,5,34} at ca. 27 mm pigment along back distinctly mottled;¹¹ at sizes up to ca. 32 mm ventral surface brilliant silver, gradually shading to greenish black toward dorsum.¹⁹

JUVENILES

Minimum size described, 37.7 mm.

Pelvis considerably shorter than in earlier stages relative to body length.⁴⁶

Pigmentation: Similar to previous stages, but with generally increased dark pigment.⁴⁶

AGE AND SIZE AT MATURITY

Minimum length at maturity, females 150 mm,⁴⁰ males unknown.

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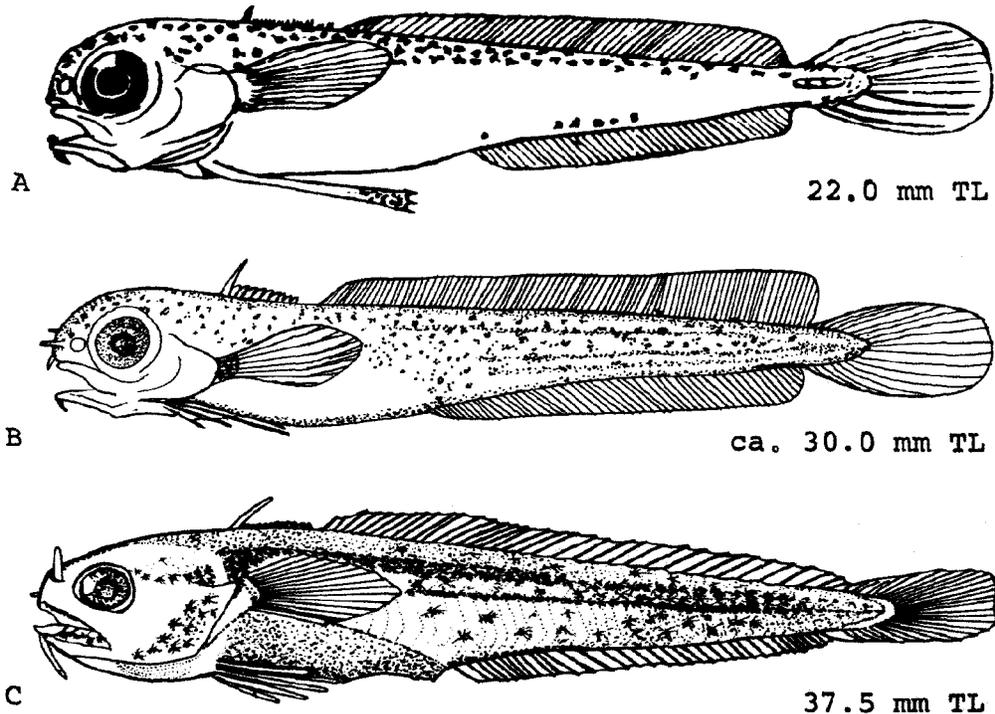


Fig. 143. *Enchelyopus cimbrius*, Fourbeard rockling. A. Prejuvenile, 22.0 mm TL. B. Prejuvenile, ca. 30.0 mm TL. C. Juvenile, 37.5 mm TL. (A, Ehrenbaum, E., 1908: fig. 1. B, Brook, G., 1891: pl. 6, Tamiko Karr, delineator. C, Original drawing, Nancy Schenk Smith.)

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Gadus morhua Linnaeus, Atlantic cod**ADULTS**

D.₁ 12–16³⁵ (w. Atlantic 13–16⁴¹), D.₂ 14²¹⁵–26²⁰⁴ (w. Atlantic 16–25²¹⁵), D.₃ 15–21³⁵ (w. Atlantic 18–21²⁴⁰); A.₁ 17–25³⁵ (w. Atlantic 20–24⁷¹), A.₂ 15–23³⁵ (w. Atlantic 17–22⁴¹); scales 150–170;⁷¹ total gill rakers outer row first arch 18–28;³⁵ vertebrae 44²⁷–57,¹⁷⁴ but lower values may reflect growth in rearing ponds;²⁷ otherwise minimum vertebrae 49;³⁵ trunk vertebrae 18–20; caudal vertebrae 32–35.²¹¹

Proportions as times in TL: Depth 4.74–5.15, head 3.53–3.76.⁷¹ Diameter of eye as percent HL: 15.5–23.6.³⁵

Body elongate, stout, slightly compressed; snout conical; head blunt,⁴¹ scaled;²⁴⁰ upper jaw and snout projecting;⁷¹ gape extending to margin or anterior third of eye;^{41,240} chin barbel equal to diameter of eye. Teeth small, pointed, cardiform, in bands on jaw and vomer; teeth of outer row of upper jaw and inner row of lower

jaw somewhat enlarged. Lateral line distinct, arched in forward two-thirds.⁴¹ Scales very small, cycloid.⁷¹ Caudal fin slightly concave;⁴¹ pelvics inserted slightly in front of pectorals;²⁴⁰ 2nd pelvic ray slightly extended and filamentous.⁴¹

Pigmentation: Color highly variable, with individual fish able to rapidly change color, shading, and pattern.²¹⁸ Two main color groups: gray-green and red²⁴⁰ (with red fish restricted to shoaler waters⁹⁶). Fish in the gray-green group may be almost black, sooty or brownish gray, oil gray, olive brown, mouse gray, ash gray, clay-colored, greenish, pale pearly, or yellow on the sides; "red" fish may have the sides dull reddish brown, orange, or brick red. In most cod, the upper surface of the body, sides of head, the fins and the tail are sprinkled with small, round, vague-edged, brownish, reddish brown, or yellowish spots.^{35,175,240} Belly whitish,⁹⁶ ashy,²⁴¹ pearl gray,⁴² or reddish tinged.²⁴⁰ In some specimens the body

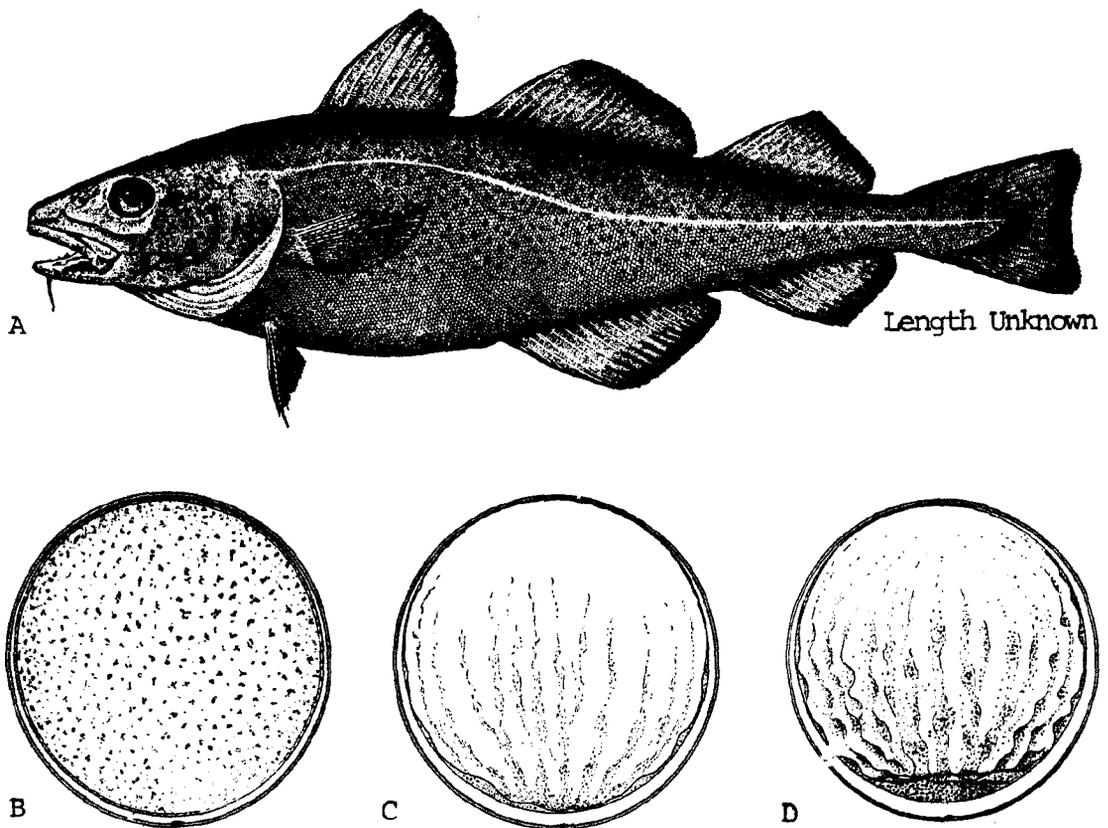


Fig. 144. *Gadus morhua*, Atlantic cod. A. Adult, length unknown. B. Unfertilized egg. C. Egg 1 1/2 hours after fertilization, protoplasmic streaming toward ventral pole. D. Blastodisc developing, 3 hours and 40 minutes. (A, Goode, C. B., 1884: pl. 58a. B-D, Ryder, J. A., 1884: pl. 1.)

may be irregularly blotched with creamy white and orange; ³⁹ others are almost black above with light gray-green mottled bars. ⁴² Fins usually same shade as ground color; ^{71,240} vertical fins sometimes with dark spots arranged in transverse rows, ³⁵ or, rarely, marked with white, orange, dull red, or greenish black streaks. ⁴¹ Lateral line always pale, never dark. ^{249,253} Peritoneum steel-gray, ¹⁷³ silvery leaden or leadened black, ³⁵ and with white dots. ⁴¹ Iris dark. ³⁹

Maximum length: Recorded to 1800 mm, ³⁵ although possibly reaching 2000 mm. ¹⁶⁶ Maximum weight, 95.8 kg. ²³²

DISTRIBUTION AND ECOLOGY

Range: Generally the North Atlantic Ocean, and the North, Norwegian, and Barents Seas. In Europe, Bay of Biscay ³⁵ (a record from Gibraltar is questioned ¹³⁸) to North Cape; in North America, Hudson and David Straits ³⁵ to Cape Lookout, North Carolina. ¹⁹⁹ Southern Greenland and Iceland. North to Jan Mayen, and the Faroe, Shetland, and Orkney Islands in the North Sea. Coastal waters of Barents Sea to Spitsbergen, shallows of Bear Island, and from Novaya Zemlya to Admiralty Peninsula. The Baltic and White seas, and possibly north to the Kara Sea. ³⁵ Within this range a number of discrete populations are recognized. Thus cod from the Mid-Atlantic Bight belong to a population which ranges, at various times of year, from Nantucket Shoals to North Carolina. ¹⁰⁵

Area distribution: Coastal waters of New Jersey, ^{10,39,71,74,91} Delaware, ¹⁴⁹ Maryland, ^{76,143} and Virginia; ¹ also in Delaware Bay, ^{74,165,201} the Delaware River as far as Trenton, New Jersey, ¹³⁸ and in lower Chesapeake Bay. ⁷¹ Although the species is now apparently uncommon in Chesapeake Bay (JDH), large incursions of adults into the Bay have been reported within relatively recent times. ^{71,201} Twenty-five thousand young cod were released at Annapolis, Maryland, about 1880 or 1881, but did not become established. ^{184,188}

Habitat and movements: Adults—typically found near bottom along rocky slopes and ledges within the limits of the continental shelf over rocky, pebbly, or gravelly areas; sometimes over sand, clay, or mud bottoms, ^{17,35,37,147,227,233,240} although, in some areas at least, mud bottoms are distinctly avoided. ²⁴¹ Occasionally forage among Irish moss (*Chondrus crispus*) and other seaweeds. ²⁴⁰ In addition to the normal coastal environments, also reported from harbors, ^{32,80,85} lagoons, ⁷⁰ brackish rivermouths, ¹²⁰ and freshwater rivers which are sometimes penetrated as much as 112 km. ^{138,251} Although primarily a ground fish, also in midwater and at surface; ^{70,252} usually in midwater when undertaking mass movements. ^{236,240} Form large, apparently loose shoals, ⁹⁶ which may be several km long and 8 or 10 km wide, ²¹⁸ shoals may form as fish approach feeding grounds, ³⁵ and

feeding shoals may strand on beaches while pursuing prey close inshore. ^{232,240} Large concentrations of cod have been reported at surface associated with drift ice. ¹⁹⁵

Although recorded from depths of up to 600 m, ^{16,17,35,71,259} prefer depths of ca. 40 to 130 m, ⁹⁶ and, in some areas at least, most concentrated between 15 and 75 m; ^{241,246} minimum depth ca. 0.66 to 1.0 m. ^{80,246} Cod have been found at surface over depths of 2000 m, ¹⁹³ and may concentrate at one particular depth in deep water, as at 460 m in water over 1000 m deep. ²⁵² In Canadian waters, near and below the border of the below-zero intermediate cold layer. ²⁷⁹ Largest cod tend to stay closer to bottom and are usually in deeper water and farthest from land. ^{52,240}

Maximum salinity ca. 35 ppt; ¹⁸⁶ typically in marine (saline) waters, but also reported in estuarine ^{74,165,201} and freshwater. ^{35,138,223,251} In northwestern Atlantic, absolute temperature range reported near -2 C ^{243,259} to $+20\text{ C}$; ^{7,186,217} however, the heart may stop beating at -1.9 C , ²⁰⁸ and both -1 C ²⁵⁰ and $+20\text{ C}$ ²⁵² may be lethal. Overall average optimum temperature may be $0\text{--}6\text{ C}$, ^{186,219,252} but this varies from area to area and season to season: in Newfoundland $2\text{--}3\text{ C}$ in March; ⁶¹ Sable Island $3\text{--}7\text{ C}$ in March and April. Nova Scotian cod appear to remain in more shallow, warmer water at all seasons: ca. $1\text{--}8\text{ C}$ in summer, $2\text{--}4\text{ C}$ in winter. ¹⁶ As a rule, the species tends to avoid temperatures over 10 C . ²⁴⁰ In European waters found at temperatures of $0\text{--}16\text{ C}$, but with optimum varying within the area ($1\text{--}5\text{ C}$ in coastal fjords as opposed to $4\text{--}7\text{ C}$ otherwise) ²⁵ and seasonally (minimum tolerance 2 C from October to June, near or below zero in summer). ^{4,262}

The local (Mid-Atlantic Bight) population of cod is apparently discrete and moves from vicinity of Nantucket Shoals to points as far south as North Carolina during the colder months. These fish are typically concentrated north of Block Island in summer and along New Jersey coast in winter. Wise regards these southern waters as "native grounds" since spawning apparently takes place there. ¹⁰⁵ Fish moving southward generally appear off New Jersey in November and pass northward again in March and April; return to Nantucket in early May; and apparently enter Chesapeake Bay only from January to March. ^{71,74,240} Movements of other cod populations are highly variable; some move great distances while others are more or less stationary. ²⁴⁰ Schroeder pointed out that all cod do not carry out the same migratory schedule and that some cod apparently do not migrate to spawn. ²⁰³ In certain New England and Canadian waters cod concentrate on local spawning grounds and disperse afterward, and these movements are frequently quite limited. ²⁰² Some spawning populations appear to move inshore, ⁶ while others apparently move offshore. ²⁶⁶ Several kinds of movements take place in Canadian waters. Some individuals make very restricted offshore movements (up

to 40 km) in autumn and early winter and return shoreward in spring and early summer; others make orderly extended migrations to offshore banks or southward along the coast in autumn and early winter; still others are "rover fish" and move at random (but most typically northeastward along the coast) at about 200 km a year.²¹⁷ Regular annual movements are highly variable in different localities. In New Brunswick, Canada there is an inshore "run" in June, while in New England cod move to offshore banks in summer. Such differences may involve preferred water temperature,^{14,146,219} thus, small cod in east Newfoundland move from deep to shoal water in spring, but larger cod remain in deep water (at depths of 200 m or more) below the cold water layer.¹⁶ Labrador cod move north and south, always remaining in cold water.¹¹ There is apparently some intermingling of various populations as a result of general movements.¹⁶⁹

In northern Europe cod movements are likewise varied. Some populations, particularly in the North, Barents, and Baltic Seas appear to be essentially nonmigratory,^{35,52,60,90,192} while others in the same area make extensive migrations. Thus, shoals assemble in Barents Sea and go to Lofoten to spawn, arriving in January and February and returning mid-April, moving as far north as Novaya Zemlya.^{11,35,68,238,267} Cod may travel from Lofoten to Finmarken in 5 to 6 weeks.²⁰² At least a part of the Baltic cod population is definitely migratory.²²⁷ There is a migration from Greenland to Iceland between October and April, although large specimens may remain in Iceland and some Icelandic specimens move only to offshore banks from which they may or may not return.^{12,64,137,146,193,208} There is also a migration from Iceland to Norway.¹⁰⁰

Migrations of 3200 km or more have twice been recorded: once from Iceland to Newfoundland and once from the North Sea to Grand Bank. In spawning migrations, larger, older fish arrive earlier in the season than smaller ones,¹¹⁸ with males arriving before females and staying longer.⁶

In northwestern Atlantic waters definite vertical movements occur.^{221,239} From mid-July to fall cod move into midwater at night and from May to July as many or more cod are in midwater during the day as at night.^{189,276} Diurnal variations in shoaling behavior also occur: compact shoals at 182 m disperse at sunset and re-form at sunrise.^{50,264}

Larvae—newly hatched larvae remain motionless, floating upright, on sides, or inverted at surface. After approximately two days become active, maintain upright position, and rest at 45° angle in water with head up.^{7,44,49,116,160,240,241} Found over deep water (as, for example, 4.0 to 5.5 mm specimens over 150 to 255 m);²⁶⁹ but also around rocks in bays,¹²⁵ in sheltered fjords,¹¹⁸ shallow sounds and coves with light bottoms,¹⁷⁹ along

beaches,²¹⁹ in very shallow water on muddy ground among weeds,¹⁶¹ and in association with jellyfish.^{84,121,213,214} "Young" ca. 12 mm long at surface near Woods Hole, Massachusetts.²²² Larvae ca. 3–8 days old positively phototactic, but are repelled by and die if exposed to very strong light.^{6,36,113} Specimens ca. 3²⁰⁵–12 mm long from surface^{17,222} to 75 m.¹⁰ Depth varies with size of larvae, time of day, and possibly, location: thus larvae 3.0–5.0 mm at 0–30 m; 3.5–8.0 mm at 0 to 20 m;²⁰⁵ 5–8 mm at ca. 10–41 m, but mostly at 15.5 m.⁵³ Larvae of unspecified size variously recorded as from 18–23 m;⁶ 20 m and up diminishing toward surface;⁵⁸ most common at 40–75 m;¹⁹ and mostly at 10–30 m.⁴⁷ Larvae also recorded from "intermediate water layers" where salinity is not sufficient to keep them afloat.¹⁸⁶ Occasionally at less than 10 ppt, but occurrence probably accidental.^{150,205} (survival at these salinities is questionable, JDH). Can survive at 22 ppt, but ca. 15–18 ppt is critical, at least at certain temperatures¹¹³ (but probably not true in Baltic where salinities are characteristically low, JDH). Rarely in salinities above ca. 35.5 ppt.²⁰⁶ Up to 7 C under natural conditions,¹⁸⁶ but apparently survived experimentally at 20.0 to 21.4 C.²⁰¹

Larvae carried considerable distances by surface currents,^{17,54} as for example, eggs and larvae from Lofoten to Spitsbergen (ca. 800 km),¹⁰⁶ also from Block Island to Long Island Sound, New York.⁵⁹ Move downward in water column with growth, thus swim at surface at 4–5 mm, but move into midwater depths as growth continues.¹³⁶ Wind as well as current may affect dispersal of drifting larvae.²⁷¹ Diurnal vertical movements have been observed;¹⁵⁰ thus specimens 3.8–4.9 mm have been found at 18–23 m by day, and from the surface to 2 m at night.⁶

Juveniles—within size range of 25–50 mm (or sometimes larger) there is generally a movement shoreward and to the bottom. Specimens in this size range have been reported, therefore, as occurring in schools at surface, under jellyfish and other floating objects,^{37,117,138,219} among vegetation in shallow coastal waters, in rock pools among sea weed at ebb tide,^{117,211,277} in shallow inlets (sometimes in company with young pollack),¹³⁸ in river mouths¹⁵⁷ and harbors, and around wharves.¹⁸² Specimens 50 to 125 mm which have moved to bottom¹³⁸ are apparently more plentiful on rough inshore bottoms than on smoother offshore banks;²⁴⁰ recorded around wharves,⁸⁰ in rock piles at low water, and in *Zostera*, *Laminaria*, and brown weed beds; also offshore in 36 to 100 m, and in association with jellyfish.¹⁰³ At 100 to 150 mm recorded from river mouths.⁵² At 150 to 175 mm in vicinity of steep ledges and rocks in 15 to 22 m.¹³⁸ At 35 to 200 mm from mud, sand, and *Zostera* beds.¹⁶⁸ Specimens up to 380 mm associated with red algae,¹² also in shallow coastal waters and bays.³⁷ "Young" and "juveniles" reported in rivers,¹³⁸ fjords,^{58,138} and in lagoons where bottom is salt, the surface fresh.⁷⁰ Yearlings in shallow

coastal water.²¹⁸ Specimens 70 to 100 mm long are "somewhat phototactic."¹¹⁹ Individuals ca. 35 to 50 mm long are reported to hang obliquely in water with head downward against the current.^{159,271} Specimens 25²¹⁴ to 300 mm²³⁸ have variously been recorded from ca. 5^{134,181,214} to 366 m;²³⁸ but depth varies from place to place and from season to season.²⁵⁰ Specimens 100 to 300 mm recorded at 183 to 366 m in the northern North Sea, but in conspicuously more shallow water in the southern North Sea.²⁴⁰ Various length/depth relationships are as follows: specimens 63–93 mm in 38 m (Nantucket);²⁰¹ at 75 to 100 mm inshore, but also at depths of 36 to 100 m (Scotland);¹⁶¹ at 100 to 190 mm as shoal as 5 m (Norwegian Sea); at ca. 150 to 175 mm in 15 to 22 m; at ca. 300 mm in 55 m (Lofoten Islands);¹³⁸ at 300 to 600 mm at 128 to 238 m (Norwegian Sea).¹⁸² Most "fry" are at an average depth of ca. 35 m, with a variation of 8 to 42 m;¹¹⁸ while one year olds have been caught at depths of 73 and 274 m.¹⁹⁶ Specimens ca. 95 mm long, 193 km offshore.^{153,163} Juveniles taken at less than 31.3 to 35.0 ppt, and through temperature range of 6–20 C⁵² (but specimens 140 to 210 mm recorded at –1.4 C).²⁶⁵ Small cod are apparently able to survive higher temperatures than larger cod.^{216,240}

In Mid-Atlantic Bight descent to bottom at 25–50 mm^{217,232} in New England at age of 2 months and size of ca. 25 to 40 mm.^{17,240} In North Sea at age of ca. 2 1/2 to 4 months,^{108,194,252} descending in relatively shallow water^{84,163} during May,²¹¹ and early July¹⁵⁴ (and remaining pelagic for a longer period in southern waters¹⁵⁸) at extreme lengths of ca. 20 to 50 mm (but usually 25 to 40 mm).^{32,163,214} In Norwegian Sea sometimes remain pelagic for up to 7 months,²⁵⁷ and to sizes of 90 to 95 mm.^{163,240} In Barents Sea descend by late summer²⁷³ (August and September⁵⁴) at lengths of 25 to ca. 75 mm.¹⁰ In or near Iceland descend in early August at ca. 45⁵⁴ to 90 mm.¹⁵⁸ In Greenland mid-August and September at ca. 25 to 30 mm.^{54,121} In Faroes descend in July,²¹¹ In the Baltic move to shallow water (shores and river mouths) at 40 to 50 mm.^{120,130} Young cod may descend both in the littoral region and at greater depths.¹⁸¹ Not all juveniles go to bottom in coastal waters: some descend on offshore banks.²⁴⁰ Two factors affect the length of "larval" life: water temperatures and the depth to which the young must descend.⁵⁴ It is possible that 0- and 1-year class fish make seasonal migrations to shallow water during summer, returning to deeper water in winter, but there is no direct evidence to support this.²⁵² Some populations may make short movements from sandy, muddy bottoms to rough areas,²⁰⁰ while others remain more or less stationary for several years^{173,251} or up to the time of maturity.^{122,196} In still other populations various movements take place: in Norway two year old fish move out into deeper water;²¹³ in the British Isles young fish winter in shallow inshore water, and spend summer offshore⁸⁴

(although some two year olds may not return inshore until the 3rd or 4th year²⁷⁷); in Barents Sea juveniles are in shallow feeding grounds from June to September, but move into deeper water along edge of shelf during winter. The extent of the annual inshore-offshore migration in the Barents Sea increases with increasing age, so that juveniles eventually make "dummy runs" toward the spawning grounds and spend winter near spawning adults. In Iceland older juveniles actually accompany adults on the spawning runs.^{115,252,259,267} "Young" apparently move from the nursery areas in Lofoten Banks to the Barents Sea,⁶⁵ and from the Barents Sea make feeding excursions to Sweden.⁴¹ In Nova Scotia, inshore cod move progressively farther offshore with age; in southern Canada smaller cod are typically in more shallow water than larger cod.²⁰⁵ Juvenile movements are not well-known in American waters; however, in Massachusetts leave coast by mid-June at sizes of ca. 75 to 100 mm.⁵¹

SPAWNING

Location: In Europe principal spawning grounds along coast of Norway (Lofoten Islands), Barents Sea, North Sea, and Faroes to north of Bear Island and possibly Novaya Zemlya;^{35,46,81,84,231,273} also the Baltic Sea,²¹⁴ around Greenland,³⁵ and Iceland.⁵⁸ On the North American coast Newfoundland Banks²¹⁴ south to at least New Jersey²⁴⁰ and, possibly, to North Carolina.²⁵³

Spawning occurs in inlets,^{6,35,217} fjords^{58,63,70,87,131} bays,^{10,232} and harbors,^{6,49} and on both coastal and offshore banks^{153,211} over bottoms of rock, clay, sand, mud, or stone, as well as over areas of aquatic vegetation;^{6,35,75,138} sometimes under ice.³⁵ Spawning fish may occur primarily in a narrow "transition zone" (thermocline, halocline) which may shift position from midwater to near bottom.^{28,54,83,97,257} Maximum distance out, 273 km.²⁷⁷

Depth: In water 1.5 (White Sea) to 330 m deep (Hamilton Bank)²⁶⁶ and highly variable on both sides of the Atlantic (although along coast of United States usually shoaler than ca. 73 m).²⁴⁰ Optimum depth over entire range estimated from 40 to 136 m.^{18,32,32,122,163} Depth may vary with season: in North Sea begins in December within the 40 m depth contour, in January extends out to 80 m, and in March to 200 m.²⁰⁶

Season: Considering the range as a whole, apparently spawns throughout year in both the northwestern and northeastern Atlantic (JDH). In American waters peaks occur from January to mid-September^{33,41,109,208,217,252,277} and in November,²⁰⁰ varying greatly from year to year and from locality to locality.²⁰¹ In European waters peaks vary from February to mid-September^{32,68,104,107,153,154,155,206,208,225,247,248,277} (depending on locality, JDH), and may shift radically in a given locality from year to

TABLE 7. Spawning season of western Atlantic *Gadus morhua*.

	J	F	M	A	M	J	J	A	S	O	N	D
Nova Scotia 40,49,208,240			X			X	X		X	X	X	X
Bay of Fundy 49,208	X	X	X	X	X							
Gulf of St. Lawrence 2,208,218,276					X	X	X		X	X	X	
Labrador 126,143,269			X	X	X	X	X	X				
Newfoundland 8,30,164,198,252			X	X	X	X	X	X	X	X	X	
Emerald Island 208			X	X								
Grand Bank 41,171,240				X	X	X	X	X				
Banquereau 208,257				X	X	X						
Sable Island 208,218			X	X								
Browns Bank 208					X							
New England (no specific location) 91,182,196,240	X	X	X	X	X	X			X	X	X	
Gulf of Maine 33,109	X	X	X	X								
Maine 240		X	X	X	X							
Georges Bank 203,218,240	X											X
Massachusetts 144,171,201,222,240	X	X	X	X		X			X	X	X	X
Rhode Island 77,144,171	X	X	X	X	X						X	X
New York and New Jersey 240	X	X									X	X
North Carolina 253	X	X	X	X	X	X			X	X	X	X

year¹⁵⁷ depending on temperature.^{104,226} On New England coast "smaller race of cod" spawns from November to April while larger cod begin in July.¹⁹⁶ For seasonal summary see table 7.

Duration: Total spawning period varies in length from place to place. Thus, on Lofoten Banks ca. 84 days⁶⁵ and in Arcto-Norwegian region 20 to 50 days.⁸¹ A single individual may continue to spawn over a period of 6 to 8 weeks^{9,65,96,277} and a captive specimen was observed to spawn 6 times in a 17 day period.²⁵²

Time: Primarily at night,^{29,276} and possibly crepuscular (thus "dusk and early morning";¹¹ "probably around day break";¹⁶⁹ and between 1815 and 2300 hours); also recorded at 1130 hours in experimental tanks,^{56,245} and eggs extruded but not fertilized on "bright sunny afternoons."³⁴

Temperature: Range, -1.1 C^{240} (or possibly as low as -1.5 C^{269}) to 12.0 C ;^{186,217} In northwestern Atlantic, $0.6\text{--}12.0\text{ C}$ (although higher temperatures are based on indirect evidence); in northeastern Atlantic, ca. $0\text{ C--}6.5\text{ C}$.¹⁸⁶ Spawning can apparently occur on either a falling or rising temperature,¹¹⁴ although sudden drop in temperature may bring about a cessation of spawning.⁶ Spawning fish may be associated with a narrow temperature band within the water column, and the temperature within this band may vary from 3.0 to 6.5 C .^{28,54,195,259}

Salinity: Range 10.0 to 35.5 ppt;^{10,18,35,45,48,57,68,218} typically somewhat lower in American than in European waters (except for Baltic populations);¹⁸⁶ optimum 32.6 ²⁴⁹ to 35.0 ppt^{18,122} (although optimums are obviously considerably less in areas such as the Baltic where total range extends from ca. 10.0 to 18.0 ppt).³⁵ Under experimental conditions complete egg mortality occurred at 9.93 ppt and high mortality at 12.47 ppt.¹⁸⁶ Sperm became immotile at 7.52 ppt.¹³⁹

Behavior: Males usually proceed females to spawning grounds,^{57,75} but in some areas, as at Lofoten Bank, large females arrive first.²⁵² Males set up and defend terri-

ories several weeks prior to spawning²⁶¹ and remain on spawning grounds longer than females.²⁴⁹ There is a cessation of feeding during the spawning period.⁴³ Behavior leading to spawning involves vertical movements, territoriality of males, and, possibly, stratification, with a group of active males above a less vigorous group of males and females.²⁴⁵ In spite of reports of spawning at the bottom,⁹⁶ the actual spawning act apparently takes place at or near the surface^{9,15,79} (one author reports spawning within the upper one meter).¹⁹⁶

Jones stated that, once mature, cod spawn every year until they die, and pointed out that the theory that older cod do not spawn every year was based on erroneously interpreted otolith studies.²⁵² Thurrow, however, noted that about 7% of all females which developed sexually in a former year were found to suspend propagation for one year.²⁴⁹

Fecundity: Total $200,000$ to $12,000,000$ ²⁴ with averages estimated at $94,000$,⁷³ $1,000,000$,²⁷⁰ and $3,000,000$ to $5,000,000$.¹⁸³ Total fecundity increases with weight¹²⁹ and length (thus $200,000$ at 510 mm, $12,000,000$ at 1400 mm).²⁴ Not all eggs ripen at once¹⁷ and at least 3, and possibly up to 8, batches of eggs are produced each season²³ (Chrzan's statement that mature females "expell their eggs at once and then leave the spawning area,"²²⁹ is probably erroneous, RRM). Estimates of the number of eggs that can be obtained from stripping varies from $11,000$ to $3,000,000$.^{33,133,136,182}

EGGS

Location: Found in bays,⁷⁸ inner parts of fjords^{17:} and in open ocean; in water a few to 2200 m deep²⁶⁰ (although few beyond the 1000 m depth contour and mostly within the 100 m contour);²¹¹ in Norway most plentiful over 90 m contour,²⁵⁵ in Newfoundland Bank over 150 to 200 m, and in Labrador over 280 to 350 m.¹⁸³ May reach concentrations as high as 4500 per square m of surface in some areas.¹⁰ Initially at or near surface,^{2,6} floating slowly upward immediately after ex-

trusion^{11,17} (sometimes as slowly as 32 mm per minute^{169,277}) but great variation in position in water column occurs; "sometimes (as in Langelandsbelt) more numerous on bottom.¹⁵⁵ Sink with age and may actually develop on bottom^{3,17,40,73,230} with descent beginning 5 to 10 days after fertilization^{111,124,133} (unfertilized eggs sink after maximum of 18 to 36 hours).¹⁹⁶ Changes in position in water column may be influenced by water movement,²⁰⁵ weight of accumulated debris, or actual changes in specific gravity of eggs.¹⁸⁴ There are geographic differences in depth at which majority of eggs are found (in Norway at 25 to 30 m,^{123,128} in Baltic at 100 to 300 m,³⁵ in Georges Bank, Gulf of Maine in upper 10 m)^{82,236} and, apparently, in minimum salinity in which they float (estimates vary from ca. 25 ppt in ocean water¹⁹⁵ to 10 to 14 ppt in Baltic^{139,190,191,214}). Other authors have pointed out that eggs will not float at specific gravities of less than 0.025 to 0.021,^{56,58,111,205} and that spring freshets cause eggs to sink.²⁴⁰

High mortalities may be associated with storms and result from mechanical injury of chorion,^{123,266,272} and large numbers of eggs are sometimes washed ashore and stranded by tides, breakers, and wind.^{91,96,138,241}

Ovarian eggs: Initially minute, clear, yolkless. At 0.3 mm yolk formation begins (eggs possibly opaque at this stage²³¹ and with finely granular yolk⁶⁹); at 0.5 mm yolk evident in all eggs. At a later stage, 2 size groups evident, some 0.8 to 0.9 mm, and others ca. 1.2 mm (with the later group perfectly clear). Size of ripe eggs estimated at 1.0 to 1.8 mm.^{23,40,46,69} Eggs ready for deposition are completely transparent¹⁷⁷ (although one author states that they have a "milky appearance"^{7,169}). Micropyle single,⁹ evident as a circular disc of yellow with somewhat raised edges⁶⁹ in lower hemisphere of eggs.^{11,169}

Fertilized eggs: Spherical⁵ or nearly so;¹⁹⁴ sometimes distinctly ellipsoidal¹¹⁴ (perhaps abnormal when so shaped, RRM). Color variable (so much that Dannevig proposed races of cod based on color of spawn):¹⁸⁴ Clear, cream color,^{120,183} pale green,^{17,96} yellowish red,²⁵⁶ or deep red (although red eggs usually die in 4 to 5 days).⁹⁶ Blastodisc light terra-cotta, but pigment lost as development proceeds.²⁴³ Diameter of egg variously estimated from 1.1 to 1.89 mm;^{5,10,17,20,32,33,41,71,72,78,109,195,197,214,243,247} average diameters estimated from 1.30 to 1.76 mm.^{11,33,66,109,156,196,277} Eggs are larger in cold water than warm water²⁴⁰ and size varies seasonally;¹⁵⁹ in Barents Sea 1.49 to 1.53 mm in March, 1.39 to 1.46 in April; in North Sea average decreases from 1.46 mm in early January to 1.30 mm by end of April;²¹⁴ in Nova Scotia 1.12 to 1.55 mm in autumn (average 1.36 mm), 1.3 to 1.7 mm in winter and early spring (average in spring 1.50 mm);⁶ in Narragansett average 1.39 mm in December and January, 1.34 mm in April and May.²⁶² Smallest fish apparently produce smallest eggs.^{96,118} Eggs adhesive (thus sometimes coated with detritus,^{73,96} although this is

atypical, RRM). Egg membrane thin,²⁶¹ fragile³² (0.00635¹¹⁴ to 0.0079 mm thick¹⁵⁹), laminated,²⁴³ non-iridescent^{78,153} (although showing faint bluish translucency¹¹⁴). Sars claimed that the chorion consisted of 4 layers;⁶⁹ while Ryder pointed out that cod eggs lack a zona radiata.⁴⁴ Yolk homogenous, variously described as clear, cream-colored,²¹⁴ or yellow,^{78,155,247} and surrounded by a thin, fragile vitelline membrane.¹²⁷ Oil globules lacking^{72,240} (although Sars noted numerous small "oil globules" scattered over the yolk of eggs in which the micropyle was still evident when viewed "with the aid of a strong microscope"⁶⁹). Perivitelline space quite narrow.¹²⁷

EGG DEVELOPMENT

Development at 5.5 C (Meek series):²⁹

1st day.	Early cleavage stages.
2nd day.	Blastomeres crowded.
3rd day.	Blastocoel, endoderm, and mesoderm formed, notochord evident.
4th day.	Germ ring around 1/2 yolk.
5th day.	Blastopore narrow; somites, optic vesicles, optic cavity, and infundibulum formed.
6th day.	Blastopore closed; heart, liver, lumen of brain, auditory placodes, Kupffer's vesicles formed.
7th day.	Tail free, median finfold evident; lens separated from ectoderm, nasal organs evident as thickened cellular masses; notochord vacuolated; pronephros formed or forming.
8th day.	Optic nerves forming, small cavity evident in each nasal thickening, heartbeat established.
9th day.	Tail extended nearly to head, body flattened posteriorly, pronephric ducts joined above anus.
10th day.	Embryo fully encircles yolk, gas bladder evident, pectoral fins forming, renal vesicles formed, blood corpuscles evident.
11th day.	Mouth closed by thin membrane, renal vesicles now in contact with cloaca.
12th day.	Hatching. ²⁹

Development from time of 2-cell stage at 6 C (Bonnet series):¹²⁴

52 hours.	Early gastrula.
62 hours.	Quarter gastrula.
83 hours.	1/2 gastrula.
130 hours.	3/4 gastrula, somites present.
136 hours.	Just prior to closure of blastopore, 11 somites.

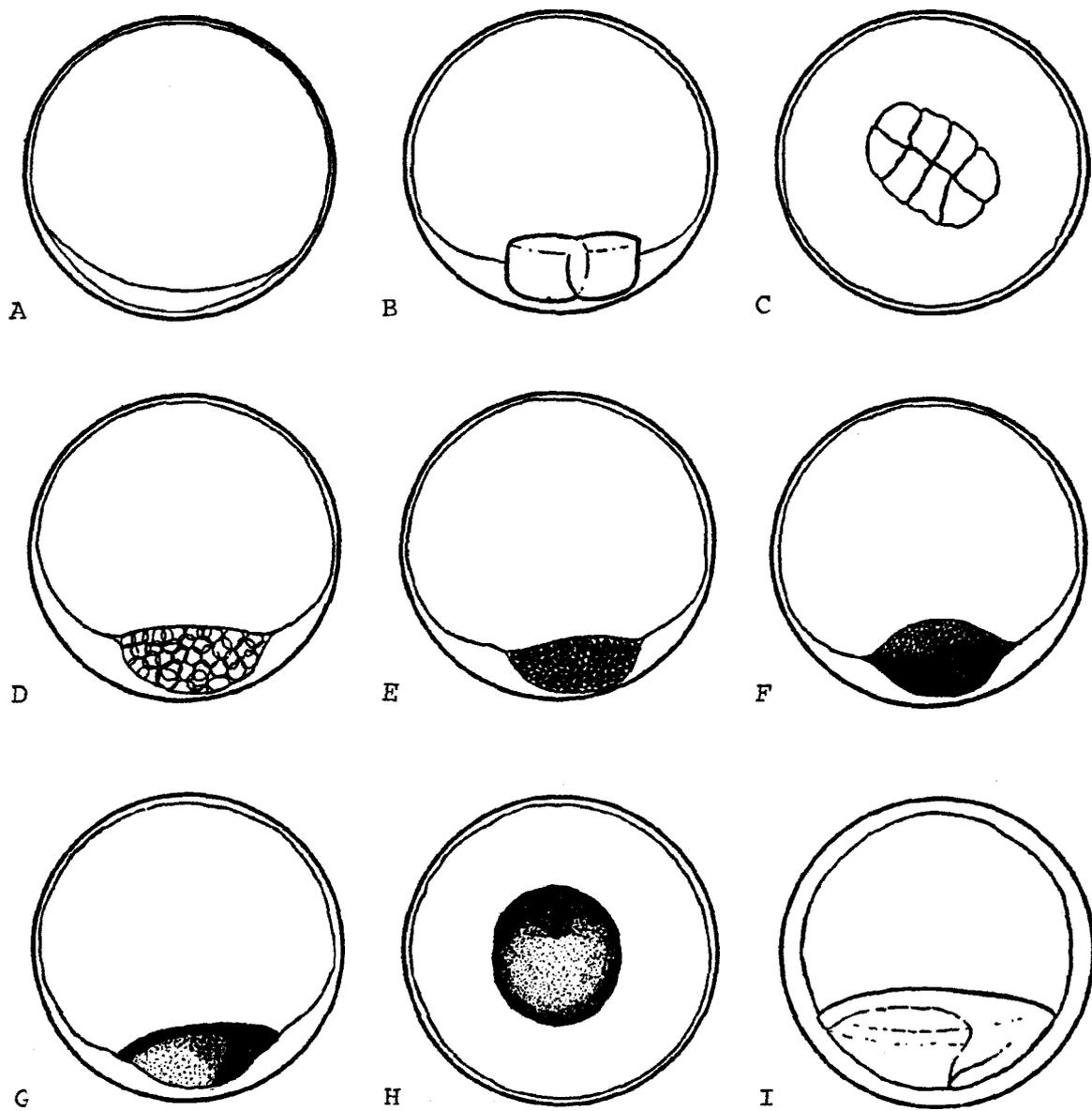


Fig. 145. *Gadus morhua*, Atlantic cod. A. Blastodisc formed. B. 2-cell stage. C. 8-cell stage. D. Early morula. E. Mid-morula. F. Late morula. G. Early gastrula. H. Dorsal view of G. I. Blastoderm extended one fourth over yolk. (A-I, Bonnet, D. D., 1939: figs. 1-8.)

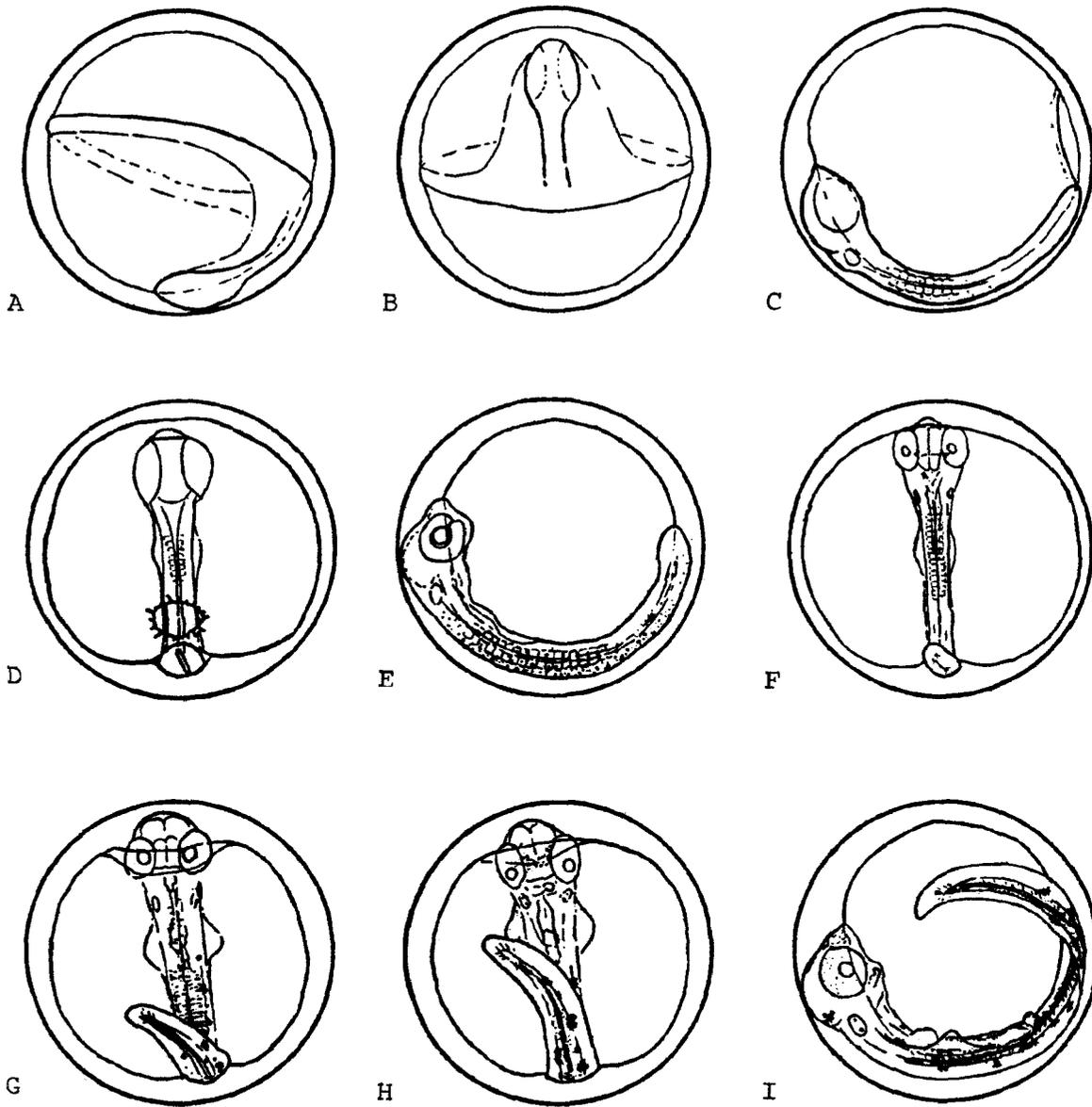


Fig. 146. *Gadus morhua*, Atlantic cod. A. Blastoderm to equator of yolk, lateral view. B. Same as A, dorsal view. C. Blastopore evident, 7 somites formed, pigment developing. D. 11-somite stage. E. 18-somite stage, pigment increased. F. Same as E, pectoral fin buds evident. G. Tail free, 35 somites. H. Heartbeat established. I. Same as H, otoliths developed. (A-I, Bonnet, D. D., 1939: figs. 9-14.)

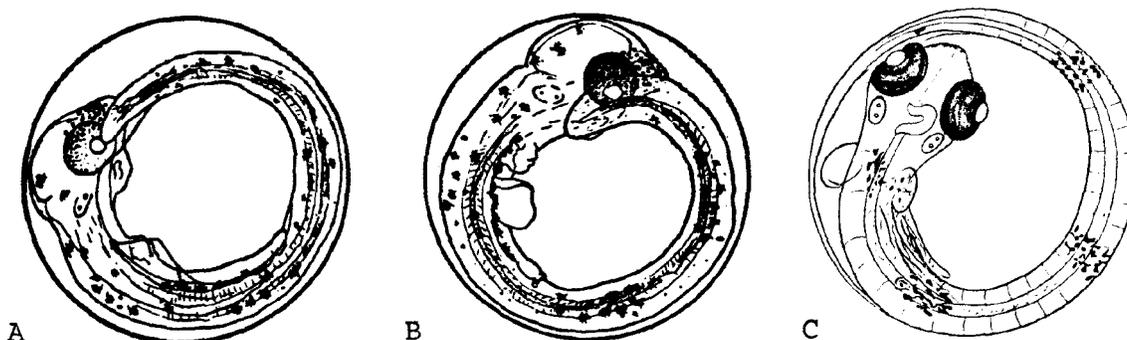


Fig. 147. *Gadus morhua*, Atlantic cod. A. Tail extended to head, pigment developed in upper part of eye. B. Pre-hatching stage, eye well pigmented, body pigment localized into bands. C. Pre-hatching stage showing more definite pigment bands. (A, B, Bonnet, D. D., 1939: figs. 17-18. C, Ehrenbaum, E., 1905-1909: 226.)

154 hours.	Pigment evident; 18 somites, pectoral buds formed.	Day 3, 1600 hours.	Otoliths evident, pectoral buds forming.
202 hours.	35 somites.	Day 4, 1500 hours.	Heartbeat, body movements established.
226 hours.	Heartbeat, tail movements established; otoliths evident; eye pigment forming.	Day 5.	Yolk decreased, pectorals pointed posteriorly, liver evident, round melanophores on head and dorso-lateral region of trunk.
298 hours.	Upper eyes well pigmented.	Day 6.	Eyes pigmented, 3 branchial clefts, nasal pits visible, some individuals hatching.
416 hours.	Pigment localized into definite bands, hatching imminent. ¹²⁴	Day 7.	Some individuals not yet hatched. 4 branchial clefts evident, stellate chromatophores on head. ¹⁵⁹
Development at 6-8 C (Nordahl series): ²⁷⁴		Development at unspecified temperature (Sars series): ⁶⁹	
Ca. 105 hours.	Blastopore nearly closed, 8-10 somites, notochord formed, future gut evident in posterior half of embryo.	"A few hours." 112 hours.	First division. Blastoderm evident as multicellular cap.
Ca. 111 hours.	13 somites, Kupffer's vesicle forming.	8 days.	Blastoderm nearly around yolk, embryo evident.
Ca. 120 hours.	Blastopore usually closed, 12-14 somites.	16 days.	Ready to hatch; iris completely pigmented, and with silvery gloss; pigment at base of pectoral fins, along upper side of gut, and on back in distinct bands. ⁶⁹
Ca. 135 hours.	Tail-free stage.	Development at unspecified temperature (Ryder series): ⁴⁴	
Ca. 155 hours.	25 somites.	3 hours.	Germinal disc defined.
156 hours.	Liver evident.	6 hours.	Germinal disc "biscuit-shaped."
177 hours.	30 somites. ²⁷⁴	8 hours.	2-cell stage.
Development at 15 C (McIntosh and Prince series): ¹⁵⁹		9 1/2 hours.	4-cell stage.
At beginning of series (day 1).	Germ ring 1/3rd over embryo.	23 hours.	14- and 18-cell stages.
Day 1, 2 hours later.	Germ ring to equator.	45 1/2 hours.	Morula.
Day 1, 1500 hours.	Keel of embryo deepened, faint indications of optic enlargements.	4 days.	Underside of germinal disc convex. Blastoderm beginning to spread laterally over yolk; segmentation cavity, epiblast, hypoblast developed.
Day 1, 1600 hours.	Optic vesicles completed.	7 days.	
Day 2, 1000 hours.	Blastopore closed, 5-6 protovertebrae.		
Day 2, 1200 hours.	10-12 protovertebrae, invagination of lens evident.		
Day 3, 1500 hours.	Otocysts, mesenteron developing.		

8 days.	Medullary plate formed.	-1.2 C
10 days.	Optic vesicles formed.	-1.0 C
"About 10th day."	First somites formed.	
14 days.	Heart, auditory vesicles, some somites, optic cup, choroid fissure, intestine, nasal organs differentiating; Kupffer's vesicle present; stellate chromatophores on body.	-0.6 C -0.56 C 0.0 C
15 days.	Heart developed as spherical cavity.	
16 days.	Tail free, liver forming, otoliths evident, pectoral fin buds developed as short lateral ridges, position of anus defined.	0.5 C 0.6 C 1.0 C 1.1 C
17 days.	Primary brain vesicles evident.	1.7 C
18 days.	Heartbeat established, no blood corpuscles, eye becoming pigmented. ¹⁴	2.2 C 2.8 C 3.0 C

Notes on development: Prince noted that complete differentiation of the notochord corresponded to the time of closure of the blastopore. Working at unspecified temperatures he observed cardiac contractions on the 6th day.¹¹⁴ Holbrook noted that the anlagen of the heart was evident on the 2nd and 3rd day, as were protovertebrae. In this series gill slits were evident on the 4th day, and the gut was flattened dorsolaterally in the gill region.⁵⁵ Kupffer's vesicle is anterior, not posterior,²⁷⁴ and McIntosh and Prince noted that a developing embryo may have more than one Kupffer's vesicle.¹⁵⁹ McIntosh and Masterman pointed out that the pectoral fins are lanceolate just before hatching.²⁷⁷ Graham noted that at unspecified temperatures cod eggs could be distinguished from haddock eggs on the 11th day of development on the basis of a small black pigment spot below the tail.¹⁹⁴ McIntosh and Masterman noted small round chromatophores on the head and dorsolateral region of trunk 5 days after fertilization and 3 days before hatching. On the following day chromatophores on the body became stellate, and pigment developed in the eyes. During subsequent development the eyes assumed a bright bronzy hue.²⁷⁷ Walford observed black pigment in 5 to 8 days (temperature unspecified)¹⁸⁷ while Prince observed no pigment at unspecified temperatures until 2 days prior to hatching and noted that it was initially confined to the dorsal aspects of the trunk.¹¹⁴ Just prior to hatching there is a group of melanophores near the pectoral fins, a 2nd group above the anus, and 2 or 3 equally spaced groups over the tail.^{32,33,214,240} The larvae hatch tail first.^{115,194}

Incubation period: 8 days (temperature unspecified)²⁷⁷ to 60 days at minus 1 C¹⁹⁷ (a report of hatching in 107 hours—slightly over 4 days—at an average temperature of 8.3 C⁷³ is questioned, JDH).

Incubation at various temperatures:

		50 days. ^{40,43}
		42 days. ¹⁸
		Ca. 50 days. ²⁶⁹
		60 days. ¹⁹⁷
		50 days. ^{44,152,196}
		50 days. ⁴³
		40 days. ^{43,196}
		40 + days. ²⁴⁰
		Ca. 43 days. ²⁶⁹
		43 days. ¹⁹⁷
		34 days. ⁴⁰
		35 days. ¹⁹⁷
		42 days. ¹⁰²
		31 days. ^{43,197}
		28 days. ¹⁹⁷
		24 days. ⁴⁰
		25 days. ⁴³
		23 days. ¹⁹⁷
		20 days. ⁴⁰
		23 days. ^{18,43,124}
		20 days. ^{44,197}
		21 days. ¹⁹⁶
		20-23 days. ^{96,253}
		19 days. ¹⁹⁶
		20.5 days. ^{18,43}
		Ca. 17 days. ^{43,196}
		17 days. ¹⁷
		16 days. ²⁵⁶
		17.5 days. ^{5,18,40,43}
		20-24 days. ²⁵⁶
		12 days. ^{6,29}
		15 days. ¹⁹⁶
		15.5 days. ^{18,43}
		16 days. ¹⁸⁸
		17.2 days. ⁶
		14 days. ^{43,196,219}
		14-15 days. ^{96,240}
		12 days. ¹⁹⁶
		13 days. ⁴⁴
		13 days. ⁴⁰
		15-18 days. ²⁵⁶
		11 days. ¹⁹⁶
		12.75 days. ¹⁸
		13 days. ⁴³
		10 days. ⁴³
		11 days. ²⁵³
		10-11 days. ^{71,210}
		10.5 days. ^{18,43}
		9 2/3 days. ¹⁰²
		9.7 days. ⁴³
		8.5 days. ^{18,43}
		6-7 days. ¹⁵⁹
	Incubation at various mean temperatures:	
	Mean -0.6 C	50 days. ²⁴¹
	Mean 0.6 C	34 days. ²⁴¹
	Mean 1.1 C	31 days. ²⁴¹
	Mean 2.2 C	24 days. ²⁴¹

Mean 3.3 C	20 days. ²⁴¹
Mean 5.0 C	16 days. ²⁴¹
Mean 7.2 C	13 days. ²⁴¹
Mean 8.3 C	10 days. ¹¹²
	11-14 days. ⁹⁶

Incubation at various temperature ranges:

0.0 to 9.4 C	216 to 762 hours. ¹⁸²
3.0 to 4.0 C	20 to 25 days. ⁵⁶
3.3 to 3.9 C	20 to 23 days. ²⁴⁰
3.0 to 5.0 C	40 days. ⁵⁵
5.0 to 6.0 C	Ca. 14 days. ²⁵²
6.0 to 7.0 C	Probably 16 days. ²⁴³
7.0 to 8.0 C	15 days. ⁵⁵
7.2 to 8.9 C	11 to 12 days. ¹¹⁶
10.0 to 11.0 C	11 days. ⁵⁵

TABLE 8. Incubation at various combinations of temperature and salinity¹²⁷

Temperature C	Salinity ppm	Time to 50% hatch (days)	Duration of hatching period (days)
2	30	21	16
2	32	22	6
2	34	21	8
2	36	24	11
4	26	18	5
4	28	18	5
4	30	17	6
4	32	13	8
4	34	13	6
4	36	13	5
6	26	12	3
6	28	12	3
6	30	12	3
6	32	12	5
6	34	12	3
6	36	12	3
8	26	10	5
8	28	10	3
8	30	11	3
8	32	10	2
8	34	11	5
8	36	10	4
10	26	9	3
10	28	9	3
10	30	9	2
10	32	9	2
10	34	9	2
10	36	9	3
12	26	8	1
12	28	8	3
12	30	8	3
12	32	9	2
12	34	9	3
12	36	8	3

Notes on incubation: Bonnet reared eggs which went from 2-cell stage to 50% hatch at 12 C in 8.5 days, at 10 C in 9 days, at 8 C in 11.5 days, and at 6 C in 17.2 days.¹²⁴ Eggs reared at minus 1.0 C for 35 days hatched in an average completion time of 2.5 days when transferred to 6.0 C.⁴⁸

Johansen and Krogh found an upper incubation temperature of 10.2 C¹²⁴ although others have observed

hatching at 14.0-15.0 C.^{18,43,135,159,186} Eggs at "high temperatures" hatch prematurely and the larvae die;²⁴¹ hatchlings from eggs reared at ca. 7.5 C are "frail and weak";²⁵⁶ and there is an increase in mortality at 8.0 to 10.0 C.¹³⁵

Johansen and Krogh noted that development stopped just after appearance of pigment in eggs reared at minus 0.8 to minus 0.2 C (mean minus 0.3 C). Incubation was apparently less successful at temperature gradients of minus 2.1 to minus 1.2 C (mean minus 1.6 C) and minus 1.7 to minus 0.8 C (mean minus 1.2 C).⁴⁸ A. Dannevig noted partial development (up to 9 days) at minus 1.4 C, and obtained complete development at 0.0 C,¹³⁵ while Bigelow and Schroeder reported 50 to 75% mortality in eggs reared at 0.0 C.²⁴⁰ The same percent mortality was observed by Howell in all eggs reared below 3.3 C.¹⁹⁶ Price reported that hatching occurred at 2.8 C, but was less successful at lower temperatures.⁹⁶ Rognerud noted that larvae hatched below ca. 2.5 C were "frail and weak."²⁵⁶ Hatching is not synchronous, and the hatching period may vary from 1 to 16 days.^{48,127,241} Optimum incubation temperatures have been estimated at 3.0 to 5.0 C,¹³⁵ 5.0 to 8.5 C,^{96,240} and 2.0 to 8.0 C.²¹⁸ The threshold of incubation has been variously estimated as minus 2.0 C¹³⁵ and minus 3.6 C.¹⁵²

YOLK-SAC LARVAE

Hatching length 3.0 mm²⁰⁶ or smaller (based on stated average of 3.0 mm)²⁰¹ to ca. 5.0 mm.¹³¹ (Cod larvae hatched on shipboard ranged from 3.30 to 5.71 mm in length with averages varying from 3.58 to 4.95 mm, but age at time of measurements was not stated.^{141,143}) Length at end of stage 4.0¹⁵⁹ (although apparently more often 4.5^{21,32,102,136,158,206,214}) to 5.19 mm.¹⁰⁹ Duration of stage 7^{44,159} to 15 days^{32,241} and varying with temperature. Twelve days at 7.2 C.²¹⁹ Feeding may begin in specimens as small as 3.0 to 3.2 mm which still retain yolk.^{208,268}

Abdominal vertebrae, 18-20.²⁷⁵

In a specimen 4.71 mm, preanal distance 1.83 mm.¹³²

Body thin,⁶⁹ curved;^{96,241} head rounded, deflected downward at hatching;⁶⁹ snout free of yolk in 3 days.¹⁵⁹ Mouth not open at hatching,¹¹⁷ open in 3 to 7 days;^{44,159} mandible extended beyond upper jaw by 4th day.¹⁵⁹ Brain with distinct mesencephalic flexure at hatching.²⁹ Choroid fissure still evident at 5.0 mm or on 3rd day.^{26,124} Otoliths closer to eyes by 3rd day than in earlier stages.¹⁶² Gills without filaments at hatching,²⁹ gill clefts distinct at ca. 4.0 mm or at 1 day.⁴⁴ Notochord multicolumnar.²⁴⁴ Forward part of dorsal finfold developed as supraceutical sinus; supraceutical sinus small at hatching, elevated at 1 day, well-developed at 4th

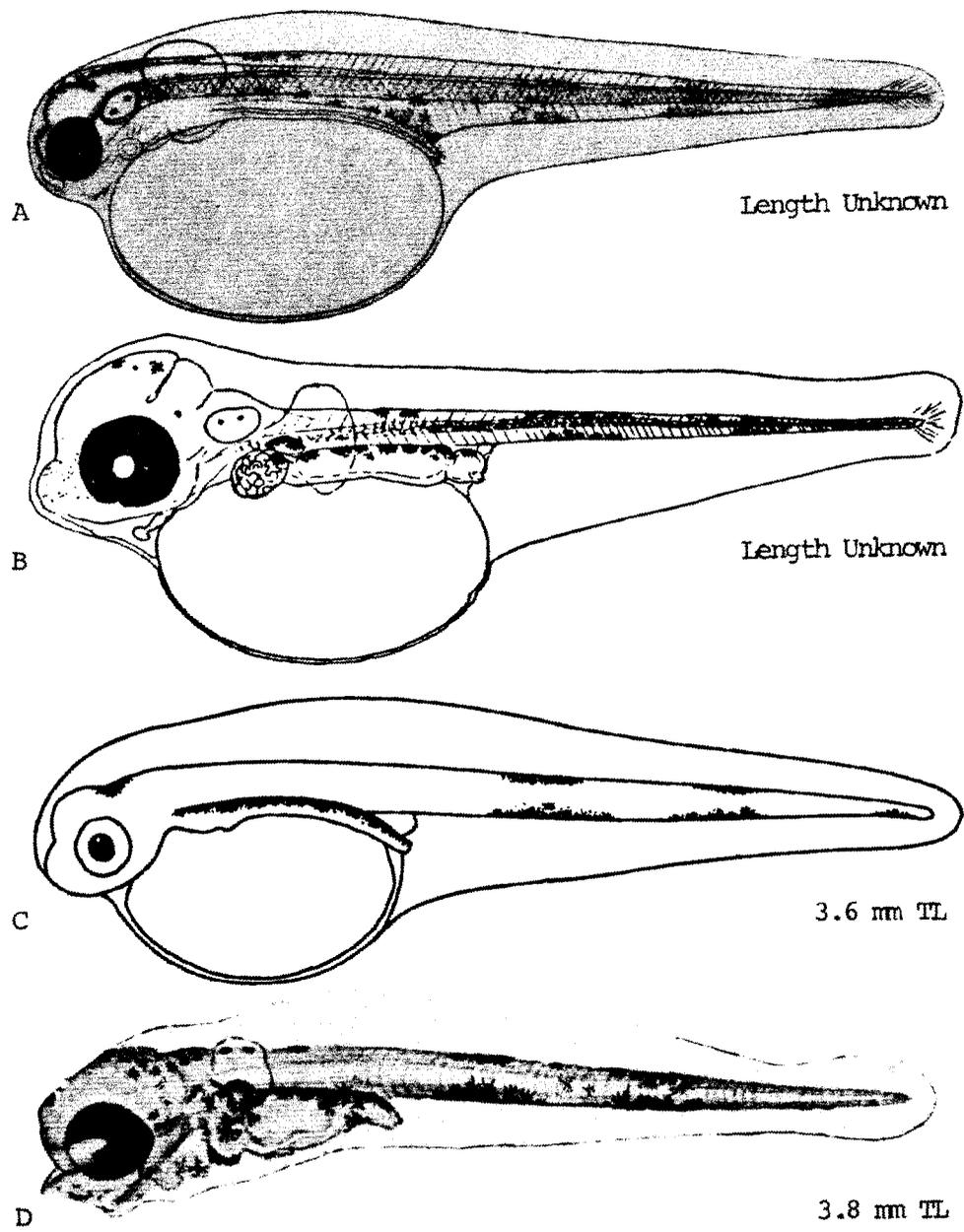


Fig. 148. *Gadus morhua*, Atlantic cod. A. Yolk-sac larva, length unknown, showing typical pigment pattern. B. Yolk-sac larva, length unknown, 3 days old. C. Yolk-sac larva, 3.6 mm TL. D. Yolk-sac larva, 3.8 mm TL. (A, M'Intosh, W. C., and A. T. Masterman, 1897: pl. 9. B, Bonnet, D. D., 1936: fig. 18. C, Colton, J. B., Jr., and R. R. Marak, 1969: 24. D, Dannevig, A., 1918: fig. 16.)

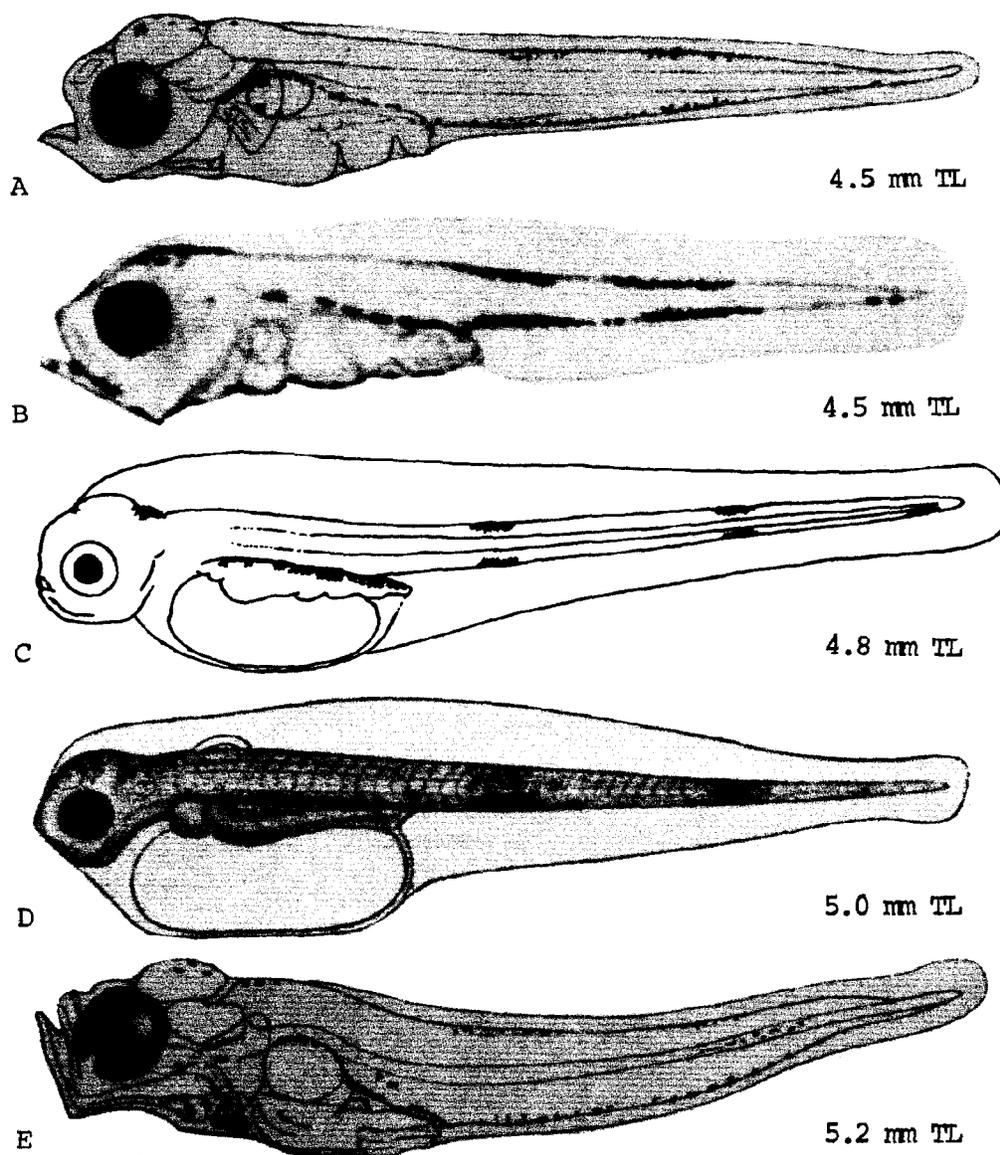


Fig. 149. *Gadus morhua*, Atlantic cod. A. Yolk-sac larva or larva, 4.5 mm, mouth well formed. B. Yolk-sac larva or larva, 4.5 mm, showing broad pigment bands on body. C. Yolk-sac larva, 4.8 mm, pigment bands narrow. D. Yolk-sac larva, 5.0 mm, pigment bands fused laterally. E. Larva, 5.2 mm. (A, E, Masterman, A. T., 1901: pl. I. B, Schmidt, J., 1905: pl. I. C, Miller, D., 1958: 9. D, Murray, J., and J. Hjort, 1912: fig. 520.)

day.^{26,277} Incipient caudal rays at ca. 4.0 mm (24 hours);⁴⁴ pectoral fin large and clearly defined at hatching,²¹⁴ circular in outline at ca. 4.0 mm,⁴⁴ with incipient rays at 5.0 mm,²⁸ and nearly vertical at 7 days.⁴⁴ Stomach just formed; intestine thick-walled, straight at hatching.^{29,69} Anus not yet formed at 7 days,¹⁵⁹ when formed, opens laterally on left side of body at base of finfold.^{29,33} At time of hatching gall bladder evident,¹⁹⁴ gas bladder still connected with enteron;²⁹ gas bladder well formed

at 4.0 mm (24 hours). Lateral sense organs evident as elevations surmounted by fine "hairs" at ca. 4.0 mm. Pronephros evident at 7 days.⁴⁴

Pigmentation: At time of hatching and throughout stage transparent²⁹ (including yolk)¹⁶⁰ with chromatophores aggregated in 4 or 5 distinct bands: one behind pectorals, one toward posterior border of yolk^{159,277} (these two occasionally continuous),²⁴³ and 2 or 3 on tail.^{159,277}

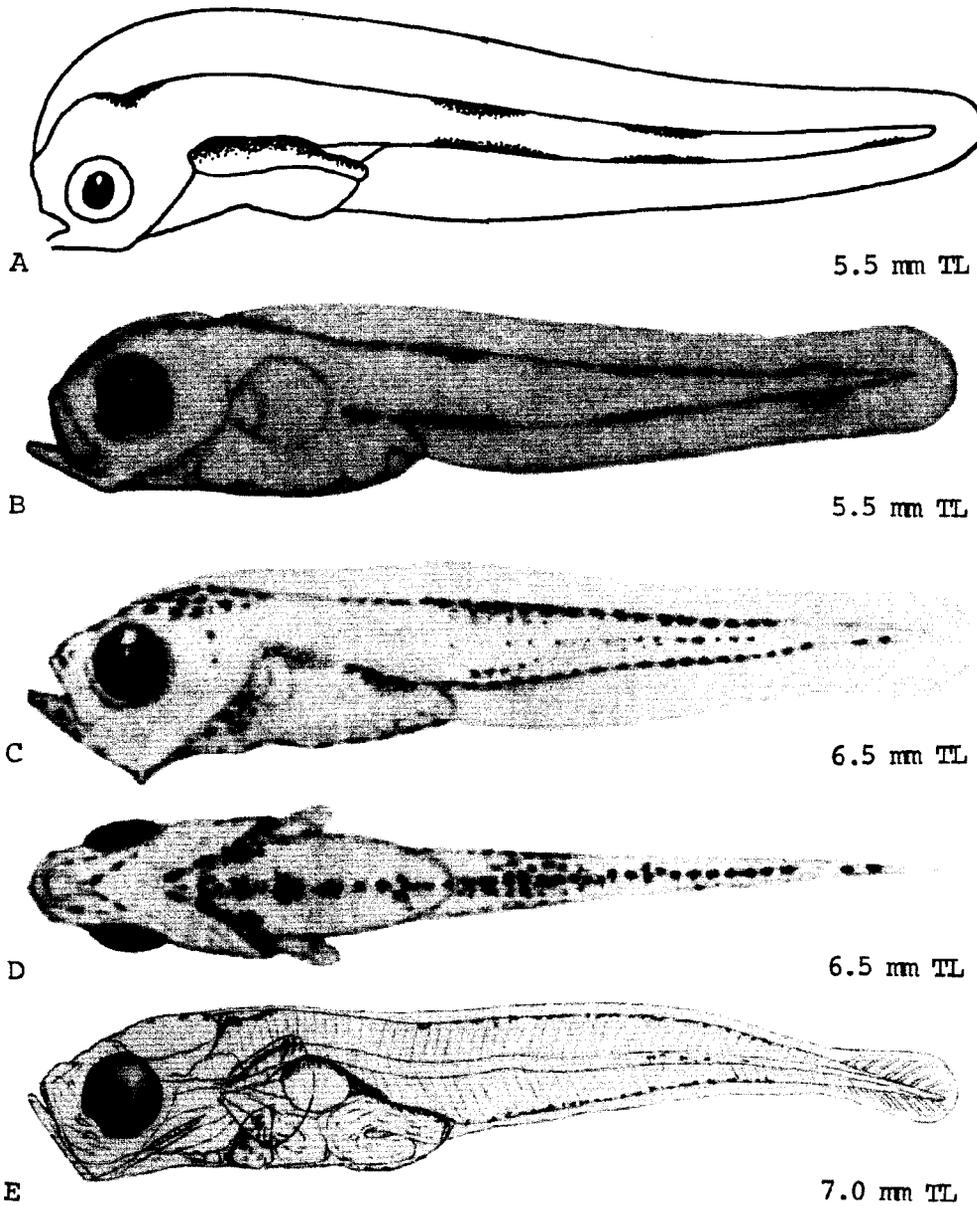


Fig. 150. *Gadus morhua*, Atlantic cod. A. Larva, 5.5 mm. B. Larva, 5.5 mm. C. Larva, 6.5 mm. D. Ventral view of C. E. Larva, 7.0 mm, incipient rays in caudal fin, gut coiling evident. (A, Colton, J. B., Jr., and R. R. Marak, 1969: 24. B-D, Schmidt, J., 1905: pl. I. E, Masterman, A. T., 1901: pl. I.)

Dorsal pigment bands shorter than corresponding ventral bands (opposite in pollock).^{34,77} Pigment bands vary geographically. In North Sea, sometimes lack postanal bands²¹⁴ (as well as mediolateral streak which develops later in stage in some populations).¹⁵⁸ In Murmansk, posteriormost band often lacking, preanal ventral pigment very light.¹⁰ Melanophores in dorsal wall of peritoneum, especially over swim bladder and, sometimes, scattered chromatophores over brain.¹³⁶ Eye deep

black;¹⁵⁶ also described, without reference to length or age of specimens, as having a bright bronze-like hue.¹⁵⁹

At 4.0 mm typical pattern with additional chromatophores on head, at angle of mandible, and on ventral surface of abdomen. Eyes deeply pigmented and with bluish silvery sheen.¹⁵⁹

At 4.5 mm pigment bars sometimes partly or completely fused, a mid-ventral line of pigment from anus to near

tip of tail, an oblique streak of abdominal pigment, and few large stellate chromatophores in occiput. Body with diffuse yellow-green tinge, especially over head.^{136,158}

At 3.30 to 5.19 mm scattered chromatophores on back of head, pigment over gut increased.¹⁰⁹

At ca. 5.0 to 5.2 mm dorsal elements of postanal bars approaching one another;¹³⁶ chromatophores present¹⁵⁹ or absent on head and jaws;²⁷⁷ row of chromatophores forming along lateral line; internal pigment increased to include liver and pericardium;¹³⁶ subnotochordal black band;¹⁵⁹ eye with purplish sheen, stomach sometimes stained pinkish by ingested copopods.²⁷⁷ Greenish yellow coloration on head, snout, and dorsal region of body.¹⁵⁹

LARVAE

Minimum size ca. 4.5²⁷⁵-5.5 mm;⁴⁴ size at end of stage 24²⁰⁶ (or possibly as small as 20 mm)^{13-30 mm.}²¹⁴

Abdominal vertebrae, 17-20, average 18.4.³³

At 9.5 mm nasal region elongated, mandible horizontal,²⁷⁷ lower jaw projecting.⁶⁹ Choroid fissure evident to at least 6.0 mm.¹⁵⁹ Teeth apparent at 19.0 mm.¹³⁶ Brachiae of gills with simple papillae at 8.0 mm.¹⁵⁹ Development of barbel variable, reported first evident over a size range of 7.0 to 19.0 mm,^{136,268} but also noted as absent in specimens up to 30.0 mm long.^{13,214} Urostyle oblique at 9.5 mm²⁷⁷ to 11.0 mm.^{152,158,211} Lateral line sharply defined at 11.0 mm.¹³⁶ At 8.0-9.0 mmanlagen of D.₂, D.₃, A.₁, and A.₂ present as thickenings in finfold;^{158,159} fin ray development in unpaired fins first evident at 9.0 mm^{190,214} (a report of many embryonic rays at 7.0 mm¹⁵⁹ is questioned, JDH). Incipient rays in D.₁ at 12.0-13.0 mm and in D.₂ and D.₃ at 11.0 mm;^{158,206,214} D.₂ and D.₃ complete at 20.0 mm;¹⁵⁸ D.₁ complete at ca. 26-30 mm.²¹⁴ Incipient anal rays over size range of 10.0-13.0 mm;^{71,158,206} anal fins complete at 20.0 mm;²⁴⁰ at ca. 15.0-30.0 mm, A.₁ not extended backward further than D.₂.^{158,211} Remnants of finfold evident at 20.0 and 24.0 mm.^{13,136,214} Incipient caudal rays at 6.5¹⁵⁸ to 9.0 mm;²⁰⁶ at 20.0 mm accessory fin rays above and below tail which exceed definitive number of caudal rays;⁶⁷ caudal fin initially rounded,²⁵ symmetrical at ca. 8.5 mm,²⁷⁷ immarginate at 9.0 mm,¹³⁶ squared posteriorly and with an essentially straight edge at ca. 15.0-30.0 mm.^{158,211,214} Pelvic buds barely evident at 8.0¹⁵⁹-8.5 mm, developed as knob-like processes at 13.0 mm; pelvic fins half diameter of eye at 16.0 mm,¹⁵⁸ with elongate rays at ca. 23.0 mm,¹⁵⁹ and "moved forward" at 24.0 mm.¹³⁶ At 7.0 mm intestine beginning to fold,²⁵⁶ at 7.0-19.0 mm stomach and pyloric caeca formed.²⁶⁸ Anus under D.₂ through size range of ca. 15.0-30.0 mm.^{158,211,214} *Ductus pneumaticus* obliterated at 6.5 mm;⁴⁷ gas bladder oval at 9.0 mm,¹³⁶ somewhat elongate at 13.0 mm.¹⁵⁹

Pigmentation: Pigment pattern of yolk-sac larvae retained to ca. 7.0³³ or 8.0 mm;^{211,240} at ca. 4.5 mm dorsal pigment bars distinctly doubled, 1-3 melanophores on ventral side of tail tip.²⁷⁵ At ca. 9.0-11.0 mm original pigment groupings barely evident, usually a single chromatophore on underside of tail.²¹⁴ By 10.0 mm pigment bars fused (so that postanal pigment is indistinguishable from that of pollock and haddock),³³ a median pigment band formed, and dorsal pigment less pronounced than ventral pigment. At 10.0-20.0 mm pigment extended on to tail^{158,211,240} and general pattern more diffuse.¹⁰⁹ Larvae translucent green and white, with bluish black eyes, and both black and yellow pigment on head and body.^{83,113,194} Pigmentation varies geographically, specimens from southern North Sea and west of Scotland may be only faintly pigmented.²¹¹ Pigment also affected by environment, paling at low temperatures and salinity.¹¹³

At 5.7 mm 2 postanal bands fused; a trace of lateral chromatophores in caudal region; chromatophores on head and on venter from jaw to anus, chiefly in midline. General color uniform greenish yellow.²⁷⁷

At 6.0 mm pigment generally as above, but mid-ventral pigment developed beyond anus, and a pair of short postanal pigment rows along lateral line.¹³⁶

At 6.5 mm ventral postanal streak extended further back on tail, mediolateral streak developing along posterior part of body, few chromatophores in dorsolateral region, yellow pigment on dorsal and ventral aspects of body.^{158,214}

At 7.0 mm pigment intensified, postanal pigment bands well-fused and forming a single dorsal and ventral streak, mediolateral streak more developed, a characteristic pigment blotch evident over pectorals, internal pigment increased, general ground color more yellowish.^{136,159,256}

At 8.0 mm black pigment on top of head, along base of dorsal and ventral finfolds (although less distinct ventrally). A mostly internal line of pigment from pectoral base to anus, few melanophores between developing caudal rays. Eyes bluish silvery. Body yellowish green with greenish translucency.¹⁵⁹

At ca. 8.5 mm pigment more pronounced, scattered yellow chromatophores over head and back.²⁷⁷

At 9.0 mm postanal pigment bars essentially obliterated; mediolateral, dorsolateral, and ventrolateral pigment now strong; a line of pigment over dorsal aspect of neural tube; yellow pigment increased; body with greenish translucency.^{136,158}

At 9.5 mm pigment more abundant and distributed mainly in dorsal and lateral bands and in large patches on head and stomach.²⁷⁷

At 11.0 mm first ventral pigment bar reduced to a single chromatophore, a conspicuous mass of black pigment

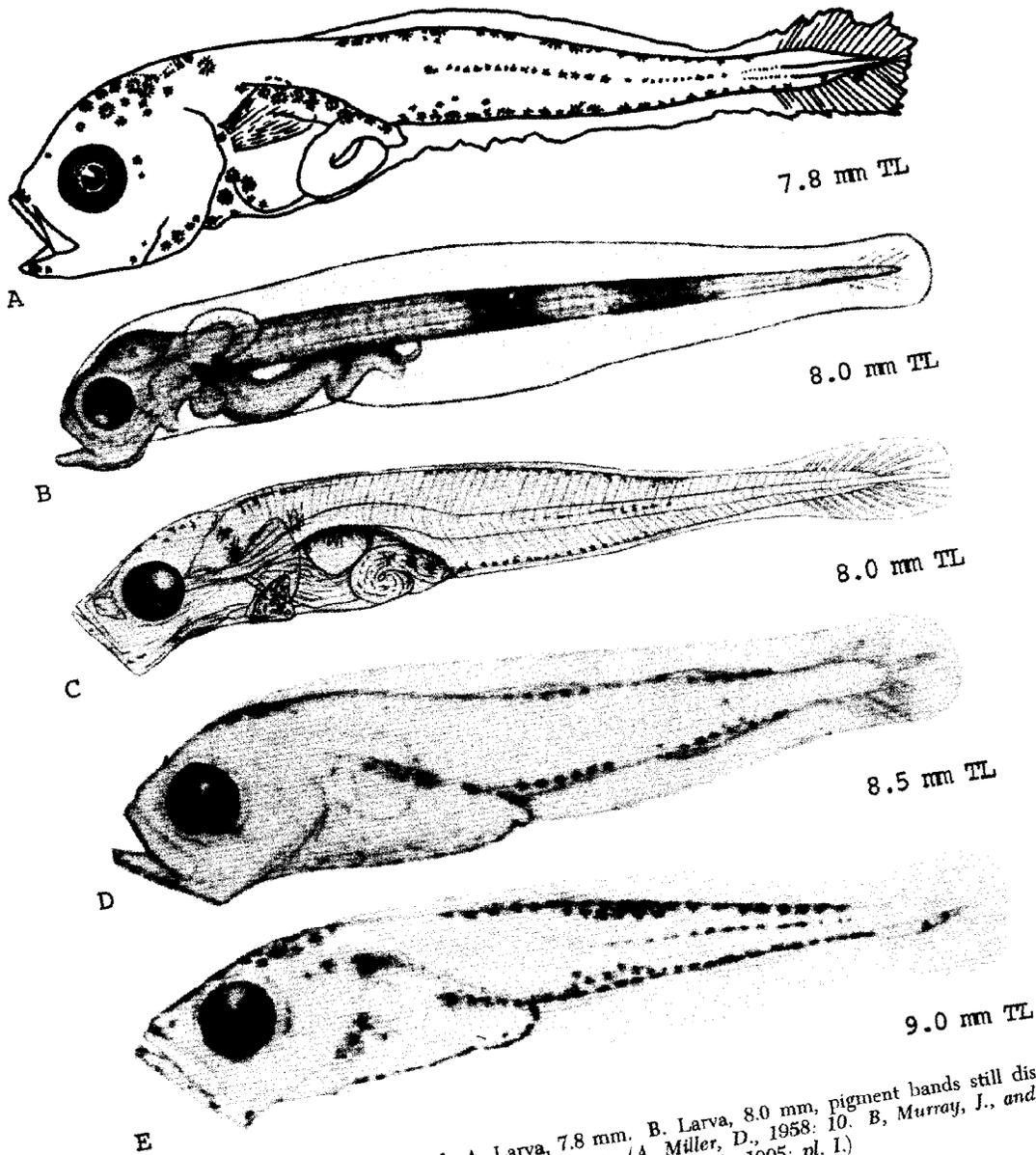


Fig. 151. *Gadus morhua*, Atlantic cod. A. Larva, 7.8 mm. B. Larva, 8.0 mm, pigment bands still distinct. C. Larva, 8.0 mm. D. Larva, 8.5 mm. E. Larva, 9.0 mm. (A, Miller, D., 1958: 10. B, Murray, J., and J. Hjort, 1912: fig. 520. C, Masterman, A. T., 1901: pl. I. D, E, Schmidt, J., 1905: pl. I.)

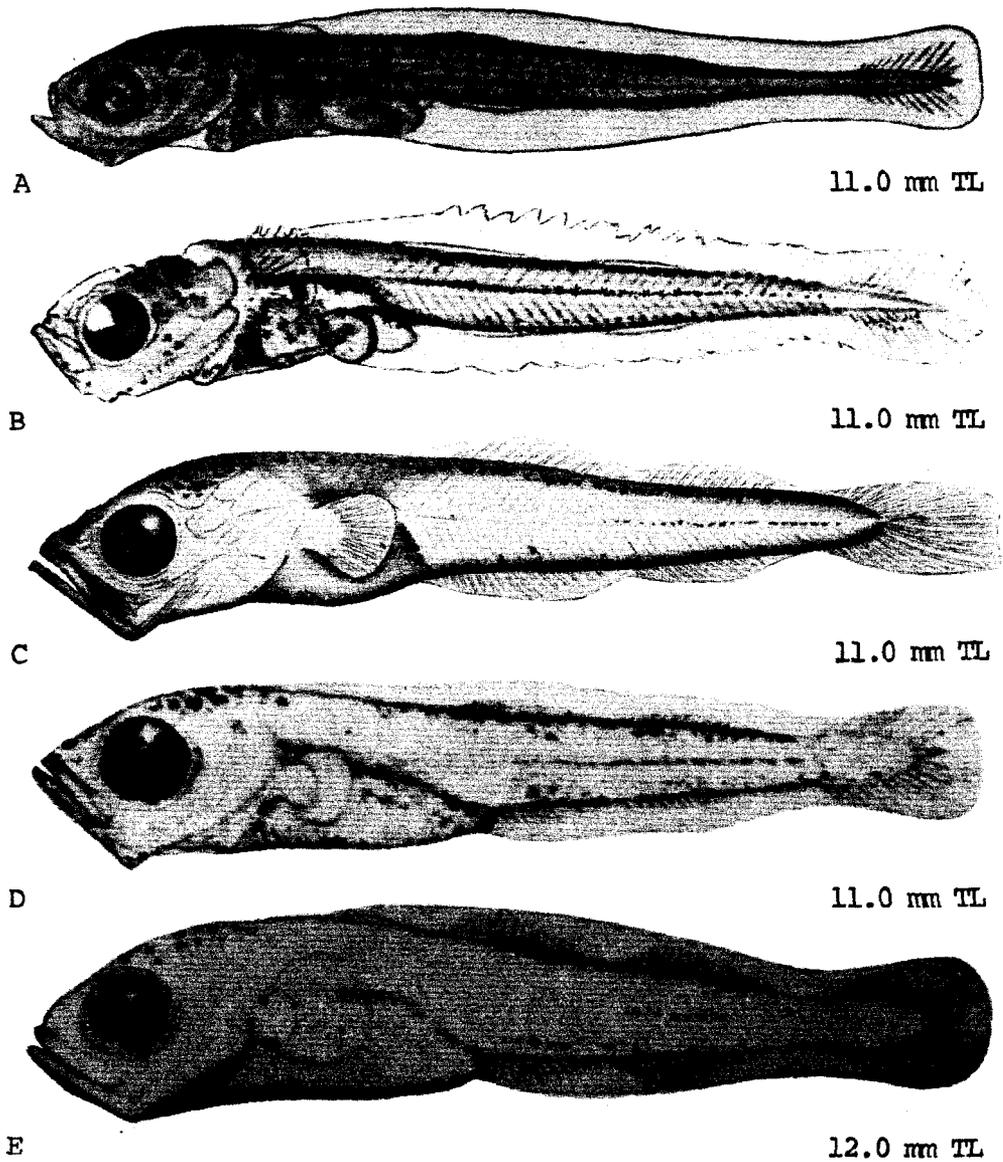


Fig. 152. *Gadus morhua*, Atlantic cod. A. Larva, 11.0 mm, anlagen of dorsal and anal fins evident. B. Larva, 11.0 mm. C. Larva, 11.0 mm, dorsal and anal fins distinct. D. Larva, 11.0 mm. E. Larva, 12.0 mm. (A, Murray, J., and J. Hjort, 1912: fig. 520. B, Dannevig, A., 1918: fig. 17. C, Masterman, A. T., 1901: pl. I. D, Schmidt, J., 1905: pl. I. E, Schmidt, J., 1906: fig. 27.)

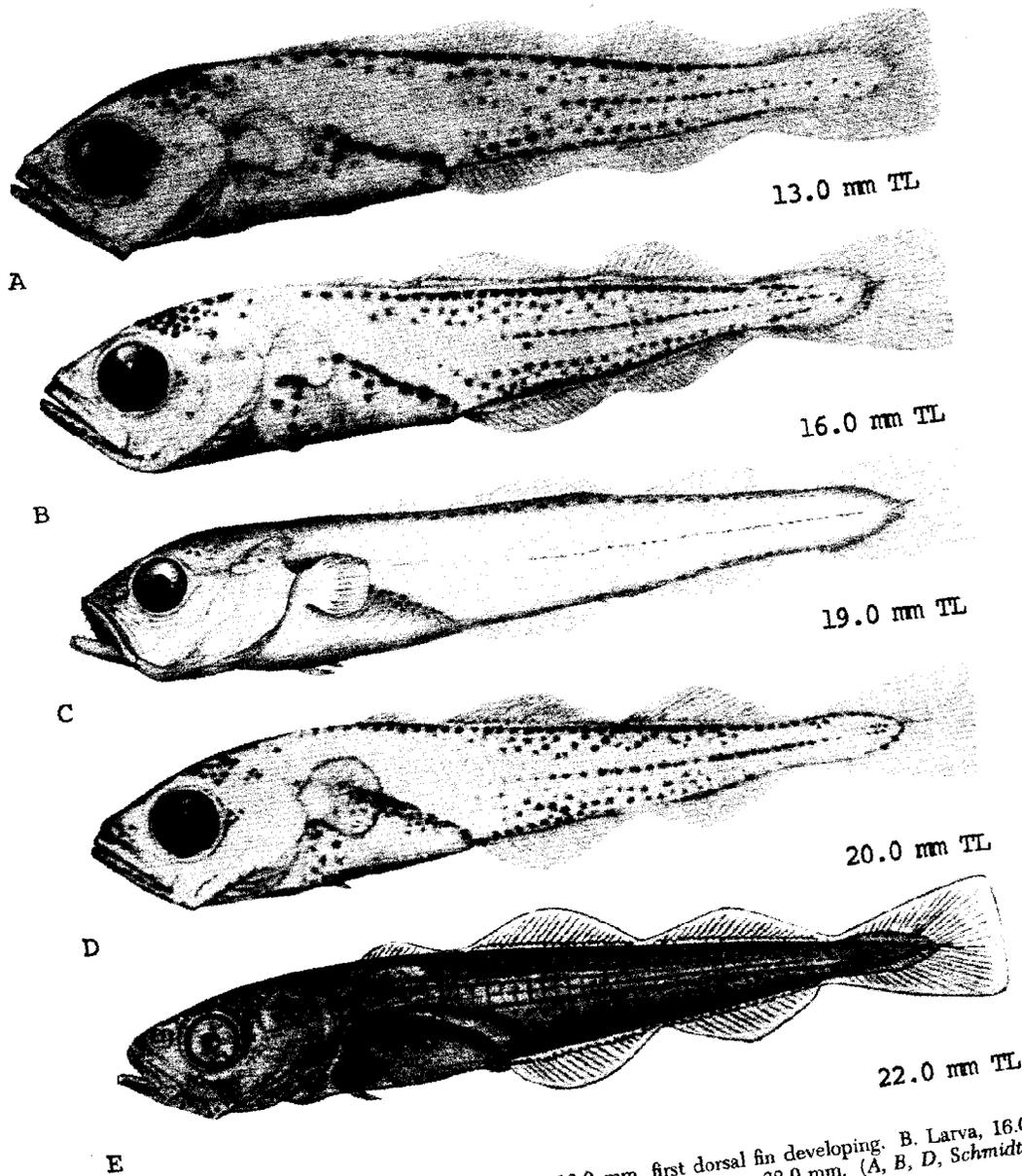


Fig. 153. *Gadus morhua*, Atlantic cod. A. Larva, 13.0 mm, first dorsal fin developing. B. Larva, 16.0 mm. C. Larva, 19.0 mm. D. Larva, 20.0 mm, pelvic fin buds distinct. E. Larva, 22.0 mm. (A, B, D, Schmidt, J., 1905: pl. I. C, Masterman, A. T., 1901: pl. I. E, Murray, J., and J. Hjort, 1912: fig. 520.)

over brain, patches of pigment on jaws and snout.^{136,158}

At 12.0–13.0 mm yellow pigment increased on flanks, silvery sheen evident in abdominal region.²¹⁴

At 16.0 mm mediolateral streak extended posteriorly toward end of tail, yellow pigment extended to middle of sides, forward part of abdominal region with slight silvery sheen.¹⁵⁸

At 20.0 mm yellow pigment diffusely scattered over entire side, dorsal surface uniformly covered with pigment.^{13,158}

At ca. 23.0 mm stellate chromatophores thinly scattered on sides.¹⁵⁹

At 24.0 mm mid-ventral line of pigment from throat to anus no longer visible.¹³⁶

At 30.0 mm mediolateral streak very distinct, occipital pigment more dense, yellow pigment extended to caudal fin, belly silvery¹⁵⁸ (note lack of checkered prejuvenile pattern at this size, JDH).

PREJUVENILES

Minimum length 24 mm²⁰⁶ (or possibly smaller).^{13,268} Length at end of stage ca. 45.0³² or possibly 95.0 mm^{163,240} and with both length at time of development of checkered pattern²¹⁴ and descent to bottom varying

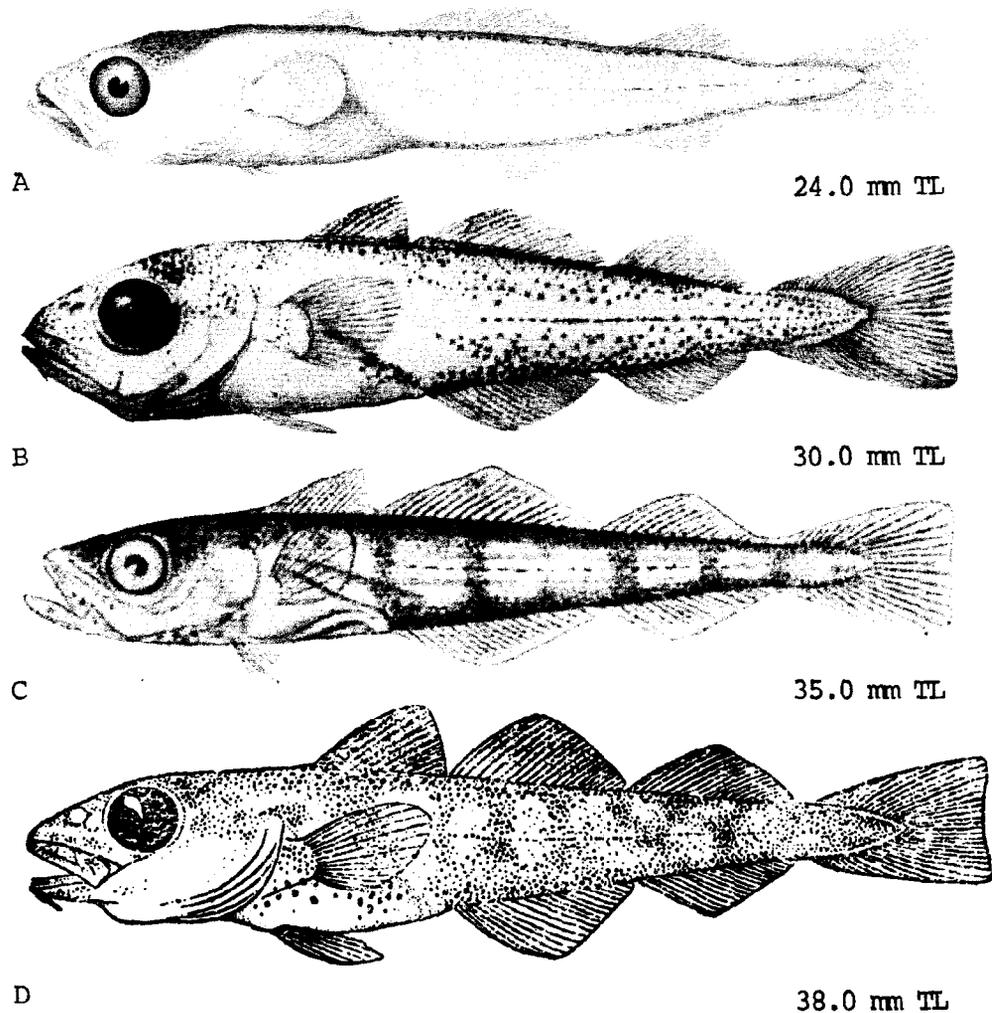


Fig. 154. *Gadus morhua*, Atlantic cod. A. Prejuvenile, 24 mm. B. Prejuvenile, 30 mm. C. Prejuvenile, 35 mm. D. Prejuvenile, 38 mm. (A, Masterman, A. T., 1901: pl. II. B, Schmidt, J., 1905: pl. I. C, Murray, J., and J. Hjort, 1912: fig. 520. D, Rass, T. S., 1949: fig. 23.)

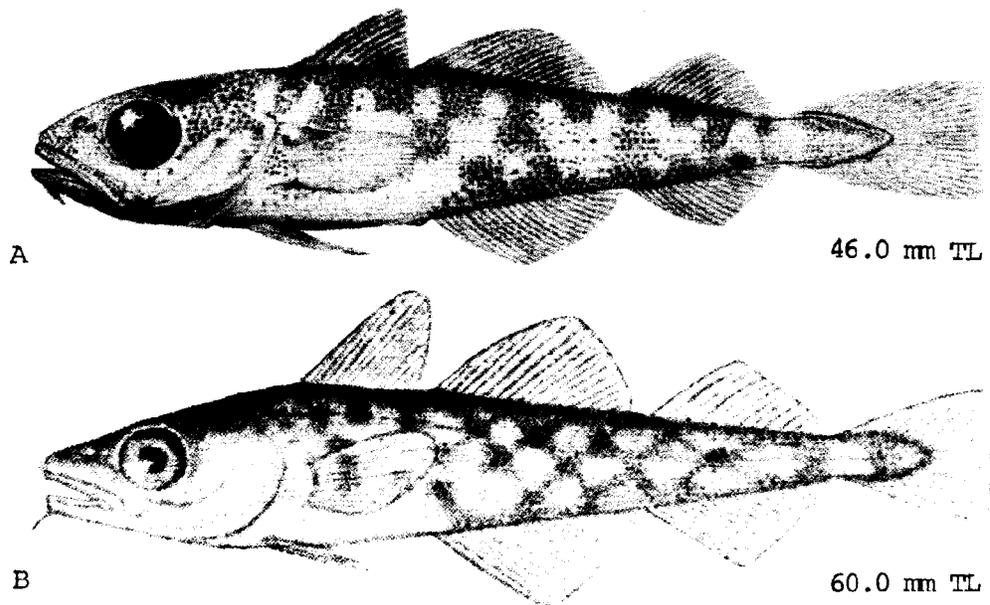


Fig. 155. *Gadus morhua*, Atlantic cod. A. Prejuvenile, 46.0 mm. B. Prejuvenile, 60.0 mm. (A, Schmidt, J., 1905: pl. I. B, Masterman, A. T., 1901: pl. II.)

geographically.^{10,17,32,54,120,130,131,158,163,214,218,232,240} Age at beginning of stage, 2^{17,240}—7 months.²⁵⁷

Body shape practically adult-like at 25.0 mm.¹⁰² Barbels just forming in some specimens ca. 25.0–30.0 mm long.^{214,277} Scales first evident at 30.0¹⁹–50.0 mm²⁰⁶ or at 6²⁰¹ to ca. 12 weeks.²⁰⁰

Pigmentation: Stage characterized by checkerboard pattern.

At 26.0–30.0 mm checkerboard pattern barely evident; pigment present in some unpaired fins, especially D.₁, D.₂, and A.₁; pigment on flanks much increased; yellow pigment fairly evenly distributed over body; belly with silvery hue.²¹⁴

Specimens 30.0 mm long described as mottled or spotted and having opaque skin.^{71,83,240}

At 35.0 mm head with reddish hue; body variegated, pale green, dotted with black. Sides with pale (pearly) blotches between dark bars; ca. 8 dark blotches along median line; 9 dark blotches above lateral line extending back from operculum, the first three of which connect with the belly. Sides sometimes with burnished silver or slightly coppery sheen. Lower part of gill region and belly silvery; a band of pigment on each side of midline of belly, particularly well-developed along anal fin bases. D.₁ and D.₂ dotted with black, primarily between rays, and touched with opalescent bluish. A.₁ flecked with black anteriorly. Pelvics translucent and with few grains

of white on 2 outer rays; caudal fin lacking pigment; pectorals translucent. Eye silvery specked with black and with iridescent orange hue when viewed laterally, blackish with minute iridescent greenish specks from above.²⁷⁷

At 35.0–63.3 mm occiput as well as gills reddish.¹¹⁷

At ca. 38 mm fins sometimes with slight marginal black band.¹⁵⁹

At 35.0–ca. 47.0 mm olive green from above; sides iridescent, with pinkish pearly lustre; upper surface and sides of head to level of eye studded with dark pigment; a series of dark pigment spots along each side of mid-ventral line to tail; ca. 8 spots in uppermost row of checkered pattern; D.₁ with black pigment toward tip; black pigment on sides and under surface of mandible; a dark streak in eye; opercular region and body silvery; eye pale olive green with specks of darker color.¹⁵⁹

At 46.0 mm pigment present on central portion of D.₁ and D.₂, less so on D.₃ and A.₁, and on base of caudal; mediolateral streak almost obliterated.¹⁵⁸

At 50.0 mm (and larger sizes) 3 to 4 parallel lines of bright reddish brown spots on sides, ground color with silvery or golden gloss.¹⁵⁹

A specimen 6 months old is described as still transparent but having overall blotched or mottled appearance, upper parts covered with minute black dots, belly nearly

white, traces of dark bands still evident, and body with golden tinge.²⁴¹

JUVENILES

Minimum length 45³² to ca. 50 mm.¹⁵⁹

Abdominal vertebrae, 17-20.¹⁰⁹

At 12 to 18 months adult-like in general appearance.²⁴¹ Scales first evident (in some specimens) beneath each melanophore above and below lateral line at 40-50 mm.²⁰⁶ Minimum sclerites at 50-80 mm, large sclerites at ca. 110-120 mm.¹⁴⁸ Pelvics nearly as long as pectorals in young, proportionately shorter with age.²⁴⁰ Sexes not distinguishable for first 2 years; ovaries evident after 2 years as very thin tubes along dorsal and caudal part of body cavity.²³

Pigmentation: Juveniles from ca. 100 to ca. 380 mm or weighing up to a few pounds sometimes reddish;^{17,30,241} "small cod" also described as "dark."³⁵ Pigmentation apparently varies with habitat: thus at 1 year (ca. 305 mm) reddish yellow when living among algae, light green or grayish over sand;¹⁵⁹ one year old fish also described as very light grayish green with silvery gloss on sides, and usually, dark spots.²⁵⁵

AGE AND SIZE AT MATURITY

2^{35,57,196} to 16 years²²⁸ with males usually maturing before females^{215,242} and sometimes with a difference of as much as one year (thus, in some populations, males in 3rd year, females in 4th^{17,228}). Averages have been estimated from 2.2 to 2.7 years²⁴⁹ and from 7.8 to 9.9 years.²⁰⁴

In Labrador, 6 to 11 years, with males usually in 7th year and females usually in 8th year.^{86,88,89} In Newfoundland 3 to 10 years,^{89,145} but with only 2% of population at 4 years;²⁴ usually in 7th or 8th years with females "a little later than males."⁸⁹ In Belle Island 6 to 10 years, but usually 7th or 8th year.⁸⁶ In Gulf of St. Lawrence 4th to 10th year, usually 7th or 8th year (and with no difference between sexes).^{24,88} In Gulf of Maine 3rd or 4th year.²⁴ In Barents Sea 5 to 15 years.²⁶⁷ In Kiel Bay males at average of 2.2 years, females at average of 2.7 years; at end of 2nd year 10% of males and 3% of females spawn.²⁴⁹ In Denmark some individuals still immature at 9 years.²³⁴ In North Sea 4 to 5 years.²⁵ In Norway coastal cod 3rd to 7th year, Arctic cod 6th to 14th year;^{93,152} but Norwegian cod variously estimated: in Arcto-Norwegian cod 6 to 15 years, but with one author stating mostly at 8, 9, and 10 years (with males an average of one year before females) and another stating mostly between 9th and 11th years.^{99,252} At Lofoten 7 to 15 years, usually 10th or 11th year.³⁵ At Oslosjord ca. 35% males and 29% females with ripe or ripening

gonads at age of 2 years.^{176,210} In Skagerrak, Kattegat, Belt Sea, and Baltic ca. 24% of age group II mature in northern area and over 75% of age group II mature in southern area.¹⁵⁷ In Skagerrak 54% of age group III spawning, 95% of age group 5.¹⁷⁵ In Faroes some as early as 2 years,¹³⁰ mostly at 5 years.²⁴² In Iceland some cod mature during 3rd year,²³⁷ but such fish probably do not spawn until 4th year.^{62,70,110,185,212,228} Saemundsson gives the following minimums for Iceland: males 3 (rarely) to 5 years on south and west coast, 5 to 6 years on north and east coast; females 4 (rarely) to 6 years on south and west coast, 5 to 9 years on north and east coast.²²⁰ Maximum age at first maturity, 16 years.²²⁸ Majority usually mature between 7th¹⁷⁸ and 10th year,²⁶⁰ with overall average estimated at 7.8 years.⁶² One author presents somewhat lower estimates: males at 4 to 7 years, females at 5 to 9 years.⁷⁰ Cod mature earlier in warmer waters of southern coast than in cooler waters of northern coast,^{110,228} and average age at first maturity may shift from year to year in a single population.^{94,180} In Greenland 5th to 11th year^{89,95,131} (although few in 5th year);¹¹⁰ usually in 7th to 9th year.^{86,88} Hansen²⁰⁴ has demonstrated a decrease in minimum size and age at maturity in Greenland cod (Table 9).

TABLE 9. Minimum size and age at maturity of Greenland cod in different years (Hansen, 1949)

	Year class	Age at maturity	Average age at maturity
Northern Greenland	1917	6-15	9.9
	1922	6-13	8.6
	1924		6.4
	1934	7-9	7.8
	1936	7-9	6.9
Southern Greenland	1922		9.3
	1932		8.1
	1934		7.8
	1934		7.8
	1936		7.6

Hjort, speaking of cod generally, pointed out that average age at maturity may decrease as fishing pressure increases.¹⁶⁶

Minimum length at maturity possibly between 156-200 mm; but this is well below other minimum estimates which vary from 240 to 685 mm (including both sexes).^{22,38,120,161,219,277} Maximum (an estimated average), 1000 mm.³⁵ In Newfoundland 500 to 800 mm, with 50% of fish above 500 mm mature,^{61,90,164,198} however, males typically at 600 to 700 mm, females at ca. 800 mm. In Gulf of St. Lawrence 50% males at 500 mm, 50% females at 520 mm.²⁴ In Barents Sea minimum 350 mm.³⁷ In Manx males at 330 mm, females 440.²⁴² In Kiel males at average of 352 mm, females at average of 378 mm.²⁴⁹ On Norwegian coast variable: on east coast 270 mm; on coastal banks 500 to 600 mm;¹⁶³ in vicinity of Lofoten usually ca. 697 to 710 mm,^{133,196} but with averages for different samples varying from 600 to 1000 mm.³⁵ In North Sea smallest mature male 500 mm (a mature male 290 mm long was considered deformed), smallest mature

female 540 mm; largest immature male 890 mm, largest immature female 970 mm; average for females ca. 740 mm.²⁵⁸ Other estimates for overall minimum length vary from 550 to 762 mm^{98,163,196} and average lengths at maturity from 600 to 750 mm.^{55,185} In the Baltic specimens between 150 to 200 mm long have been included in a chart of "spawning cod";²²⁴ but other Baltic estimates are males at 270 mm, females at 300 mm.⁵⁷ In Kattegat many fish mature at 305 mm.¹⁵³ In the Shetlands, 520 mm.¹⁶³ In Iceland males at minimum of 490 to 540 mm (but mostly at 700 mm), females 590 mm (mostly at 800 mm). Some females still immature at 900 mm²²⁰ (other estimates for Iceland, however, include ca. 500⁶² to 600 mm;¹⁶³ males 600 to 700, females 700 to 800⁷⁰). Greenland variables: males 640 to 660 mm,¹³¹ females 530 mm,¹⁹⁸ although in other studies total population (both sexes) 700 to 800 mm.^{24,193}

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Melanogrammus aeglefnus (Linnaeus), Haddock**ADULTS**

D.₁ 13–18⁸⁰ (w. Atlantic 14–17),^{17,114} D.₂ 19–25^{14,80} (w. Atlantic 20–24),^{17,114} D.₃ 18⁵¹–23⁸⁰ (w. Atlantic 19–22),^{17,114} A.₁ 21¹⁷–28⁵¹ (w. Atlantic 21–25),¹¹⁴ A.₂ 19⁵¹–24¹⁷ (w. Atlantic 20–24).¹¹⁴ P. 19–21.¹²⁵ Scales in lateral line, ca. 160;¹⁷ gill rakers, 24–27;¹⁴ preanal vertebrae 19–22, postanal vertebrae 32–35 (based on Icelandic population),^{80,94} total vertebrae 50–57 (excluding hypurals),⁴² average vertebrae counts vary from 53.58 to 54.12 in the western Atlantic.¹²⁰

Proportions expressed as percent body length: Predorsal distance 26.1–28.2; preanal distance 41.7–45.5; base of D.₁, 12.2–13.8; base of D.₂, 19.7–23.5; base of D.₃, 13.6–16.4; base of A.₁, 21.1–22.8; base of A.₂, 13.8–16.5. Eye diameter as percent HL, 20.0–28.2.¹⁴

Body laterally compressed; upper jaw projecting, lower jaw with single barbel, its length less than diameter of eye; gape not extending below eye. First dorsal fin pointed, higher than 2nd dorsal, and with its margin slightly concave; pelvics in front of pectorals; caudal fin lunate.^{17,114,125}

Pigmentation: Top of head and dorsal surfaces down to lateral line dark purplish gray or dark gray with violet shadings; lateral line black; sides below lateral line silvery gray with pinkish reflections; belly and lower parts of head milky white. A large, conspicuous dark blotch on each shoulder between lateral line and middle section of pectoral fin. Dorsal, pectoral, and caudal fins dark gray; anal fin pale and with black specks at base; pelvics white, more or less dotted with darker color. Peritoneum black. Occasional specimens with 1–4 transverse bars or splotches in addition to shoulder patch. Rare individuals golden on back and sides and with lateral line golden.^{9,14,80,114,125}

Maximum length: Ca. 1118 mm.¹⁰⁷

DISTRIBUTION AND ECOLOGY

Range: In western Atlantic, Gulf of St. Lawrence and Newfoundland Banks to Cape Hatteras, North Carolina. In Europe from vicinity of Matochkin Shar in Novaya Zemlya to the Bay of Biscay, France, and including the Orkney, Faroe, and Shetland Islands, England, Ireland, and Scotland, the western Baltic, Bear Island, Spitsbergen, the western coast of the White Sea, and, possibly, the Kara Sea. Also Iceland and the southern tip of Greenland.^{6,14,19,35,50,114,125}

Area distribution: Worcester County, Maryland;⁵⁵ offshore waters of Virginia;³² and offshore waters of New Jersey^{30,90} and Delaware Bay.⁶⁰

Habitat and movements: Adults—a bottom species^{1,6,27}

found in marine waters and, sometimes, fjords⁹¹ over bottoms of sand, rock, pebbles, gravel, or broken shell. Sometimes associated with banks and ledges and sometimes over smooth areas between rocky patches;^{6,9,47,57,107,108} also reported from “slimy” bottoms.⁹⁹ Deep water channels apparently act as barriers to movement.¹⁷ Sometimes form large compact schools.^{9,31,35} Usual depths variously estimated, but ranging from 20–275 m,^{9,27,47,63,92,108,110} although at least one author regards it as rare below 185 m.⁹⁸ Maximum reported depth, 1000 m,¹⁴ but other reported maximums from 323–402 m.^{9,126,128} Reported from less than 25 ppt to over 34.5 ppt^{1,105} (Damas gives an optimum salinity of 35.0 to 35.2 ppt⁴⁹). Reported from range of 0⁹⁸ to 13 C,¹⁰⁵ but known to survive experimentally at 20 C;⁹⁷ optimum 4 to 7 C,^{14,25,97} most abundant at ca. 2 to 9 C,¹⁷ feeding range 2.2 to 11.9 C.¹¹² There are apparently seasonal shifts in preferred temperature. In Canadian waters winter temperatures vary from 3 to 6 C, summer temperatures from 6 to 8 C.¹³⁹

Haddock undertake only relatively short inshore-offshore or coastwise movements and there are no extensive long distance mass migrations.⁹ In the western Atlantic there are apparently three distinct stocks of haddock (New England, Nova Scotia, and Newfoundland), all with limited migrations.²³ The more extensive migrations occur in Canadian waters, while those in New England are noticeably less. Generally, haddock spend the winter in deeper water, and move shoreward in summer, spreading into warmer, shallow, coastal water.¹⁷ In Nova Scotia there is an apparent spawning migration to offshore banks during early spring,⁴ with spent fish returning inshore in May and June,⁴¹ however, those on Georges Bank do not migrate.¹¹³ Inshore and offshore migrations have also been documented for St. Pierre Bank and Southern Grand Bank with the movement to shallow water beginning in April in the latter locality.^{130,135,139} A southern migration from Passamaquoddy Bay takes place in March and April.³ Individuals from New England move southward to New York, New Jersey, and, rarely, Cape Hatteras in winter (and it is this migration which accounts for the regional records).¹⁰⁷ Colton concludes that haddock on Georges Bank seek shoaler water during the spawning season than during the summer months.¹¹³ In the North Sea a northward spawning migration occurs in January and April,²¹ and there is a general tendency for older individuals to migrate into deeper water.⁸⁸ In Iceland there is a migration from Faxa Bay to Selvogsbanki from April to May.¹⁰⁹ Icelandic haddock apparently move into deeper water to spawn.²⁷

Diurnal movements may occur with the species rising to midwater at night,¹³⁴ although, in some areas at least, this pattern may be reversed during the spring months.¹⁰¹

Larvae—typically oceanic,⁴⁶ although also recorded from

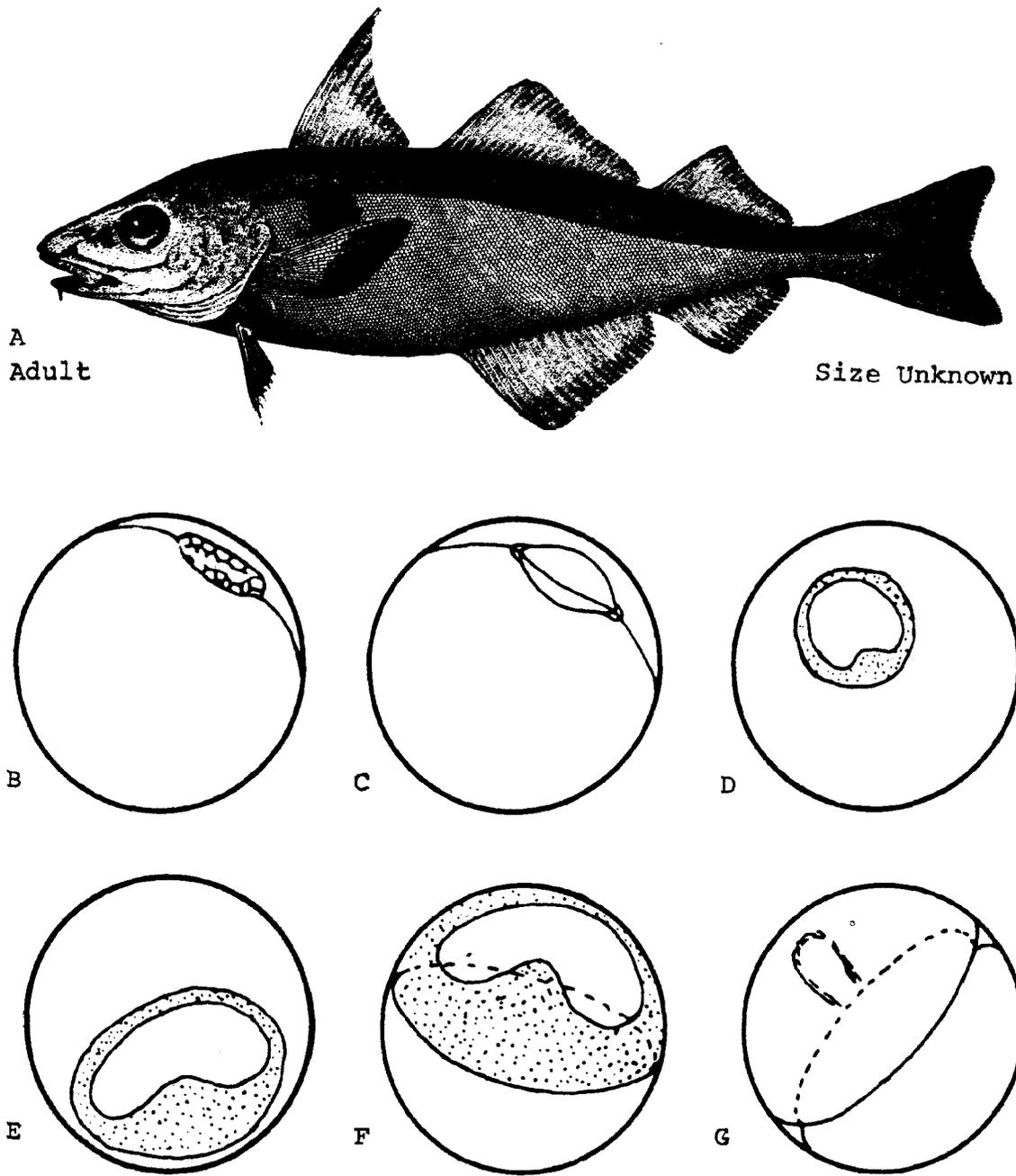


Fig. 156. *Melanogrammus aeglefnus*, Haddock. A. Adult, size unknown. B-G. Development of the egg. A. Early morula. B. Late morula. C. Dorsal view of developing egg. D, E. Early gastrula. F, G. Early embryo formation. (A, Goode, G. B., 1884: pl. 59A. B-G, Westernhagen, H. V., 1968: fig. 4a.)

estuaries.¹⁴ Yolk-sac larvae float upside down except when intermittently attempting to swim.^{8,20} In aquarium experiments Schwarz observed that hatchlings did not swim toward the surface,¹²¹ while McIntosh and Masterman commented that, under aquarium conditions, hatch-

lings descend to the bottom after one week.²⁰ Larvae are generally pelagic,⁴⁷ and are sometimes associated with medusae.¹⁴ Maximum depth ca. 150 m.⁸ Larvae less than 8 mm over greater depth range than larger larvae.¹²⁹ In Georges Bank area found at depths of less than 10 m⁵⁸ to

possibly 75 m, with over 80% at 10 to 40 m, the maximum concentration at 20 to 30 m, and the maximum density at 20 m.^{34,90} Over 80% of specimens 8 to 21 mm long are concentrated in the thermocline, while specimens 4 to 8 mm long tend to be below the thermocline.^{34,90,129} In the North Sea larvae are concentrated at 20 to 50 m.⁹² Minimum reported salinity 15 to 18 ppt.⁵⁹

Drift with surface currents.^{14,125} In some areas wind direction and intensity can affect survival of larvae,¹⁴¹ as, for example, on Georges Bank where survival is lowered when larvae are carried into slope water.⁹⁰ Some vertical movement occurs but varies from area to area.³⁴

Juveniles—on Georges Bank small juveniles tend to concentrate in water column in depths shoaler than 20 m⁹⁰ and specimens 40 to 77 mm long have been collected in Narragansett Bay.²⁸ Juveniles of various sizes (see movements and depth) reported from deep offshore waters,⁹⁴ coastal areas, bays, inlets, and fjords.^{53,104,125} Holt reports numerous young ca. 125 mm long cast ashore during a storm in England.³⁸ In Nova Scotia specimens 200 to 400 mm long are found on bottom along shore during summer months.⁹⁷ A specimen ca. 160 mm long and individuals in year class I have been reported over muddy bottoms at depths of, respectively, 51 and 134 m.^{21,78} Specimens ca. 20 to 100 mm long may be in the water column and associated with jellyfish, and up to several dozen fry may hide under a single *Cyanea*. On Georges Bank juveniles larger than 20 mm were never found in areas where *Cyanea* was not present.^{6,40,48,90,125} Various reported from 5⁸² to 177 m⁷³ although specimens 30 to 60 mm long may be found over depths of 4000 to 5000 m,⁹⁴ and recently descended juveniles may survive at depths of up to ca. 293 m.⁵⁸ Specimens ca. 60 to 90 mm long have been recorded from ca. 19 to 177 m, and Holt has suggested a nursery area between ca. 40 and 98 m in European waters.⁷⁴ Members of year class I have been taken at 134 m,²¹ year class II at 5 to 30 m,⁸² and specimens ca. 250–425 mm long at ca. 7–8 m.¹¹¹ In the northwestern Atlantic over 75% of all “juveniles” up to 124 mm were found at 10–40 m, with none below 80 m in studies of the upper 100 m.²⁰¹ In one study specimens 24 to 80 mm, 40 to 48 km offshore.²⁰ North Sea specimens recorded from 32.1 to 35.1 ppt.²¹ Recorded from 6.5 to 15.7 C, but tend to avoid temperatures above ca. 10 to 11 C. Survive experimentally at 20 C.^{21,68,111}

A definite descent to the bottom occurs, and the youngest bottom stages are further out and in deeper water than in some other related species.⁸³ Descend at an age of 3 to 5 months, with the transition itself apparently taking 1 to 2 months.^{6,9,17,85} Size at the time of descent has been variously estimated, in European waters size at descent varies from 30 mm or less to 40 mm,^{11,89,96} in Iceland specimens descend at ca. 50 mm,⁷² and in the western Atlantic at 28¹⁷ to 130 mm.^{34,85,90} Descent occurs in August and September in Georges Bank³⁴ and in “autumn” in Barents Sea.¹⁴ Some European specimens

110–120 mm long may occur pelagically, but this may represent a return to the surface after descending.^{21,92} Descent usually occurs in water 10 to 120 m deep (based on Icelandic observations),⁷¹ although seldom in water less than ca. 20 m deep.¹⁰⁷ Apparently can sound to depths of ca. 293 m, but cannot survive following soundings in greater depths.⁵⁸

Small juveniles initially remain in the open sea and are more or less stationary.^{87,98,103} Specimens up to and during their 2nd year of life may ascend to surface, particularly during autumn.⁶⁶ In North Sea and other areas a general shoreward movement takes place, primarily at the beginning of the 2nd year^{14,33,89,104} with “small juveniles” concentrating at depths of 20 m or less in some areas,⁹⁰ but this does not hold true for Georges Bank specimens (RRM). Specimens ca. 190–225 mm long are reported to move inshore in “immense shoals.”²⁹ Young which have moved inshore return (with rare exceptions) to deeper water in winter.^{14,89,137} In the Barents Sea individuals from the beginning of their 3rd year to the time of maturity undertake seasonal migrations, moving from east to west as the water cools in autumn.¹⁴

In the northwestern Atlantic, diurnal variations have been reported. Juveniles were found at an average depth of 40 m by day and 30 m at night.¹²⁹

SPAWNING

Location: At or near bottom^{9,34,63,75} over rocks,^{52,118} gravel, smooth sand,¹⁰⁷ or soft mud.⁸⁹ Usually 8 to 32 km from shore, although sometimes up to 96 km out,²⁶ and typically over offshore banks and slopes.^{6,17,16,61,111,141} Inshore spawning has been reported,²⁴ but is apparently of little importance.¹⁷ In European waters spawning probably occurs northward to at least 65° N latitude, and has been observed southward to the English Channel and the waters south of Ireland.^{19,79,106} In the Faroes there are distinct loci of spawning density near edges of shelves, and these loci do not vary significantly from year to year;^{8,79} Georges Bank populations also quite consistent about sites (RRM).

Depth: In American waters ca. 30 to 211 m, but mostly at less than ca. 48 m.¹¹³ In European waters from 20³³ to 250 m,¹⁴ but usually at 60^{36,49} to 200 m.^{49,94} Estimates for the North Sea are 20 to 200 m,^{11,33,49,52,83,84} for the Barents Sea 80 to 150 m,⁵ and for Norway an optimum of 60 to 200 m.⁴⁹

Season: Throughout the range, January^{6,19,20,21,82,87,89,92,103,124} through July^{4,17,52} (however, in some areas adults may arrive in the spawning area as early as December⁷¹). For specific locations and seasons see Table 10. On Georges Bank there are fluctuations of up to one month due to slight temperature changes.¹³² In European waters spawning begins about one month later in deeper waters

TABLE 10. Spawning season of *Melanogrammus aeglefinus*. P indicates peak spawning period.

	J	F	M	A	M	J	J	A	S	O	N	D
North American waters 4,6,17,52,85,107,124,131			P	P	P	P	P					
New England 3,9,11,63,100,115,118												
Gulf of Maine 122												
Georges Bank 10,97												
Nova Scotia 14,61,63,97												
Newfoundland and Grand Bank 61,63,130,131,140												
Iceland 11,70,71,84,94,140												
North Sea 11,19,21,83,84,87,103,123		P			P							
German Coast 52,106,118												
Norway 56,64,88												
Sweden 47												
Northern USSR 125												
Finland 5,65												
Great Britain 13,20,74,96		P	P	P								
Ireland 74,94			P	P								
Faroes 94,95												
European waters 7,14,35,89,94												

than in more shallow areas.^{87,92} and the season varies considerably from year to year⁸⁵ and with latitude.¹²⁵

Temperature: In North America 2.5 to 6.5 C,^{14,90} with maximum activity (in the Georges Bank area) at 3.3 to 5.6 C.¹⁴³ A 1.5 to 2.0 C temperature change can mean a difference of one month in the spawning season.¹³² In European waters 4 to 10 C, with optimum temperatures varying from 4 to 8 C in some areas to as high as 10 C in others.^{5,7,10,14,49,88,125} In Iceland, minimum favorable temperature 5.5 C.¹⁰²

Salinity: In American waters 32.0 to 32.5 ppt.¹¹ (In the Grand Bank area most successful year classes are correlated with low numbers of icebergs passing south of 48° N in eastern Newfoundland,¹⁴⁰ an effect which may result from salinity changes.) In European waters generally somewhat higher than in American waters (34.00 to 35.25 ppt)^{7,49,59,92} although reported at ca. 32.0 to 33.0 ppt in the Barents Sea.⁵

Frequency: Eggs are released at intervals over a period of about three weeks.¹⁴³

Fecundity: Extreme counts, 12,000 to 3,000,000. Estimated averages vary from ca. 31,000 in 2 year olds to as high as 2,158,000 in older fish. Although fecundity increases with age and size, it may vary significantly in same-size fish from year to year and this may be correlated with temperature.^{61,125,136} There are apparently differences in fecundity between populations on opposite sides of the Atlantic.¹³¹ Two types of eggs (opaque-yolked and transparent yolkless) appear in the ovaries simultaneously.¹³⁶

EGGS

Location: Initially at bottom, but become buoyant a few minutes after fertilization³⁴ (which may be delayed up to 16 hours^{9,73}); in Georges Bank area rise at rate of ca. 3 m per hour, thus from 70 m depth to surface in ca. 24

hours.⁷⁵ After arriving at surface buoyant,¹⁷ pelagic,^{6,29,44} but density varies with stage of development⁷⁵ and eggs may descend to mid- or bottom depths as development proceeds.⁹² Normally concentrated in upper 10 m,⁵⁸ relatively abundant down to ca. 50 m, maximum depth 115–170 m.¹²⁹ In eastern Atlantic normally found between latitudes 58–50° N⁹⁶ over depths of 17 to 360 m, but mostly over 50 to 200 m and at temperatures of 5 to 10 C and salinities greater than 34.5 ppt.^{71,94} Eggs may drift at surface for a week or more¹⁷ and at times, as in area of Georges Bank, may be carried into deep water where only a few survive.⁹⁰

Ovarian eggs: At less than 0.1 mm gray, yolkless; at 0.5 to 1.0 mm opaque, yellow; at ca. 1.5 mm translucent.⁶¹

Unfertilized eggs: 1.20¹⁹ to 1.50 mm.¹¹⁷ Running ripe eggs transparent or light amber.¹⁰ Micropyle shaped like reverse funnel, small opening on outside, large opening on inside; area around micropyle granular.⁷⁸

Fertilized eggs: Diameter 1.10^{12,44} to 1.72 mm,⁸⁶ averages ca. 1.46 mm^{12,20,44} (although average size decreases with advancing season,¹¹ from 1.54 to 1.45 mm or 6.0 percent in North American waters,⁷⁶ 1.526 to 1.342 mm in North Sea⁹⁶), spherical,²⁹ sometimes ellipsoidal;⁴⁵ blastodisc light terra cotta, but only in very early stages;^{26,116} zona radiata extremely thin;⁷⁵ egg membrane comparatively fragile,¹¹ soft,⁹⁶ thin, and breaking up into flakes as hatching approaches;⁷³ no oil globules.^{13,29,100}

EGG DEVELOPMENT

Development at 5.5 C (Schwarz series):¹²¹

- 7th day. Blastopore closed.
- 11th day. Anlagen of swim bladder evident as shallow evagination of dorsal gut wall at level of pectoral fins.
- 12th day. Anlagen of swim bladder a hollow inverted "U."

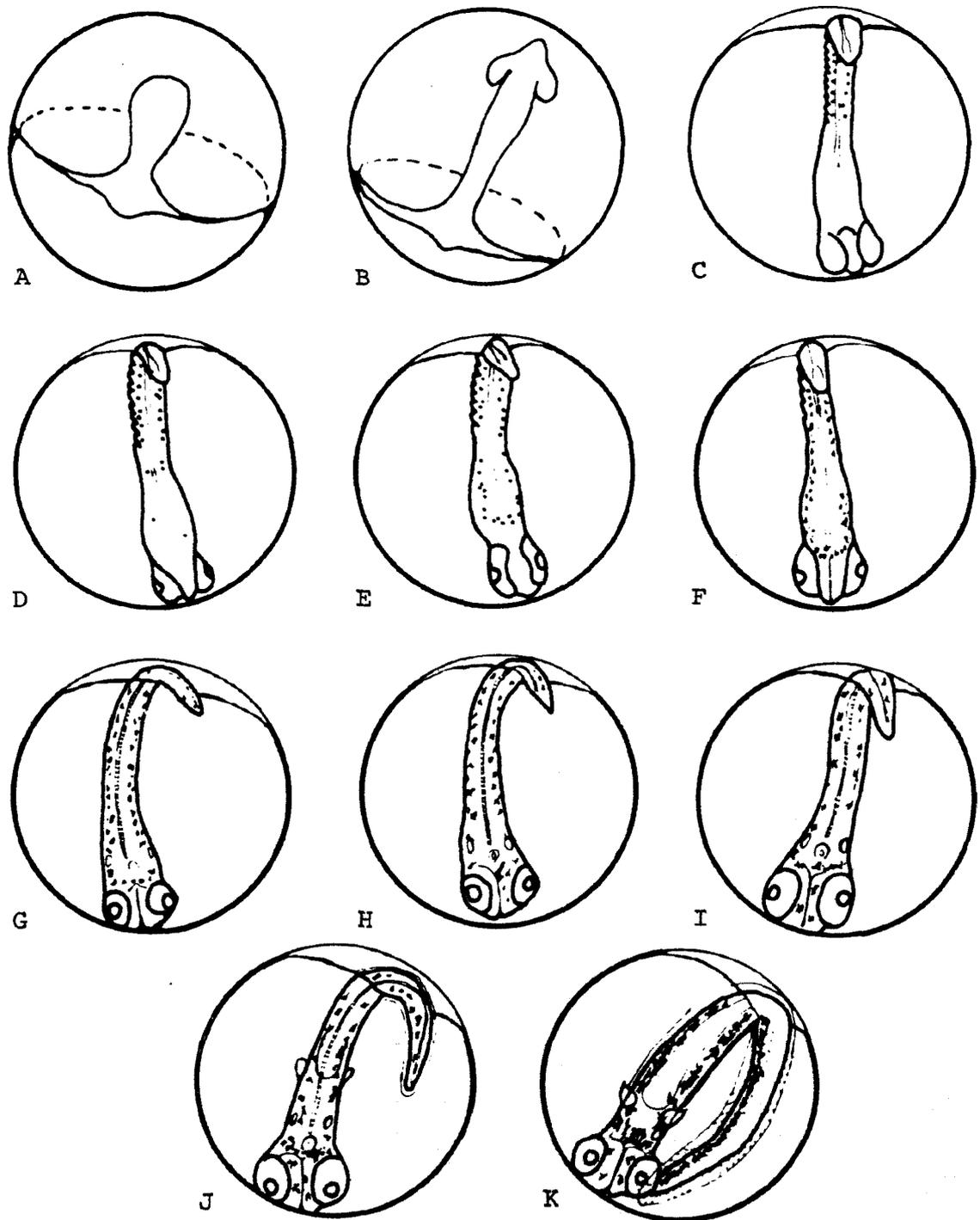


Fig. 157. *Melanogrammus aeglefinus*, Haddock. A-K. Development of egg. A. Early embryo. B. Head differentiating. C. Eyes developing, pigment on body. D. Lenses formed. E. Pigment increased anteriorly. F. Pigment forward to head. G. Otocyst developed. H, I. Pigment developed on head. J. Pectoral buds evident. K. Advanced embryo. (A-K, Westernhagen, H. V., 1968: figs. 4a, 5.)

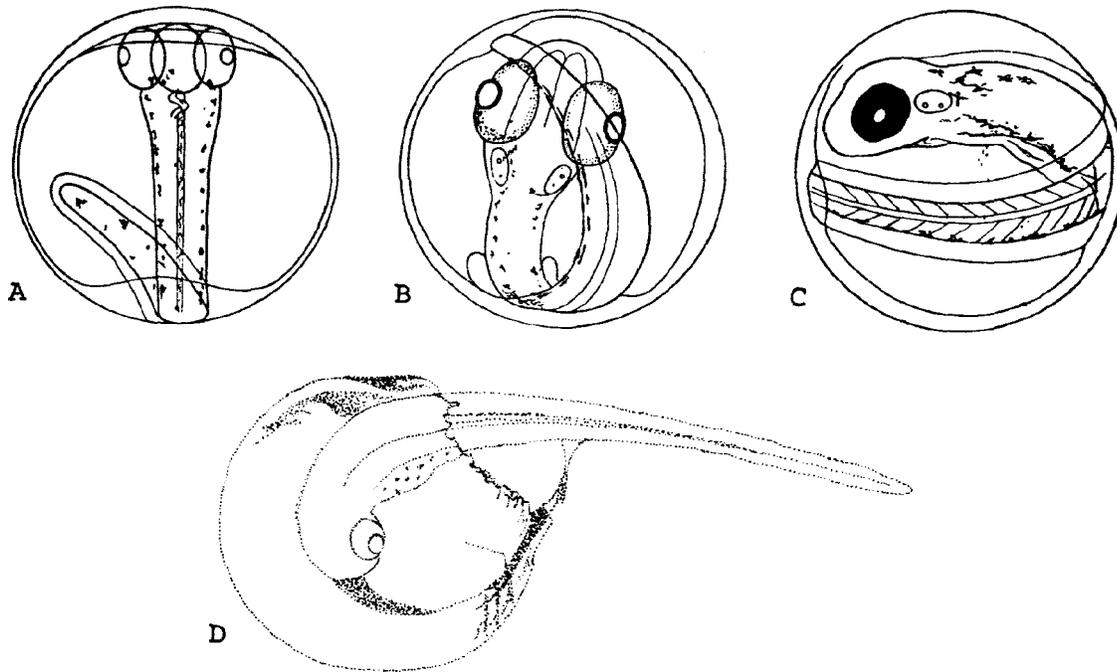


Fig. 158. *Melanogrammus aeglefinus*, Haddock. A-C. Development of egg. A. Early pigment formation, lenses formed. B. Pigment developing in eyes, otoliths evident. C. Body pigment in characteristic pattern, eye fully pigmented. D. Yolk-sac larva hatching. (A-C, Heincke, F., and E. Ehrenbaum, 1900: fig. 12. D, McIntosh, W. C., and A. T. Masterman, 1897: pl. 3, Tamiko Karr, delineator.)

13th day.	The "U" elongated.		
14th day.	Swim bladder more dorsal in position; first evidence of distinction between pneumatic duct and swim bladder.		cially in dorsolateral region above pectorals.
15th day.	Swim bladder expanded.	13th day.	Lumen of mesenteron enlarged.
16th day.	Swim bladder more expanded.	15th day.	Cephalic region enlarged, body elongate.
17th day.	Hatching. Swim bladder lengthened anterior-posteriorly, pneumatic duct enters approximately at midpoint. ⁷³	16th day.	Eyes pigmented, first branchial cleft distinct.
		18th day.	Eyes black.
		19th day.	Three branchial clefts visible, buccal chamber evident, urinary vesicles well advanced.
		20th day.	Hatching. ⁷³
Development at unspecified temperature (McIntosh and Prince series): ⁷³		Marak and Livingstone ¹³² have described six major stages of development (based on temperature of 3.3 C):	
2nd day.	Blastodisc 0.4 mm in diameter.	I.	From fertilization to formation of early blastodermal cap. 0-72 hours
4th day.	Blastoderm to equator, embryonic keel indented into yolk, head defined.	II.	From complete blastodermal cap to development of segmentation cavity. 4-7 days
5th day.	Optic lobes distinct, indications of 4-5 somites in anterior caudal region, scattered black pigment on sides and dorsum.	III.	From appearance of early embryonic axis to approach of germinal ring to equator. 7-9 days
7th day.	Blastopore closed.	IV.	From equatorial position of germinal ring to just before closure of blastopore. 10-13 days
8th day.	Kupffer's vesicle evident.		
10th day.	Regions of brain defined; nasal pits, otocysts, opercular cleft, liver evident; no cavity in heart.		
11th day.	Heart pulsations established.		
12th day.	Chromatophores more stellate, espe-		

- V. From closure of blastopore to early scattered pigment. 14-17 days
 VI. From formation of characteristic pattern to hatching.¹³² 18-21 days

Miscellaneous comments on development (all at unspecified temperatures): At 6 1/2 hours blastodisc uniform, prominent.⁷³ Complete differentiation of notochord occurs at time of closure of blastopore.⁴⁵ In series in which blastopore closed on 6th day, irregular black spots appeared in dorsolateral region on 8th day. Time of initial appearance of pigment apparently variable: sometimes by 5th day;⁸⁶ but in series having 14 day incubation period, not until 10th day.⁴⁵ At time at which embryo surrounds egg, a double row of chromatophores on ventral side in postanal region.^{11,96} Before hatching black pigment appears in peritoneum.⁶⁷ Typical yolk-sac larval pigment is developed before hatching.¹²

Incubation period 6^{20,73,89} to 42 days.^{7,18}

Incubation period at various temperatures:

At -1 C	42 days ^{7,18}
At 2.2 C	25 to 32 days ¹⁷
At 2.8 C	15 days ^{14,89,124}
At 3.0 C	23 days ^{7,18}
At 3.3 C	18 to 21 days ¹³²
At 4.0 C	20.5 days ^{7,18}
At 5.0 C	13 days ^{6,89,124} 17.75 days ⁷ 17.8 days ¹⁸
At 5.4 C	13 days ¹⁴
At 5.5 C	17 days ¹²¹
At 6.0 C	15.5 days ^{7,18}
At 6.0 to 7.0 C	probably ca. 16 days ¹¹⁶
At 6.0 to 9.0 C (\bar{x} 7.5 C)	12 days ¹¹⁹
At 8.0 C	13 days ^{7,18}
At 10.0 C	10.75 days ⁷ 10.8 days ¹⁸ 9 to 12 days ¹⁷
At 12.0 C	9.7 days ³⁹
At 14.0 C	8.75 days ^{7,30}

Reports of incubation in 42 days at 1.0 C³⁹ (not -1.0 C) and in 93 days at 12 C⁷ are apparently based on typographical errors (JDH and RRM).

YOLK-SAC LARVAE

Size at hatching 2.0⁸⁶-4.08 mm,²⁰ and apparently with some geographic variation; thus minimum in American waters (Georges Bank) 2.0 mm,⁸⁶ in Europe and Faroes 3.5 mm.^{8,11,20} Average lengths given as 3.5¹²¹-4.08 mm.^{12,44} Length at end of stage 4.5 mm⁸¹ to 5.0¹¹ or 5.5 mm.¹⁴² Duration of stage, ca. 10 days at 5.0 C;^{6,9,24} 6 days at unspecified temperature.¹²¹ In American waters a 14%

decrease in hatching length has been noted from March to May.⁷⁶

In a 3.6 mm hatchling, anus just anterior to midpoint of TL;¹³ in a 4.0 mm hatchling, snout-vent length ca. 38 percent of TL.⁹⁶

At hatching body very plump,⁶⁷ blunt;⁹⁶ head deflected downward over yolk. Mouth initially not evident,¹³ open by 5th day,^{20,73} lower jaw well-developed by 4.19 mm.¹¹⁷ By 5th day anterior nares indicated by lenticular mark.⁷³ Dorsal finfold forward to posterior part of head throughout stage.⁴⁴ Incipient caudal rays present²⁰ or absent¹³ at hatching; dorsal and anal fins without incipient rays throughout stage.⁴⁴ Pectorals initially small, rounded;¹³ large, lobate, and rayed by end of stage. At 4.19 mm notochord multicolumnar, developing gut slightly convoluted;¹¹⁷ anus not open at hatching;¹³ opened laterally at base of finfold by end of stage.¹² At time of hatching gas bladder more anterior than previously, pneumatic duct far posterior; by 3rd day (average TL 3.8 mm) gas bladder still further forward, tapered caudally to meet pneumatic duct; at average length of 4.3 mm "*rete mirabile*" (a collar almost surrounding the gas bladder) evident.¹²¹

Pigmentation: Generally scattered chromatophores on back of head and over gut; stellate chromatophores over sides of trunk; a row of small or dendritic chromatophores along each side ventrally from anus to tip of tail; stellate chromatophores scattered over sides of trunk; eyes pigmented.^{12,13}

At time of hatching dense pigment over and behind otocysts²⁰ extending back along anterior part of body;⁷³ chromatophores sometimes on sides;¹¹⁷ few chromatophores on dorsal part of abdominal region;⁷³ a row of chromatophores along each side of mid-ventral line from abdominal region to near tip of tail;²⁰ no pigment on yolk or marginal fins;⁹⁶ eyes either with black dots or dense pigment throughout.²⁰ Pigment may be very pale.⁹⁶

At 2 days stellate chromatophores in cranial region and greatly increased in region posterior to otocysts and on lateral region of trunk; posterior pigment chiefly confined to lower half of caudal trunk, with only 2 or 3 chromatophores above level of notochord; occasional melanophoric processes extended into finfold.⁷³

At 7 days melanophores on head, in region of otocysts, on dorsal wall of abdominal cavity, and ventrally behind anus.²⁰

In a specimen 4.19 mm long a patch of chromatophores dorsally above pectorals; pectoral base pigmented; stellate chromatophores on sides and top of head; eyes deep black with bluish reflections.¹¹⁷

In a specimen 4.8 mm long pigment concentrated in small

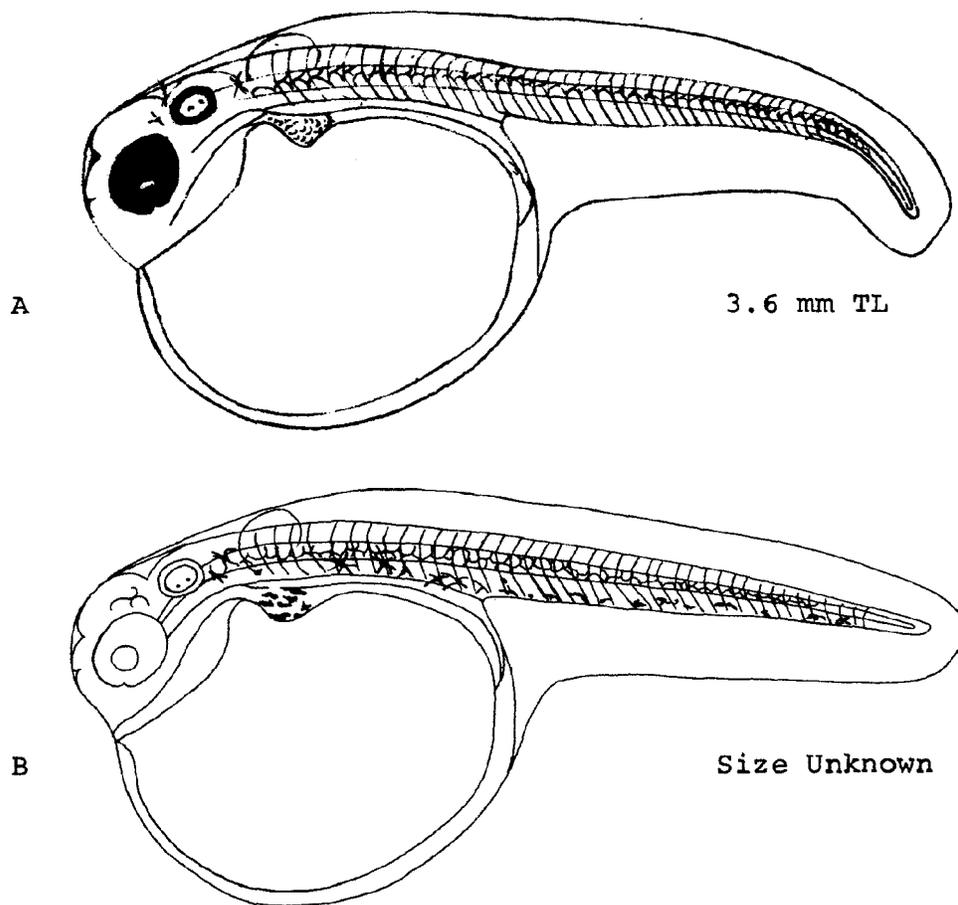


Fig. 159. *Melanogrammus aeglefinus*, Haddock. A. Yolk-sac larva, 3.6 mm TL, ventral pigment not shown. B. Yolk-sac larvae, pigment illustrated, size unknown. (A, Cunningham, J. T., 1888b: pl. 6. B, Cunningham, J. T., 1896: fig. 131, Tamiko Karr, delineator.)

patch on top of head directly above eyes, in region more or less above pectoral fins, and over gut.¹²

LARVAE

Size range 4.0 mm (average size at loss of yolk 4.3 mm)¹²¹ to ca. 28 mm.¹⁷

Abdominal vertebrae 19–22, average 20.3.¹²

At 6.75 to 11.0 mm body thick, plump; head large.^{20,72,94} At 6.75 mm finfold quite broad; dorsal finfold extended forward to front of eye.⁷² At sizes up to 19.0 mm finfold continuous;⁹⁶ at 25.0 mm unpaired fins entirely separated.⁷² Incipient rays first evident in caudal at 4.2 mm, in other unpaired fins at ca. 9.0 to 10.0 mm.^{72,87,96} At 11.0 mm not all rays in dorsal, anal, and caudal formed; first dorsal last unpaired fin to develop.²⁰ At 25.0 mm corners of caudal fin rounded, posterior border almost straight;⁷²

at ca. 25.0 mm 1st dorsal acutely pointed.¹⁷⁰ Pectorals with incipient rays at 6.75 mm;⁷² at ca. 16.0 mm to 19.0 mm pectorals extended to anterior border of D₂.⁹⁶ Pelvics first evident at 6.75 mm⁷² to ca. 8.0 mm;²² rays evident at ca. 11.0 mm. At 9.0 mm pelvics wart-like; at 10.0 mm length equal to ca. 1/2 diameter of eye; at 13.5 mm ca. 3/4 diameter of eye; at 19.0 mm longer than diameter of eye and more than half way to anus;⁷² at 26.0 mm to anus.⁷⁶ Notochord oblique and extended into caudal fin at ca. 8.0 to 11.25 mm.^{22,72,96} At sizes of ca. 8.0 to 20.0 mm, anus under 2nd dorsal fin.⁶⁷ At 10 days (average length ca. 4.8 mm) lining of cavity of gas bladder somewhat folded; at 12 days (average length still 4.8 mm) lining more convoluted, pneumatic duct greatly constricted or entirely closed; minimum length at closure of pneumatic duct in field caught specimens 4.5 mm; former position of pneumatic duct evident as thickening in outer wall of gut in specimens up to 17.5 mm long.

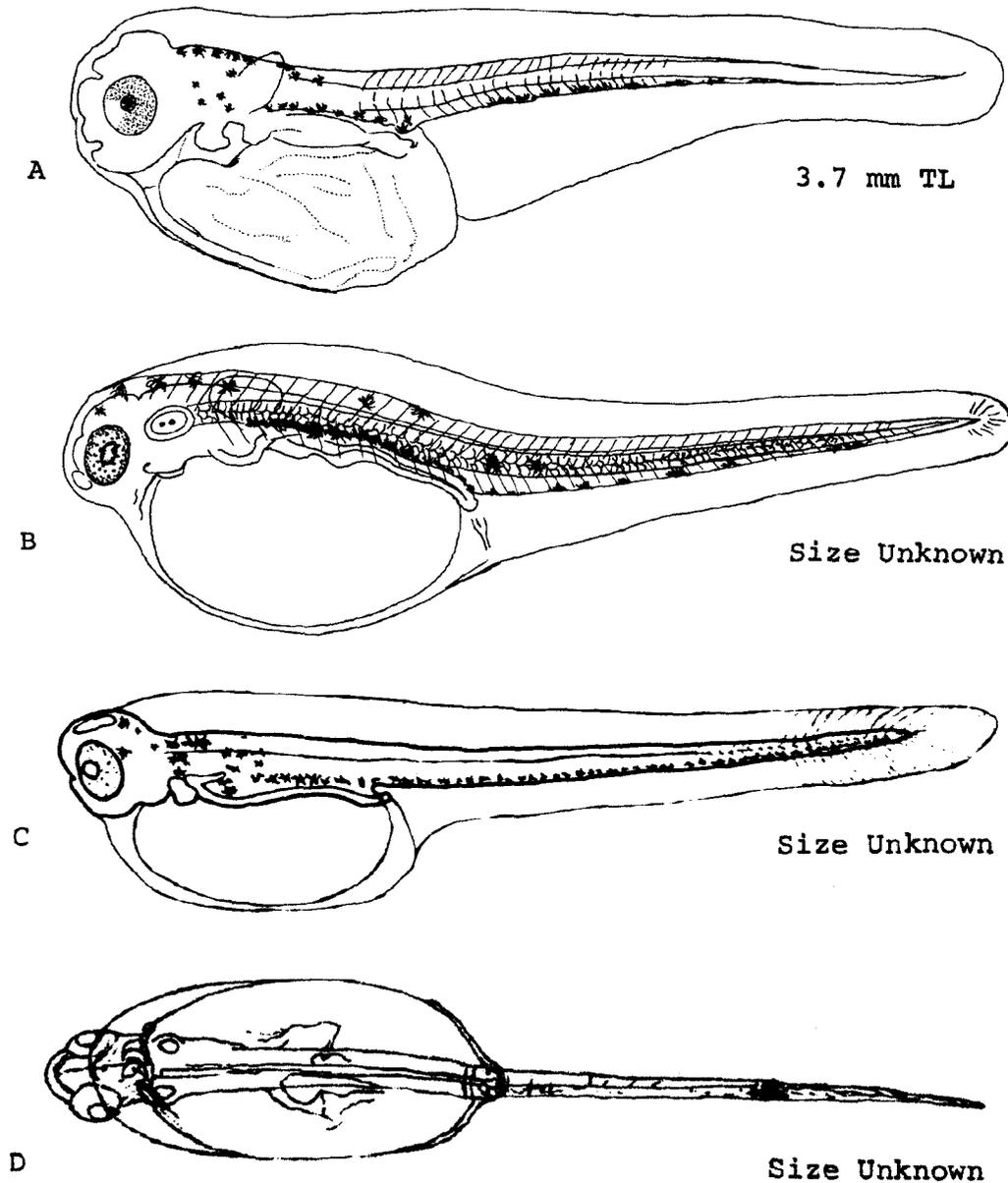


Fig. 160. *Melanogrammus aeglefinus*, Haddock. A. Yolk-sac larva, 3.7 mm TL. B. Yolk-sac larva, size unknown, eye poorly pigmented, caudal rays developing. C. Yolk-sac larva, size unknown apparently just hatched, yolk reduced. D. Yolk-sac larva, ventral view, size unknown. (A, Dannevig, A., 1918: pl. 3, Tamiko Karr, delineator. B, McIntosh, W. C., and A. T. Masterman, 1897: pl. 9. C, Westernhagen, H. V., 1968: fig. 5. D, McIntosh, W. C., and E. E. Prince, 1887-1888: pl. 19, Tamiko Karr, delineator.)

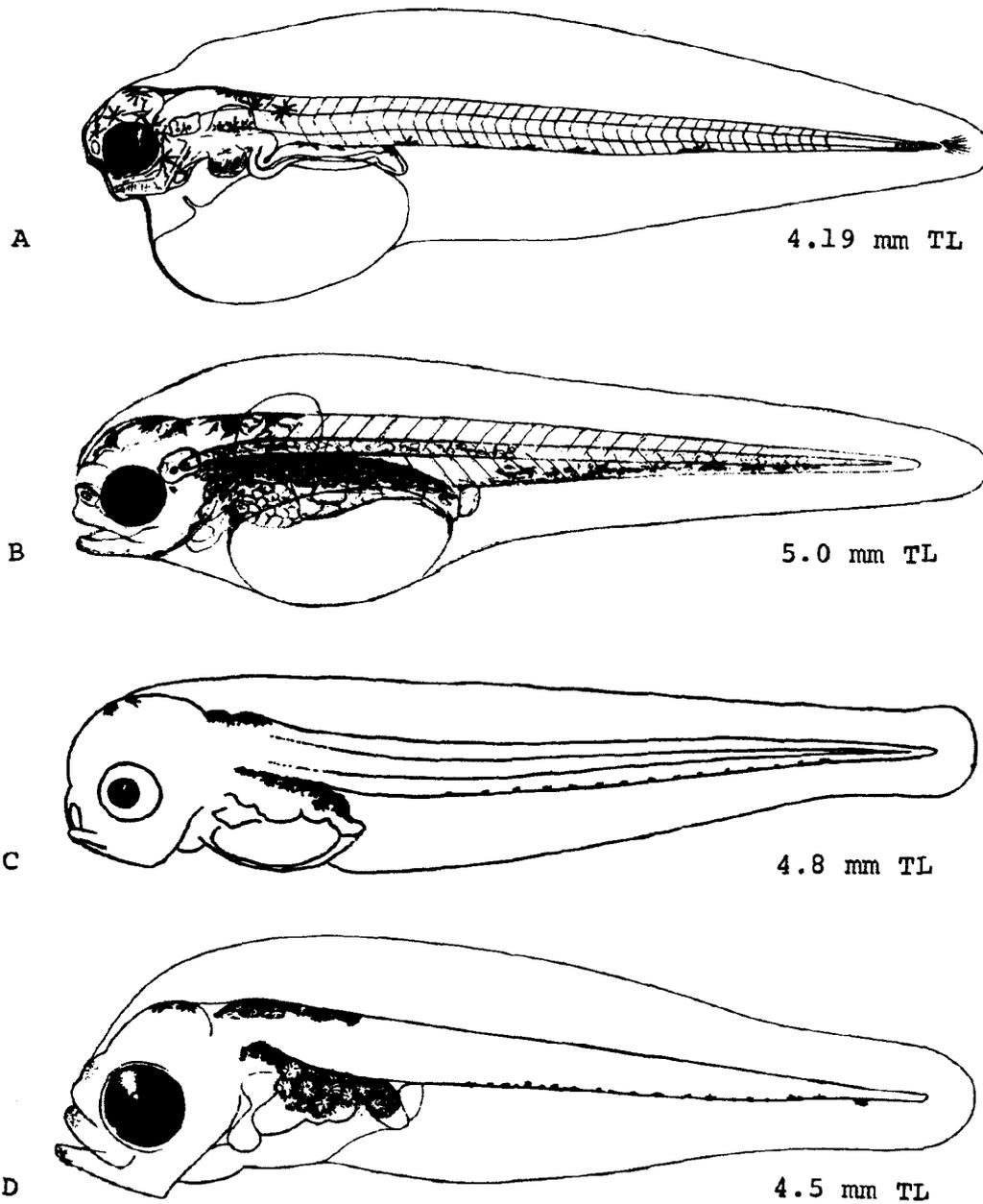


Fig. 161. *Melanogrammus aeglefinus*, Haddock. A. Yolk-sac larva, 4.19 mm TL. B. Yolk-sac larva, mouth well formed, 5.0 mm TL. C. Yolk-sac larva, 4.8 mm TL, yolk greatly reduced, ventral pigment condensed and forming definite row of dots. D. Larva, 4.5 mm TL, pigment increased over gut and anterior part of body. (A, Holt, E. W. L., 1893b: pl. 6. B, Heincke, F., and E. Ehrenbaum, 1900: pl. 9. C, Miller, D., 1958: 25. D, Schmidt, J., 1905: fig. 10.)

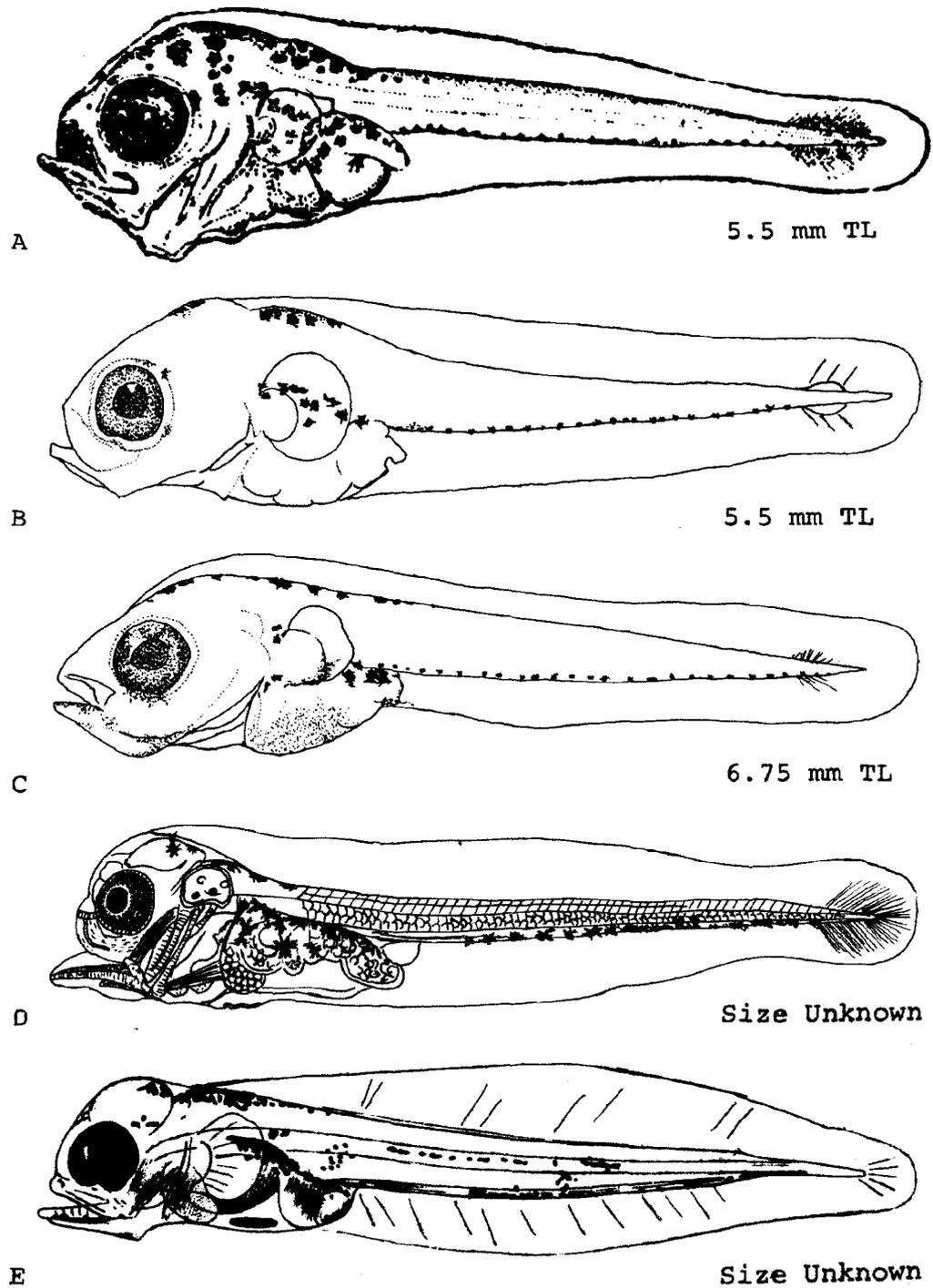


Fig. 162. *Melanogrammus aeglefinus*, Haddock. A. Larva, 5.5 mm TL, gut coiled. B. Larva, 5.5 mm TL. C. Larva, 6.75 mm TL. D. Larva, size unknown, specimen apparently pug-headed. E. Larva, size unknown, incipient pectoral rays. (A, Rass, T. S., 1949: fig. 27. B, Schmidt, J., 1906: fig. 17, Tamiko Karr, delineator. C, Schmidt, J., 1905: pl. 2, Tamiko Karr, delineator. D, McIntosh, W. C., and A. T. Masterman, 1897: pl. 9, Tamiko Karr, delineator. E, Holt, E. W. L., 1893b: pl. 6.)

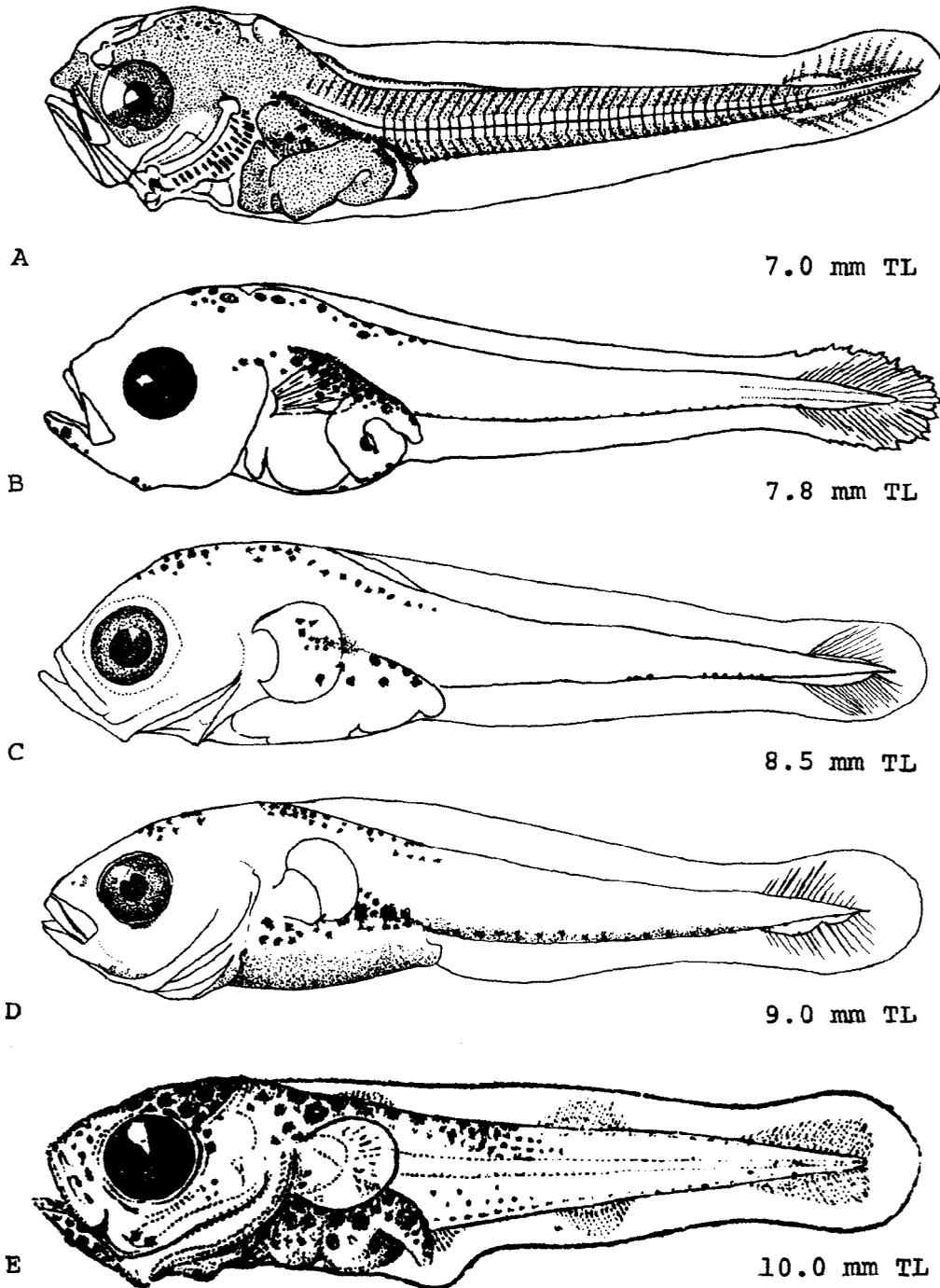


Fig. 163. *Melanogrammus aeglefinus*, Haddock. A. Larva, 7.0 mm TL. B. Larva, 7.8 mm TL, well formed rays in caudal fin, finfold reduced. C. Larva, 8.5 mm TL. D. Larva, 9.0 mm TL. E. Larva, 10.0 mm TL, earliest indications of dorsal and anal rays. (A, *Dannevig, A.*, 1918: pl. 3, *Joan Ellis, delineator*. B, *Müller, D.*, 1958: 26. C, *Schmidt, J.*, 1906: fig. 18, *Tamiko Karr, delineator*. D, *Schmidt, J.*, 1905: pl. 2, *Tamiko Karr, delineator*. E, *Rass, T. S.*, 1949: fig. 27.)

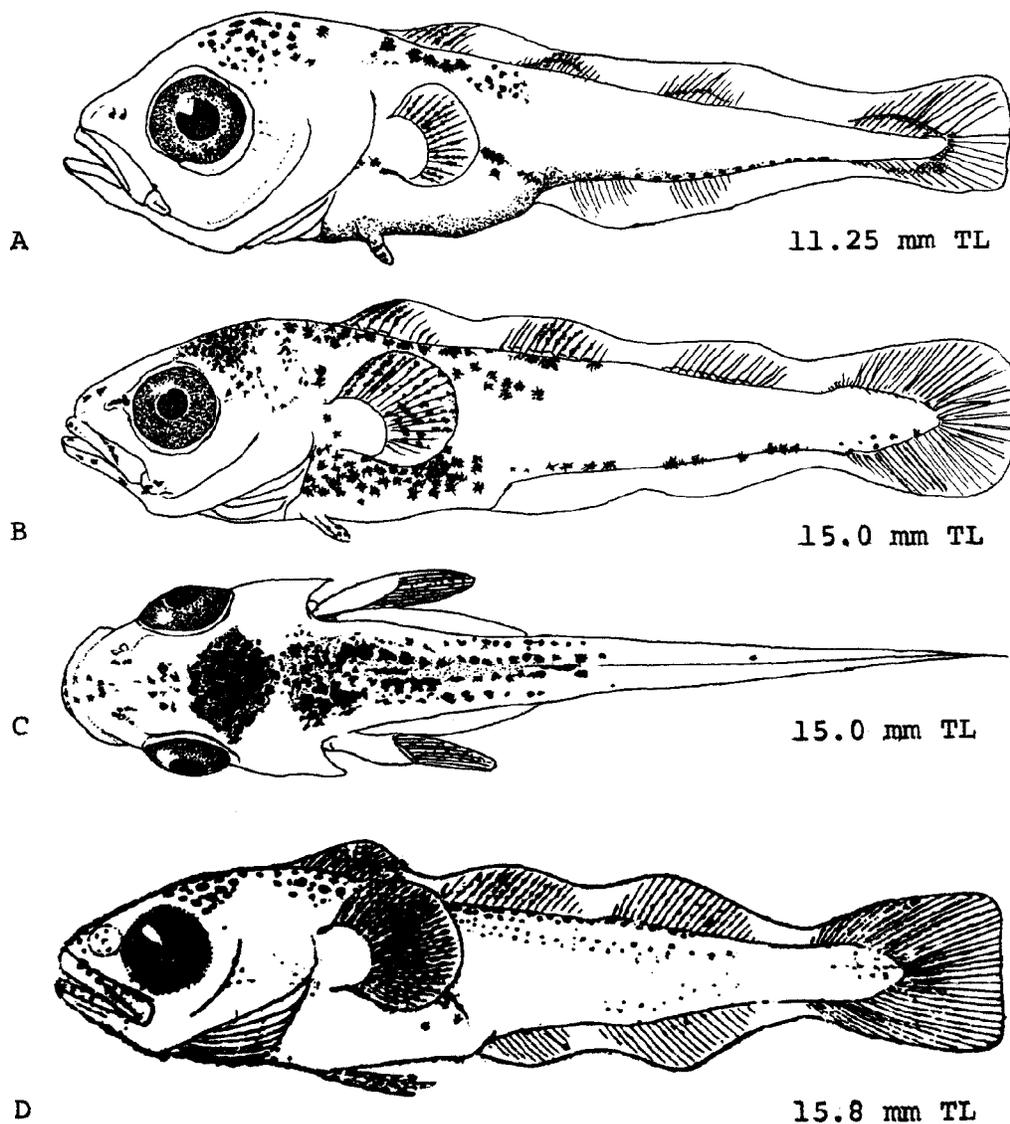
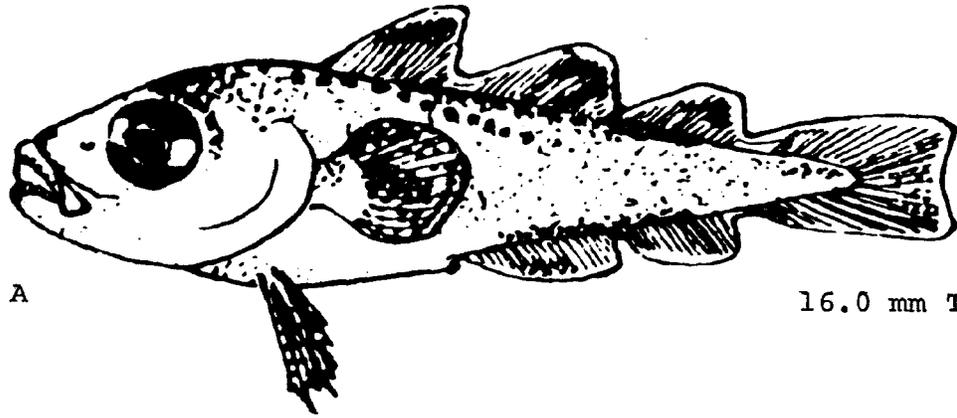
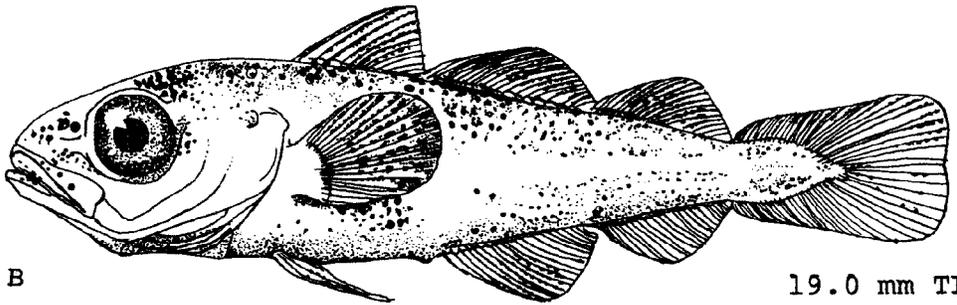


Fig. 164. *Melanogrammus aeglefinus*, Haddock. A. Larva, 11.25 mm TL, pelvic fin developing. B. Larva, 15.0 mm TL, pectoral fins expanded. C. Larva, 15.0 mm TL, dorsal view. D. Larva, 15.8 mm TL. (A-C, Schmidt, J., 1905: pl. 2, Tamiko Karr, delineator. D, Rass, T. S., 1949: fig. 27.)

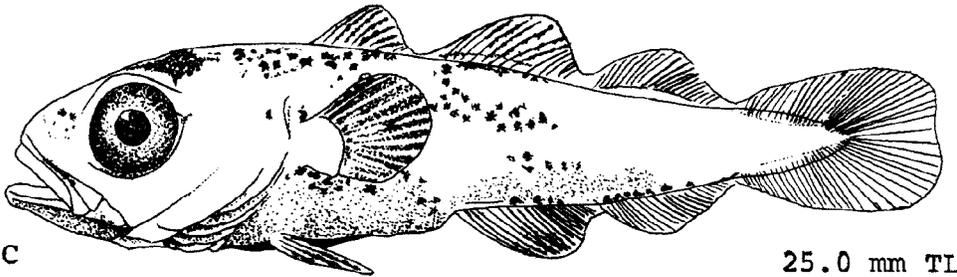
Fig. 165. *Melanogrammus aeglefinus*, Haddock. A. Juvenile, 16.0 mm TL, pelvic fins elongate. B. Juvenile, 19.0 mm TL, dense pigment patches in some vertical fins. C. Juvenile, 25.0 mm TL. D. Juvenile, 26.0 mm TL. (A, D, Ehrenbaum, E., 1909: fig. 83, after Heincke, F., 1909. B, C, Schmidt, J., 1905: pl. 2, Tamiko Karr, delineator.)



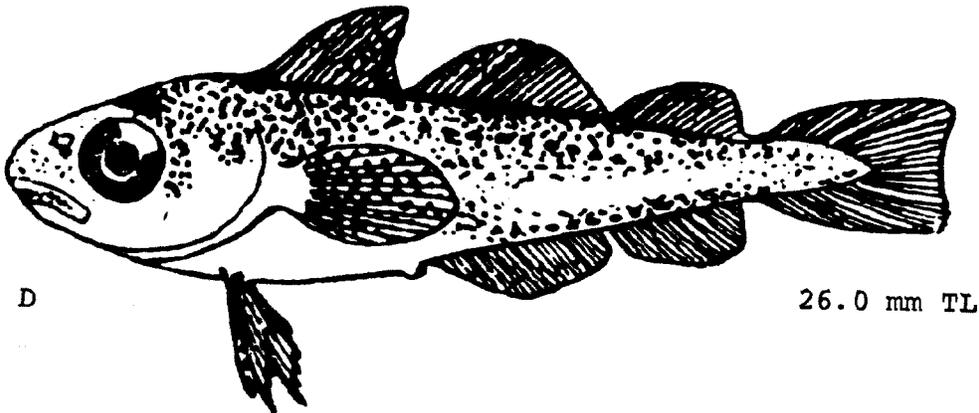
16.0 mm TL



19.0 mm TL



25.0 mm TL



26.0 mm TL

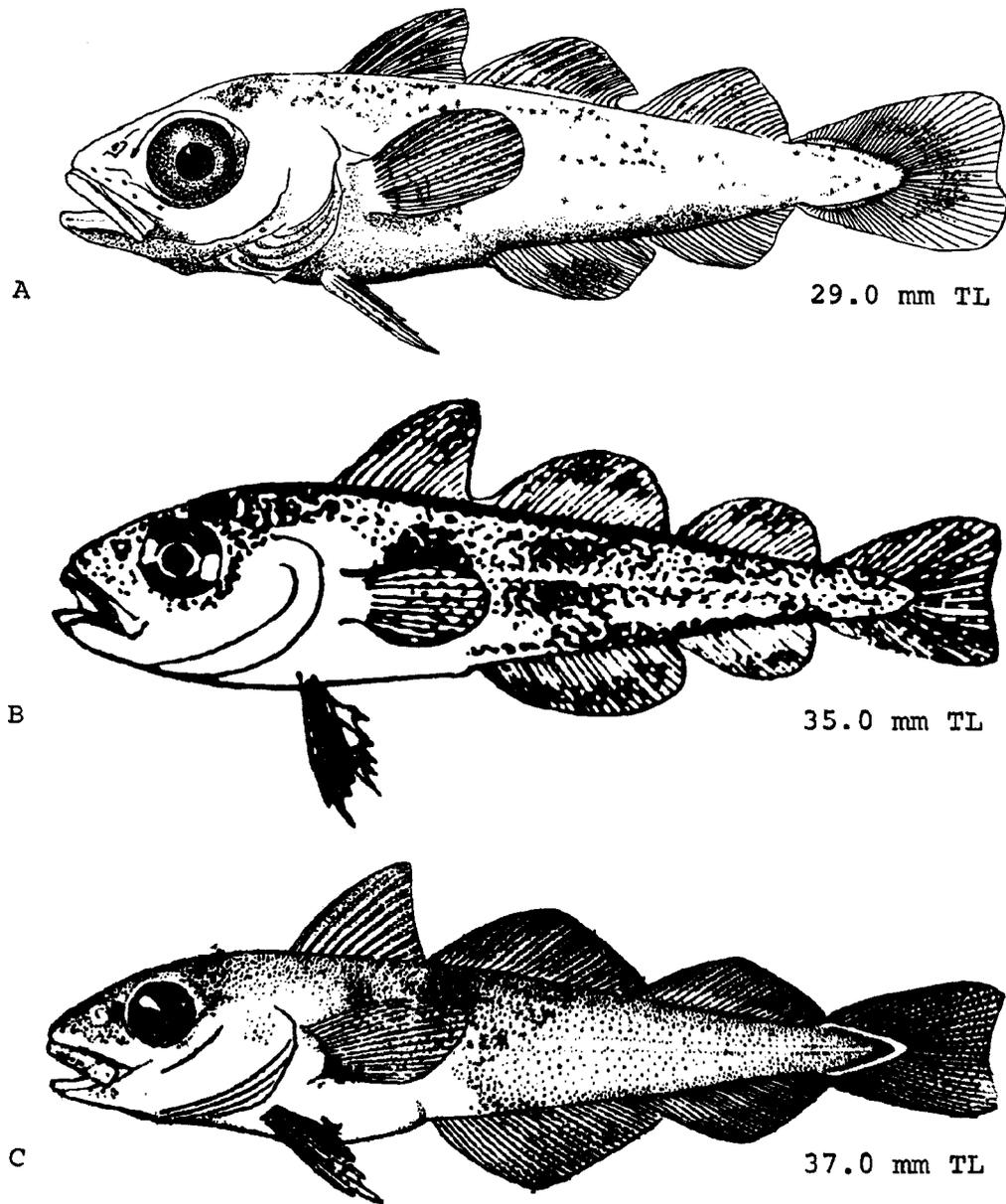


Fig. 166. *Melanogrammus aeglefinus*, Haddock. A. Juvenile, 29.0 mm TL. B. Juvenile, 35 mm TL. C. Juvenile, 37 mm TL. (A, Schmidt, J., 1905: pl. 2, Tamiko Karr, delineator. B, Ehrenbaum, E., 1909: fig. 83, after Heincke, F., 1909. C, Rass, T. S., 1949: fig. 27.)

The gas bladder probably becomes functional at ca. 4.0 to 9.0 mm, and may bring larvae of less than 8.0 mm toward the surface.¹²¹

Pigmentation: Generally yolk-sac larval pigment persists to ca. 8.0 to 10.0 mm, thereafter pigment becomes diffuse and resembles that of cod and pollock.^{12,44} In larger individuals (ca. 8.0 to 20.0 mm) posterodorsal and preanal pigment weak or absent, pectorals and pelvics strongly pigmented.⁶⁷ Shortly after absorption of yolk, diffuse orange or yellow pigment (live or newly preserved specimens) on head, anterior part of body, and in visceral region.^{87,96}

At 6.75 mm a patch of large, round chromatophores on occiput and a double row of chromatophores extending back from this patch to just behind posterior margin of pectorals; double row continued, but much fainter, from this region to a little beyond level of anus; a row of small chromatophores ventrally from anus to hypural elements in tail; in life yellowish brown pigment on neck, abdominal region, and, to some extent, in anterodorsal streak.⁷²

At ca. 8.0 mm roof of peritoneum densely pigmented.²²

At 9.0 mm occiput and abdominal pigment as before; preanal pigment weak, consisting of ca. 5 small dots; a small branch of dorsolateral pigment developed above anus.²⁰

At 10.0 mm pectorals sometimes with strongly marked stellate chromatophores; pigment otherwise as in previous stage; in life yellowish brown pigment on nape and anterior part of back.²⁰

At 11.25 mm D₁ and D₂ with strong black pigment between rays, also chromatophores between rays of distal end of pelvic fin.²⁰

At 13.5 mm pigment developed in pectorals, otherwise pigment essentially as before, but sometimes with scattered chromatophores on sides.²⁰

At 15.0 mm occipital, abdominal, anterodorsal, and anterodorsolateral pigment well-developed, dense; no pigment in posterodorsal region; behind pectorals an anterodorsal branch of pigment (from which adult pattern will develop); A₁ pigmented.²⁰

At ca. 16–19 mm fins except A₂ clearly pigmented, dorsolateral pigment spread over posterior part of body; pectorals and pelvics with deep black pigment.²⁰

At 24.0 mm sides with numerous chromatophores from pectoral fins backward; dorsum with similar pigment forward to snout; belly pale, silvery; future "dark spot" (typical of species) developing a little above and behind pectorals.²⁰

At 26.0 mm all unpaired fins except A₂ pigmented.^{72,96}

PREJUVENILES

Size range ca. 28.0 (based on minimum size at descent to bottom)¹⁷ to 43.0 mm (body adult-like),⁷² but limits highly subjective, based more on morphology than behavior, and not taking into account that western Atlantic populations do not begin descent to bottom until 90.0 to 130.0 mm.^{34,85,99}

Scales developed at 39.0 mm.²⁰

Pigmentation: At 29.0 mm conspicuous in pelvic fins.²⁰

At 35.0 mm pigment on body beginning to concentrate in spots; characteristic black spot of adult developing below D₁; in some specimens pigment developed in A₂.²⁰

At 39.0 mm sides silvery.²⁰

At 43.0 mm dense pigment on sides arranged in three distinct blotches, the anteriormost of which is the developing dark spot of the adult.⁷²

JUVENILES

Minimum size 43.0 mm.⁷²

At 53 mm pelvics proportionately shorter than in earlier stages (probably reflecting change from pelagic life); shorter still at 100 mm. At 80 mm 2nd ray of pelvic fin elongate, but failing to reach vent.²⁰

Pigmentation: Shoulder spot evident at 45–50 mm.¹⁴²

At 53 mm dark shoulder spot well-developed; pectorals with yellowish brown hue and with black spots along edges; pelvics pale, but with few melanophores in center; head and body minutely and uniformly dotted with black; eyes with silvery sheen.²⁰

At 80 mm body with coppery sheen; pectorals, pelvics, and first anal with black pigment.²⁰

AGE AND SIZE AT MATURITY

In North Sea mature at an average of about 3 years; ^{2,46,102,138} 10% of females at age 2, 75% at age 3, 95% at age 4, 99% at age 5; 60% of males at age 2, 95% at age 3, 99% at age 4, 100% at age 5.¹¹⁹ North of North Sea, earliest 6 years.¹²⁵ In Barents Sea minimum 4 to 5 years, but usually not until 8 or 10 years.¹⁴ In Scotland 50% by end of second year, remainder at end of 3rd year.¹⁰³ In Iceland 4 to 6 years,^{1,43,71,102,125} mostly at 5 years.^{2,137} In Canada (generally) males at 4 years, females between 4 and 5 years ^{77,93} but with specific areas in Canada showing wider variation. In Nova Scotia some males at 3 years, 50% at 4 years; 25% of females at 4 years, more than 50% at 5 years.¹⁶ In Newfoundland 15.5% of both sexes at 3 years, 44.5% at 4 years, 95.0% at 5 years, 100% at 6 years.² Grand Bank males and females apparently

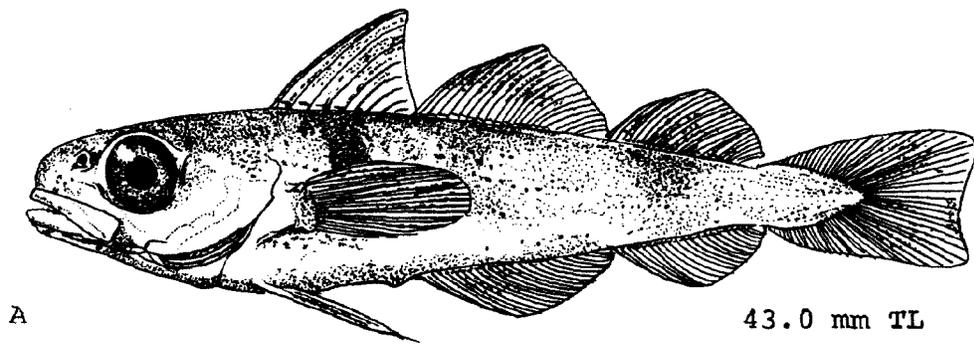


Fig. 167. *Melanogrammus aeglefinus*, Haddock. A. Juvenile, 43.0 mm TL. (A, Schmidt, J., 1905: pl. 2, Tamiko Karr, delineator.)

mature at same age: "few" at 3 years, 90% at 5 years.¹³¹ On Browns Bank, males and some females at 4 years, all at 5 years.² On Porcupine Bank earliest maturity in 3rd year.¹²⁶ On Georges Bank some of both sexes at 2 years, but with higher proportion of males; ² most 3 year old fish mature.¹²⁷

In Canada (generally) 50% of males mature at ca. 406 mm, 50% females at 457 mm,⁷⁷ but with specific areas in Canada showing greater variation. In Nova Scotia minimums a little less than 350 mm for males, 360 mm for females; 50% total population at 400 mm, over 90% at 450 mm;¹³³ 50% males at 410 mm, 50% females at 460.¹⁶ In Newfoundland minimum 500 mm.²⁵ On Georges Bank males at minimum of 280 mm, females at 350 mm² (also, in terms of weight, mostly at 0.7 to 0.9 kg).¹¹⁰ In North Sea females generally at 330–381 mm, males at 279 mm³⁷ (although specimens of unspecified sex at minimum of 230 mm); in Barents Sea minimum 370 mm; on Norwegian coast minimum 280 mm;¹⁴² in Manx females 450 mm, males 400 mm;¹⁵ in Iceland ca. 500–600 mm.^{27,137}

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Microgadus tomcod (Walbaum), Atlantic tomcod**ADULTS**

D. ₁, 11–15; D. ₂, 15–20; D. ₃, 16–23; ^{5,7,11} A. ₁, 17³³ (a count of 12¹¹ is questioned, JDH)–23; A. ₂, 16–20; ^{5,11} P. 16–19; ⁴³ gill rakers 16–21; ^{5,11} branchiostegal rays 7; vertebrae 53–57.⁴³

Proportions as times in TL: Head 4.75, depth 5; ⁷ as percent TL, head 20.1–22.2.⁴³ Proportions as times in HL, eye 5.5–7.0; ⁷ as percent HL, eye 14.8–19.7, snout 33.3–38.5, interorbital width 29.4–33.3.⁴³

Body moderately elongate,⁷ slender,¹¹ only slightly compressed; snout rounded; eye small; upper jaw projected.⁷ Numerous fine teeth on jaws and vomer; ⁴³ mouth extended to pupil.³³ A short barbel on chin.²⁷ Lateral line moderately arched over pectoral fin.⁴³ All vertical fins, especially caudal, rounded; ²⁷ origin of first dorsal over middle of pectorals or further back; pelvis narrow, tapering, and with one filamentous ray; ¹¹ vent under interval between first and second dorsal.³³

Pigmentation: Brown, olive brown, muddy green, olive, or yellowish brown above with green or yellow tinges; mottled with indefinite black spots or blotches which may extend on to pectorals, anals, and pelvis. Lateral line white. Lower sides with decidedly yellowish cast in larger fish. Belly grayish or yellowish white and without spots. Dorsal and caudal same as back; anal pale at base, olive at margin.^{5,7,11,43}

Maximum length: Ca. 380 mm,^{2,5} or possibly 447 mm.⁴⁰

DISTRIBUTION AND ECOLOGY

Range: Southern Labrador ⁴³ to Virginia.²⁸

Area distribution: Coast of New Jersey; ^{9,20} up Delaware River to vicinity of Philadelphia; ^{17,18} near Ocean City, Maryland; ¹⁰ at mouth of Chesapeake Bay.^{21,25,28}

Habitats and movements: Adults—an anadromous, inshore, bottom dwelling species ^{2,11,34} found along shores, in brackish estuaries, and freshwater rivers,^{5,31} inlets tributary to bays,¹ streams,^{11,22} lakes,³⁵ and shallow, muddy harbors; ^{2,11} sometimes over eelgrass beds.³⁵ Landlocked populations are known in Nova Scotia and Quebec.^{6,28} In winter, in only a few inches of water, slush, and floating ice, and sometimes shelter under ice.^{9,28} Maximum recorded depth, 2.7 m,²⁸ but possibly to 3.6 or 5.5 m. Not more than 1.6 km beyond headlands.¹¹ Recorded at salinities of 0.0–31.4 ppt,³⁷ and can withstand abrupt salinity changes.³⁸ Recorded from –1.2 C or slightly lower ³⁶ to ca. 25.5 C.⁴⁰

Anadromous,^{5,34} coming inshore ²⁹ and entering streams ¹⁴

and rivers ^{7,15} in October,⁸ November and December.^{23,29} Return to coastal areas primarily in late January.¹⁵ In the United States may ascend rivers in winter for at least 95 km,^{10,13} and, in former times, up to ca. 225 km (at Albany, New York).³² In St. Lawrence River undertake regular seasonal movements: upriver, appearing at Quebec City toward end of September and at Lake Peter in early December; downriver from February to May.⁴⁰ In Maritime Provinces and Gulf of Maine no offshore movements throughout year; south of Cape Cod move slightly offshore into deeper water in spring, returning in autumn. Enter Weweeantic Estuary, Massachusetts, in autumn and from October to May move with tide, these movements apparently associated with spawning and feeding; move into deeper water at mouth of estuary by late June. In New Jersey move inshore in September and October, apparently in response to drop in temperature to 17.2 C.^{2,11,35}

Larvae—in surface collections at Woods Hole from December or January to April (with earliest occurrence varying from year to year); ^{14,25} in Mystic River, Connecticut, larvae of unspecified size mostly at bottom;³ also, in same river, pelagic stages and planktonic larvae from January to early April with greatest concentrations up river and in channels.²⁸ Yolk-sac larvae apparently show preference for bottom waters during the day.⁴¹ Reported from 0.5 to 30.0 ppt, with average surface salinity of 12.0 ppt and average bottom salinity of 22.5 ppt,²⁸ and 1.1⁴⁴ to 11.7 C, with average surface temperature of 5.8 C and average bottom temperature of 5.1 C.²⁸ Larvae 44 hours old and older were able to withstand temperature increases of at least 14.4 C above an ambient temperature of 1.1 C for 30 minutes.⁴¹

At hatching swim toward surface, fall back head first.²⁸ Larvae may change to benthic habitat at 10 to 20 mm.³⁵

Juveniles—generally recorded from shoal areas, in coves near mouths of rivers, and on subtidal flats; found over bottoms of eelgrass, sand, and silt.³⁵ Young-of-the-year may remain in brackish river water for some months; ⁷ also specimens ca. 71–110 mm long along low tide line on Connecticut beaches. Possible maximum temperature 25.8 C; possible maximum salinity, 26.3 ppt.²⁸

Specimens 24 to 76 mm long are reported to approach shores from late May to June in New England.²⁶ Larger juveniles probably undergo fall and winter movements with the adults.³⁵

SPAWNING

Location: Various reported from along shores,²² at mouths of streams, ^{2,11} at head of tide,⁷ in creeks among

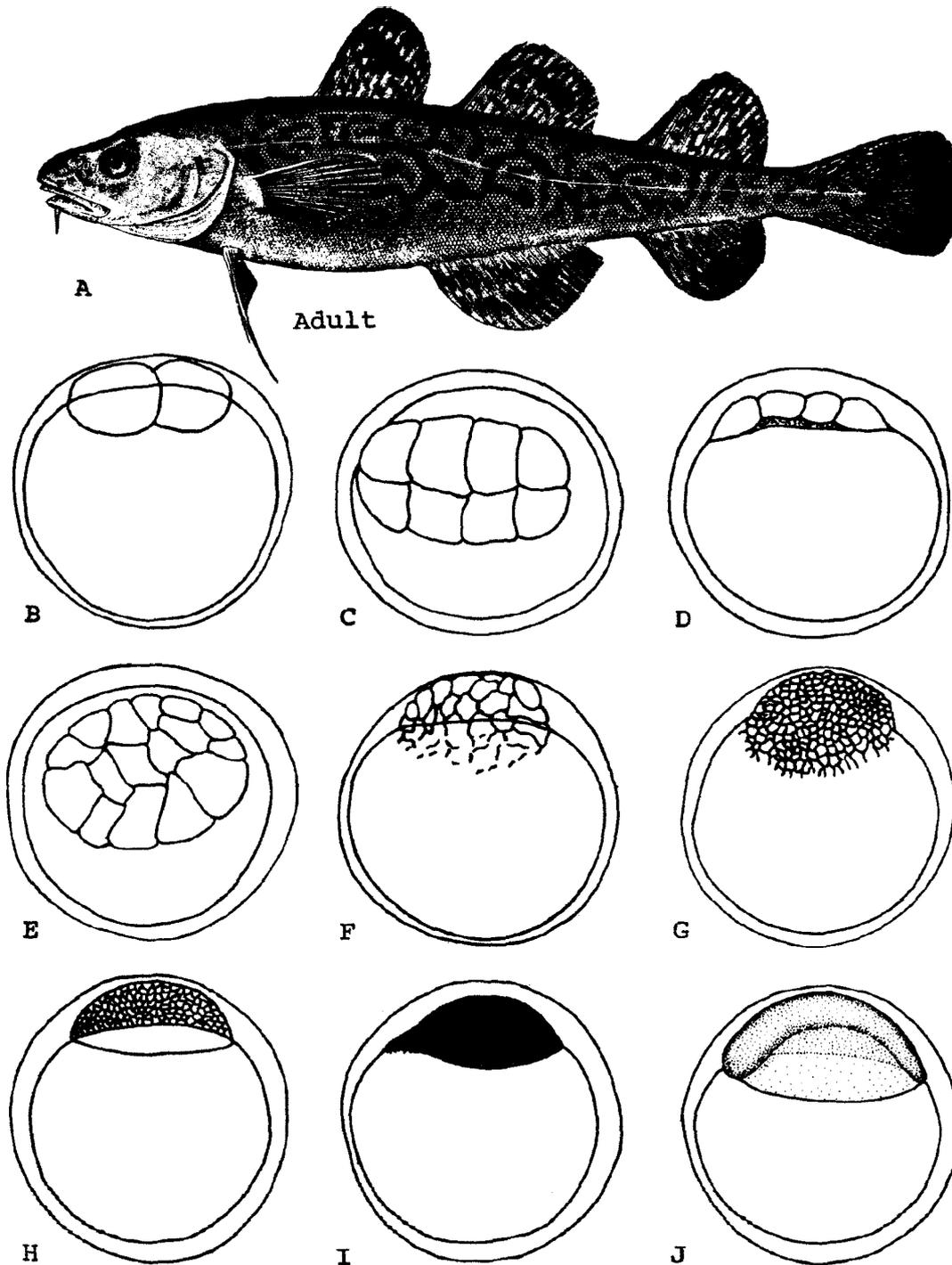


Fig. 168. *Microgadus tomcod*, Atlantic tomcod. A. Adult, ca. 277 mm TL. B. 12 hours (0.5 days), 2-cell stage. C, D, E. 24 hours (1 day), 8- to 16-cell stage. F, G. 36 hours (1.5 days), early morula stages. H. 48 hours (2 days), late morula. I. 72 hours (3 days), blastocoel formed. J. 144 hours (6 days), blastoderm descending over yolk. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 890. B-J, Original drawings, J. D. Hardy, Jr.)

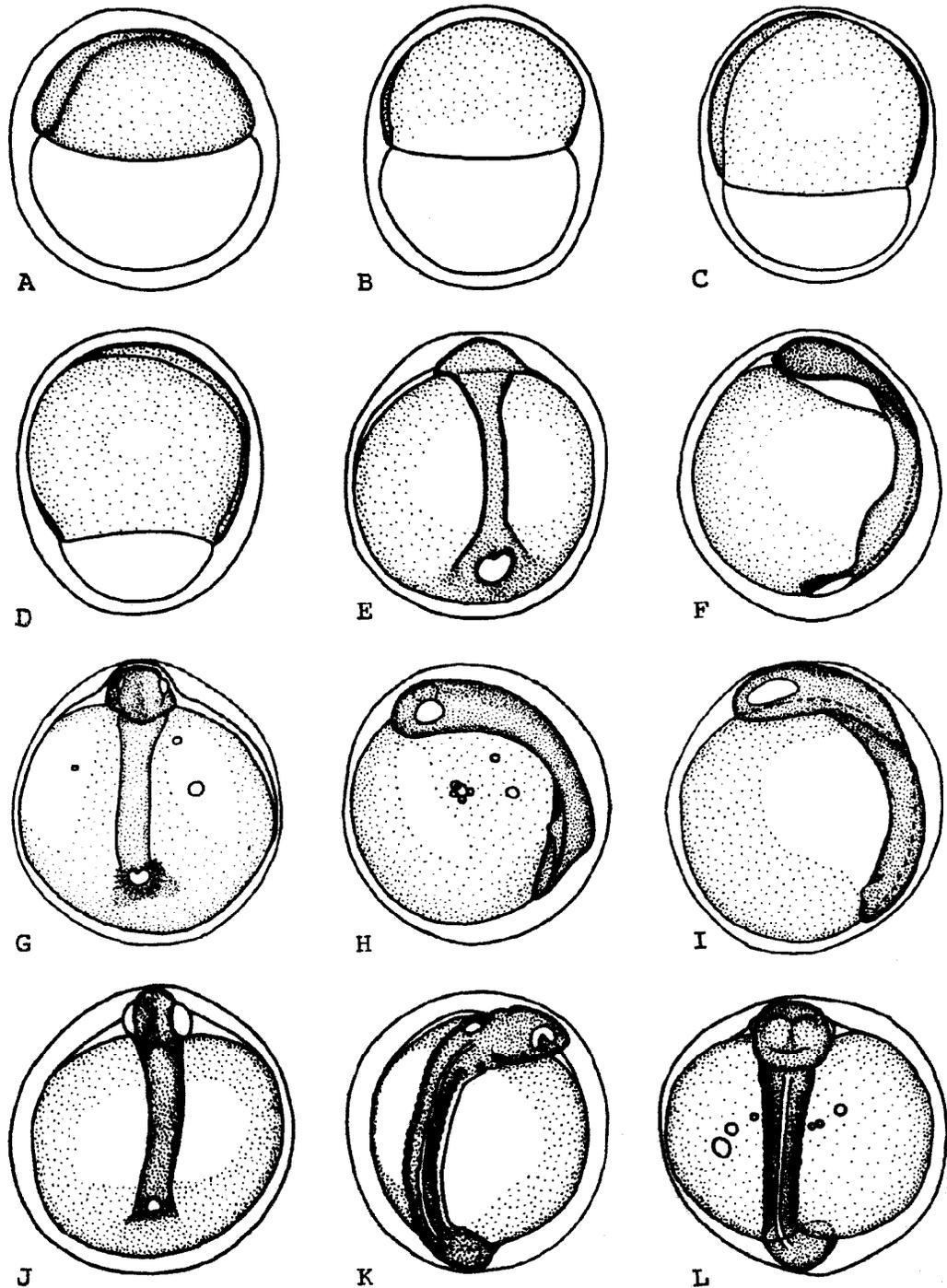


Fig. 169. *Microgadus tomcod*, Atlantic tomcod. A. 144 hours (6 days), somewhat more advanced than previous figure of equal age. B, C, D. 192 hours (8 days), blastoderm descending below equator (note constriction in yolk). E, F. 216 hours (9 days), blastopore small. G, H. 240 hours (10 days), blastopore closed or nearly closed, Kupffer's vesicle formed, oil globules evident. I, J. 264 hours (11 days), blastopore still evident in some specimens, somites present or absent. K. 336 hours (14 days), lens forming, 21-23 somites. L. 360 hours (15 days), tail free, 22-24 somites. (A-L, Original drawings, J. D. Hardy, Jr.)

emergent cordgrass (*Spartina alterniflora*),³⁵ and, in New York harbor, around docks and in weeds;¹² typically over sandy⁴⁰ or gravel bottom,⁴³ and usually associated with ice.^{28,40}

Season: November through February^{2,12,29,30} with peak activity in December^{4,15,22} or January.^{5,11,28}

Time: Unknown, but running ripe males and females collected at night.²⁸

Temperature: Running ripe males and females at 0 C;²⁸ spawning observed at 2.5 C; bottom temperature during spawning period 1.0 to 5.0 C.³⁵

Salinity: In freshwater, at least in landlocked populations. Otherwise run into freshwater, but spawn exclusively in estuaries. Ripe males and females have been taken in water having a salinity of 15.7 ppt. Optimum salinities probably correspond to those salinities which permit greatest sperm activity: 1 or 2 to 13 or 14 ppt. Salinity at the moment of fertilization is probably more important than average values during the incubation period.^{2,28} Reports of spawning at any salinity¹⁸ and in both brackish and salt water⁵ are probably in error since sperm are not active at salinities greater than 19 or 20 ppt.²⁸

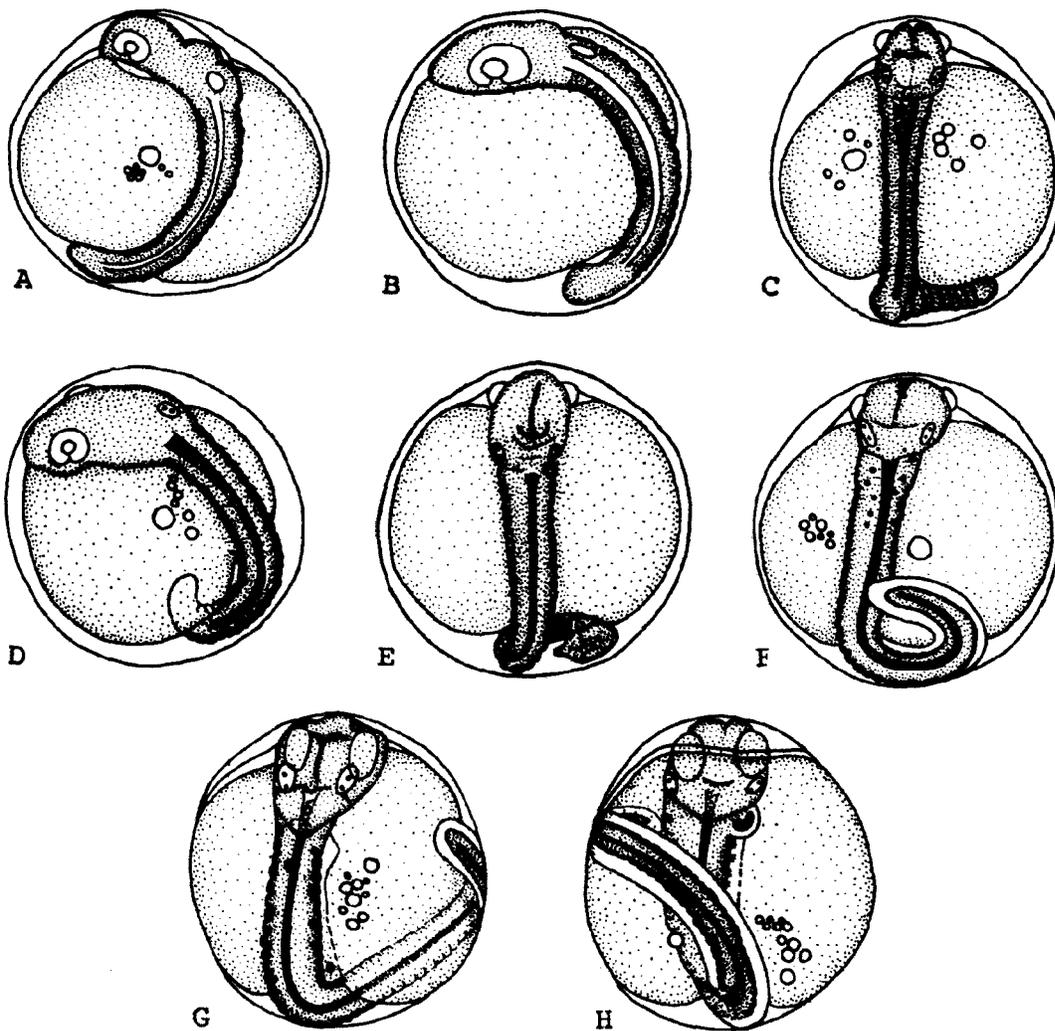


Fig. 170. *Microgadus tomcod*, Atlantic tomcod. A, B. 360 hours (15 days), showing formation of choroid fissure and otocyst. C, D. 384 hours (16 days), otoliths formed. E. 408 hours (17 days), heart developed. F. 504 hours (21 days), pigment developing, thoracic region. G, H. 600 hours (25 days), heartbeat established. (A-H, Original drawings, J. D. Hardy, Jr.)

Fecundity: 5075⁴ to 75,000;¹² estimated averages vary from 9000 to 30,000.^{2,4,5,12,41} Fecundity increases with size: at ca. 175 mm, 6000; at ca. 225 mm, 14,000; at ca. 350 mm, 65,780.⁴¹

EGGS

Location: Demersal;⁴¹ under experimental conditions initially attached to each other in large sheets, rarely attached to rearing vessel;⁴² also reported attached to sand and gravel on bottom.⁴³

Ovarian eggs: In October, 0.6 mm in diameter, in December, 1.4 mm; ripe ovarian eggs 1.4–1.5 mm in diameter.⁴

Fertilized eggs: Spherical⁷ or somewhat oval; diameter 1.39⁴²–1.7 mm,¹² reported averages 1.47⁴² and 1.66;² reported as nonadhesive by some authors,^{12,28,29,30,39} otherwise adhesive,³ adhering to one another but rarely to substrate; adhesiveness lost within one to five days after fertilization in some samples, retained until time of hatching in others;⁴² according to some authors, oil globule (or globules) absent,^{5,23} in some specimens, however, 3–12 small oil globules evident after gastrulation, but not evident in all batches of eggs or all eggs within a single batch, and with number possibly increasing as development proceeds⁴² (a report of an apparently single "distinct oil globule"⁴⁶ is questioned, JDH).

EGG DEVELOPMENT

Development at temperatures of 1.0–4.5 C (average 3.4 C):⁴²

12 hours (0.5 days)	2-cell stage—blastomeres large, equal, somewhat flattened.
24 hours (1 day)	8- and 16-cell stages—in 8-cell stage, cells distinctly flattened, aligned in rows of 4, more or less equal in size, and slightly raised from yolk. In 16-cell stage, cells distinctly unequal and arranged in oval mass over yolk.
36 hours (1.5 days)	Morula stage, peripheral blastomeres spreading downward over yolk.
48 hours (2 days)	Blastoderm peaked up over yolk, its edges sharply delineated.
72 hours (3 days)	Blastocoel formed, germ ring just beginning to move down over yolk.
144 hours (6 days)	Blastoderm over 1/4 to 1/3 of yolk; developing embryo thick and conspicuous.
192 hours (8 days)	Blastoderm extended to equator of egg or beyond; yolk noticeably constricted by passage of germ ring; developing embryo more elongate, less conspicuous.

216 hours
(9 days)
240 hours
(10 days)

264 hours
(11 days)

312 hours
(13 days)

336 hours
(14 days)

360 hours
(15 days)

384 hours
(16 days)

408 hours
(17 days)

504 hours
(21 days)

600 hours
(25 days)

864 to ca.
1008 hours
(36–42 days)

Incubation period:

At 0.0 C	ca. 44–70 days. ⁷
At 1.0–4.5 C (\bar{x} 3.4 C)	36–42 days. ⁴²
At 2.2–7.8 C	ca. 25 days. ^{29,30}
At 4.4 C	30 days. ^{11,40}
	22–35 days. ⁷
	35 days. ^{2,22}
At 4.5 C	30 days. ⁵
At 6.0 C	24 days. ⁵
At 6.1 C	24 days. ⁴⁰
At \bar{x} 6.1 C	25 days. ¹¹

Notes on incubation: Eggs have been hatched in fresh-water^{11,12} and development will proceed at a salinity of ca. 24.0 ppt.²⁸

Head distinct, embryo around one half of yolk diameter, blastopore small. In some specimens blastopore nearly closed, eyes just forming; in others Kupffer's vesicle well-developed, optic vesicles large. In this and subsequent stages minute oil globules may be present.

Optic vesicles somewhat elongate, both blastopore and Kupffer's vesicle evident in some specimens, somites present or absent.

Somites evident in all specimens, brain divisions forming.

Otocyst and lens forming, tail still attached but peaked up over yolk, 21–23 somites.

Embryo sunken into yolk, giving yolk a bilobed appearance, tail free, choroid fissure closing, 22–24 somites.

Number of somites noticeably increased, uncountable; choroid fissure closed; notochord hyaline; otoliths developed; length of tail noticeably increased.

Heart well-developed, number of somites and length of tail increased.

Pigment evident in thoracic region (also, rarely, on head).

Heartbeat established; pigment spread over ventral part of body; prominent melanophores on developing gut. In some specimens pigment appeared to develop in the eye at this stage, but this is apparently transitory, as the eyes of hatchlings are unpigmented.

Hatching.⁴²

YOLK-SAC LARVAE

Minimum reported length, 4.12 mm,⁴⁴ although average hatching length reported as ca. 5.0 mm.^{2,11} Maximum length ca. 6.45 mm.²⁸ Duration of stage, 4^{2,22} to possibly 6 days.¹² (Part of the following description is based on three newly hatched fish of unknown size, all of which hatched from the same sample over a period of six days.)⁴²

Mouth not evident in earliest hatchling (size unknown), well formed in another hatchling six days older. Yolk sac large, elongate in earliest hatchlings, round in later (older) hatchlings. In earliest hatchlings dorsal finfold

extended on to head;⁴² in other yolk-sac larvae dorsal finfold terminated at point about half way between anus and posterior border of otic capsule. Pelvic finfold carried to left of anus. Pectoral fins present²⁸ or absent at hatching. In earliest hatchling notochord hyaline.⁴² Anus first evident just behind yolk sac and to right of finfold between margin of finfold and ventral edge of myomeres.²⁸

Pigmentation: In earliest hatchling (size unknown) two rows of large stellate melanophores above gut and two disjunct rows of melanophores ventrally between anus and tip of tail; no pigment on dorsum, head, or in eye. In a somewhat more developed newly hatched specimen,

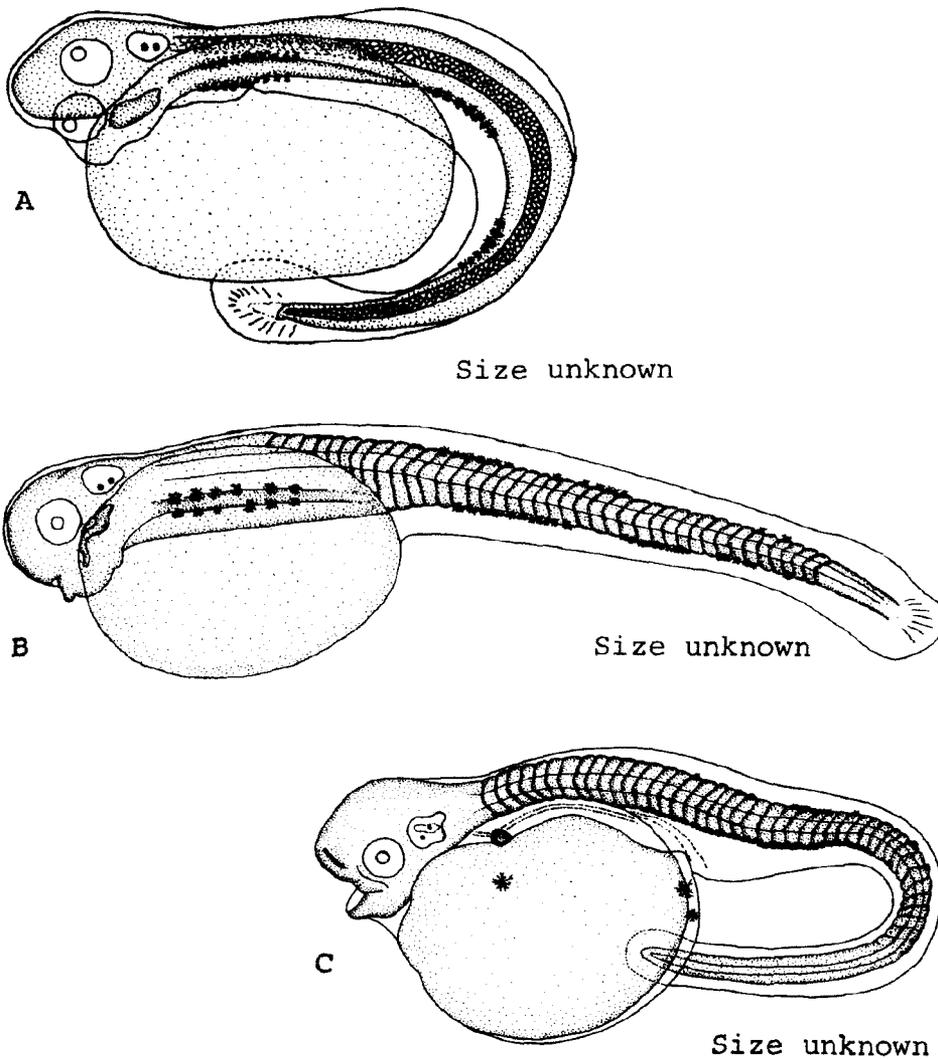


Fig. 171. *Microgadus tomcod*, Atlantic tomcod. A. Newly hatched yolk-sac larva, 864 hours (36 days) after fertilization. B. Newly hatched yolk-sac larva, 936 hours (39 days) after fertilization. C. Newly hatched yolk-sac larva, 1008 hours (42 days) after fertilization. (A-C, Original drawings, J. D. Hardy, Jr.)

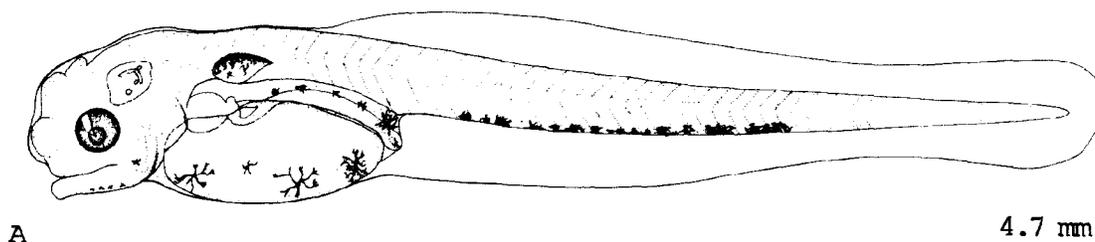


Fig. 172. *Microgadus tomcod*, Atlantic tomcod. A. Yolk-sac larva, newly hatched, 4.7 mm TL, showing pigment on yolk sac, body, and gas bladder. (A, Original drawing, J. D. Hardy, Jr.)

3 disjunct rows of pigment ventrally beyond anus, and pigment developed along mid-dorsal line. In the largest recent hatchling pigment similar except ventral pigment rows more or less continuous, and few large stellate melanophores on yolk.⁴² In a hatchling 4.9 mm long, pigment as described above, also on eye and gas bladder (JDH).

Yolk-sac larvae otherwise described as having prominent melanophores on yolk; a row of stellate or reticulate melanophores mid-dorsally and mid-ventrally along tail (but these sometimes absent in specimens up to 5.95 mm long); sometimes one to a few small punctate melanophores on head, and a few minute elongate black spots mediolaterally. Twenty percent of individuals 5.00 to 5.94 mm long with lower jaw pigmented.²⁸

LARVAE

Size range described ca. 7.0–12.1 mm.

Order of fin appearance: Pectoral (in yolk-sac larvae), pelvic, caudal, first anal, second anal, third dorsal, second dorsal, first dorsal. D_2 and D_3 first evident at 9.00–9.45 mm (with D_2 slightly preceding D_3); D_1 , first evident at 10.45 mm but still lacking incipient rays at 12.10 mm; A_1 evident in 8 percent of specimens at 8.00–8.45 mm, A_2 in 4 percent at 8.50–9.95; C. evident in some specimens at 7.50–7.95 mm, in all at 9.00–9.45 mm; P. rounded to ca. 10.00 mm, becoming elongate thereafter; V. first evident in some specimens at 6.50–6.95 mm as pair of small round buds just behind developing cleithra, in all specimens at 9.00–9.45 mm, but lacking rays throughout size range described. (Cultured and wild-caught larvae show the sequence of fin development outlined above, but the fins are more advanced in wild-caught than cultured larvae of similar sizes.)²⁸

Pigmentation: Larvae in general show several distinct pigment areas: on top of head, along dorsal side of digestive tract, over swim bladder, on ventral region anterior to anus, along mid-dorsal line of body, along mid-ventral line of body, mediolaterally on body (but also scattered elsewhere on sides), and along jaw.²⁸

At 6.5–7.95 mm 4 melanophores develop on isthmus, as well as on ventral ends of developing cleithra. All specimens 7.5 mm long or longer with lower jaw pigmented. At 6.00–6.45 mm one or a pair of small stellate or reticulated melanophores on dorsal wall of intestine just above the anal opening. Melanophores at the angle between body wall and the descending terminal portion of the gut, and in the area where the gut runs parallel to and against the ventral body wall before turning downward to the anus (note that some of these markings are sometimes visible in advanced yolk-sac larvae); in most specimens 7.5 mm long and longer pigmentation visible only at angle between gut and venter. In early larvae melanophores visible above swim bladder. At 8.5 mm and larger mid-dorsal and mid-ventral melanophores tend to occupy right and left positions, but are not conspicuously paired; subsequently dorsal and ventral melanophores form unbroken pigment bars, their ends either equal or with ventral bar extended slightly further toward tail. In some specimens up to 7.95 mm long a short unpigmented gape between vent and anterior end of ventral pigment bar. In specimens 6.50 to 6.95 mm and longer prominent melanophores just behind eyes and over optic lobes; at 7.50 mm and larger a pair of small stellate melanophores dorsal, anterior, and medial to olfactory pits. In nearly all specimens 8.50–8.95 mm long and longer mediolateral pigment forms a conspicuous line of black spots or very small stellate melanophores posterior to vent and anterior to posterior ends of dorsal and ventral pigment bars.²⁸

JUVENILES

Minimum size described, 23 mm TL.

At 23 mm TL, barbel well-developed.⁴²

Pigmentation: At 23 mm TL, a distinct, broken row of melanophores mid-laterally on posterior part of body, and a short row of pigment near caudal base; numerous large melanophores on top of head and few melanophores in throat region; pigment evident near bases of first and second dorsal and second anal. At 41 mm TL, body with

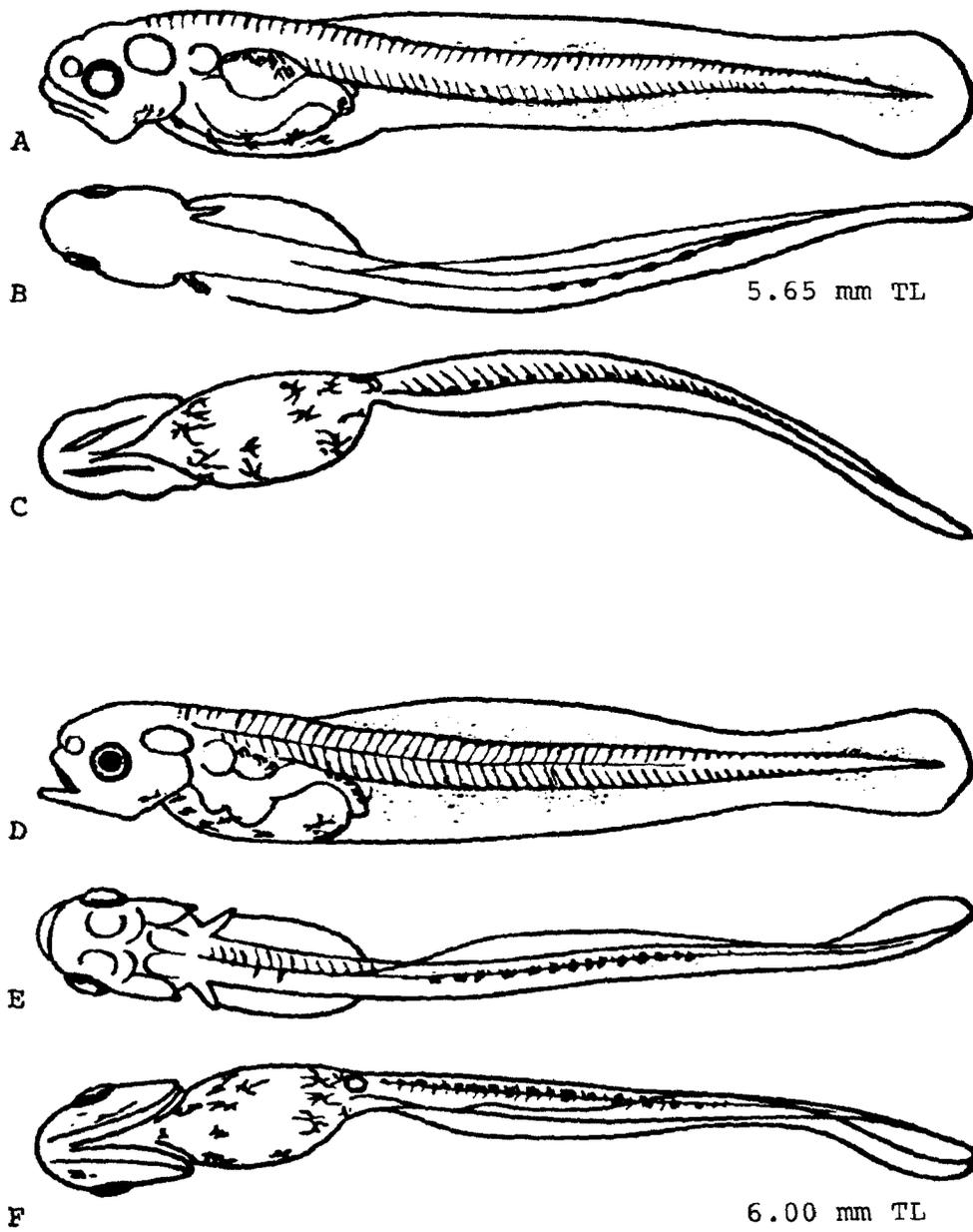


Fig. 173. *Microgadus tomcod*, Atlantic tomcod. A, B, C. Yolk-sac larva, 5.65 mm TL, lateral, dorsal, and ventral views. D, E, F. Larva, 6.00 mm TL, lateral, dorsal, and ventral views. (A-F, R. A. Booth, 1967: pls. 1-3.)

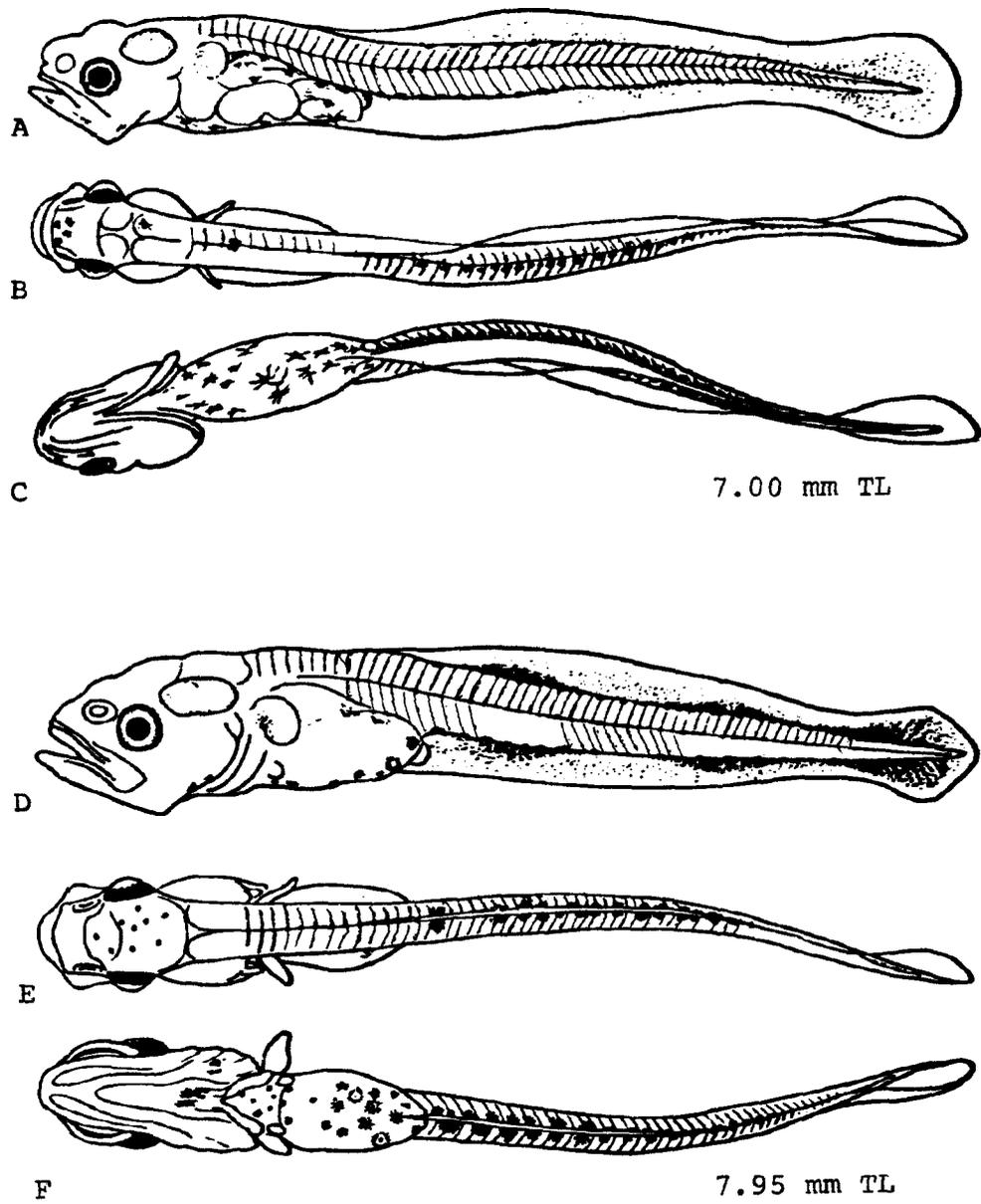


Fig. 174. *Microgadus tomcod*, Atlantic tomcod. A, B, C. Larva, 7.00 mm TL, lateral, dorsal, and ventral views. D, E, F. Larva, 7.95 mm TL, lateral, dorsal, and ventral views. (A-F, R. A. Booth, 1967: pls. 1-3.)

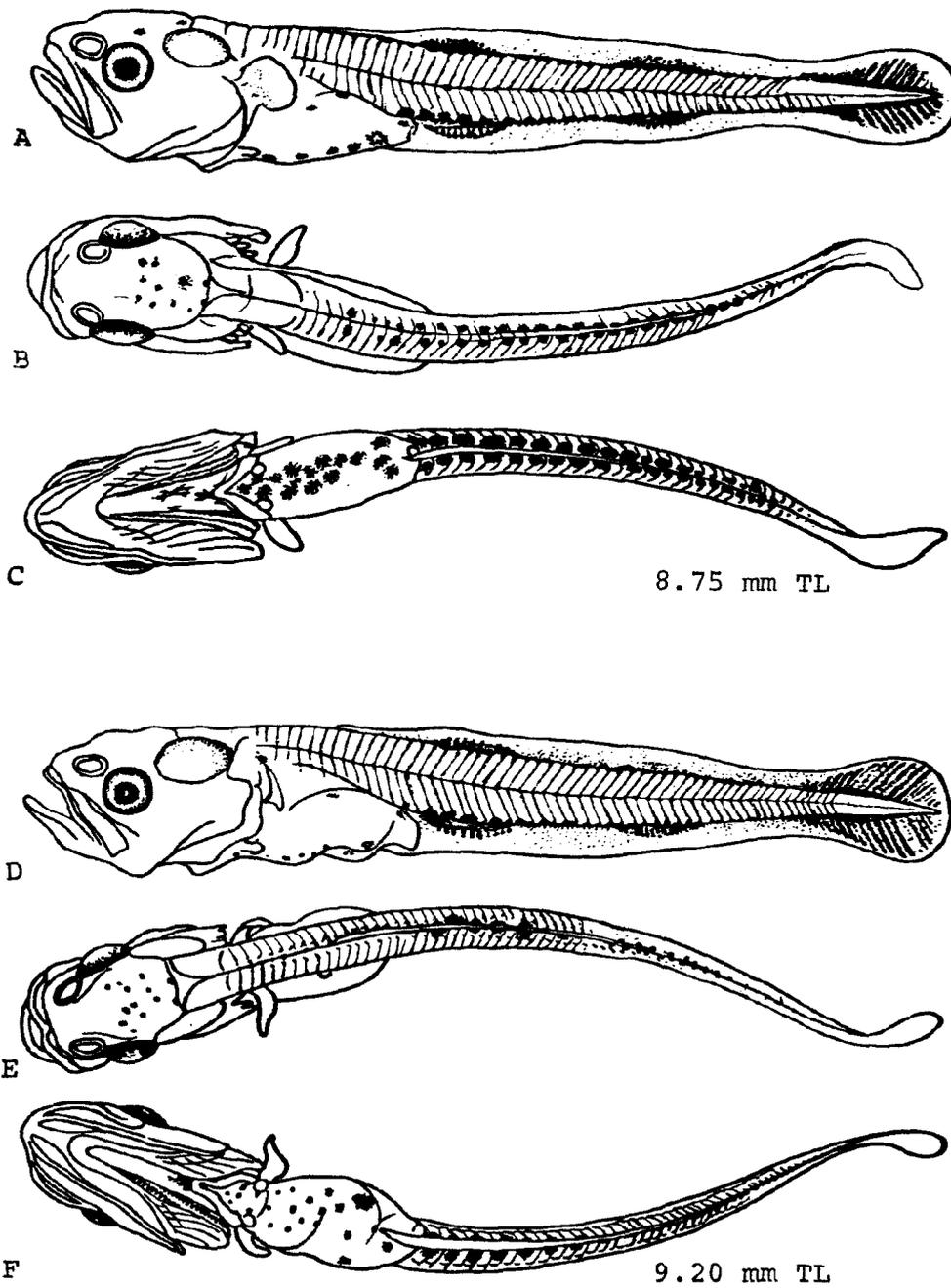


Fig. 175. *Microgadus tomcod*, Atlantic tomcod. A, B, C. Larva, 8.75 mm TL, lateral, dorsal, and ventral views. D, E, F. Larva, 9.20 mm TL, lateral, dorsal, and ventral views. (A-F, R. A. Booth, 1967: pls. 1-3.)

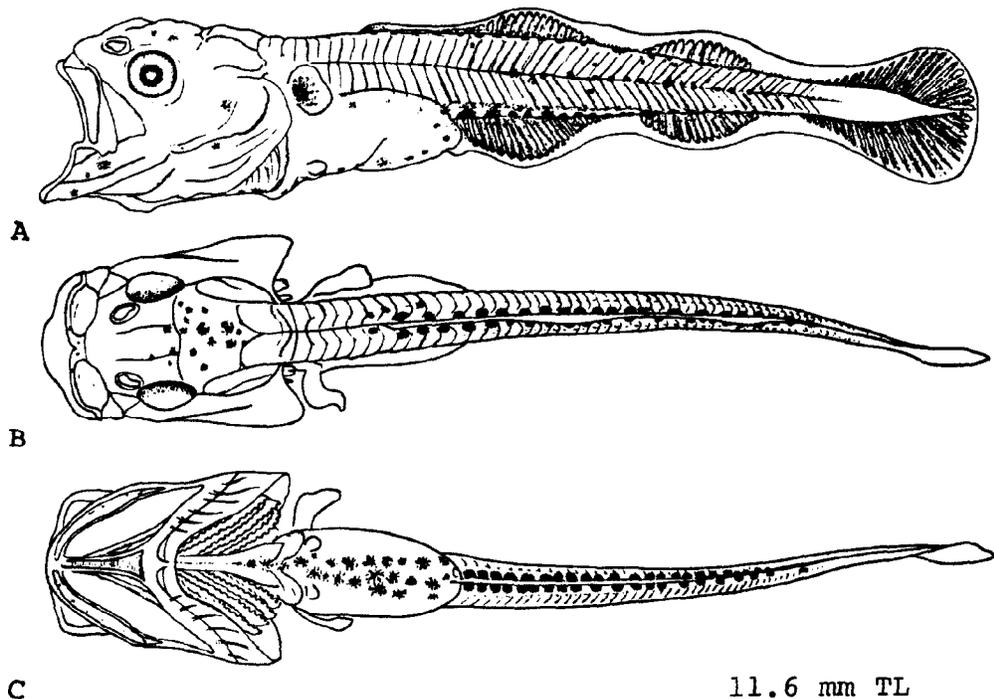


Fig. 176. *Microgadus tomcod*, Atlantic tomcod. A, B, C. Larva, 11.6 mm TL, lateral, dorsal, and ventral views (note presence of pelvic buds). (A-C, Booth, R. A., 1967: pl. 4.)

about 11 narrow blotches, sometimes forming chain-like pattern, over back, these extending ventrad below the mid-lateral region; pigment on head increased forming a prominent blotch on crown; pigment evident on first dorsal, and in all pigmented median fins melanophores have migrated outward from fin bases.⁴²

AGE AND SIZE AT MATURITY

Minimum age at maturity: 11 to 12 months in Hudson River,⁴⁵ although apparently at end of third year or during fourth year in Quebec.⁴⁰ Minimum length at maturity: Smallest female 170 mm.⁴

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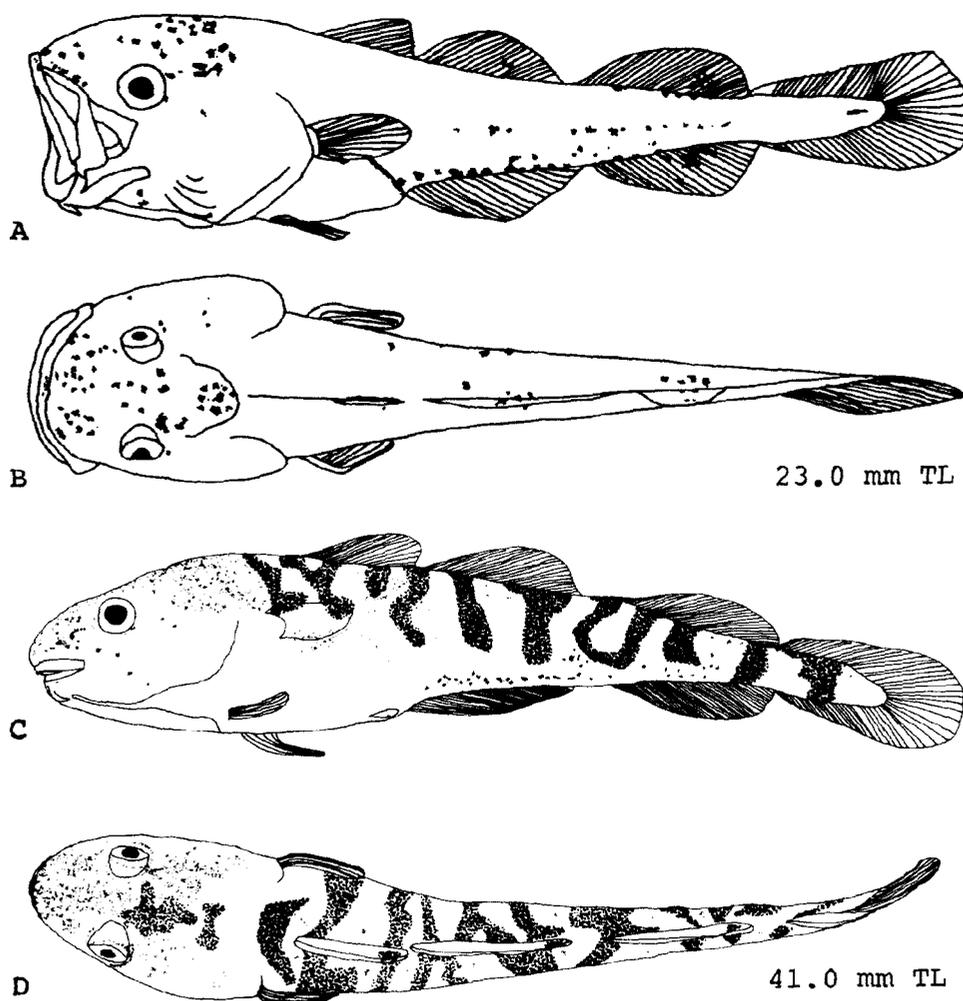


Fig. 177. *Microgadus tomcod*, Atlantic tomcod. A, B. Juvenile, 23.0 mm TL, lateral and dorsal views (note presence of barbel). C, D. Juvenile, 41.0 mm TL, lateral and dorsal views. (A-D, Original drawings, L. L. Hudson.)

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Phycis chesteri Goode and Bean, Longfin hake**ADULTS**

D₁ 9-10; ⁴ D₂ 54³-59; ² A. 47³-56; ⁴ C. 5+18-21+5; P. 16-18; V. 3; scales ca. 90-91; scales above lateral line 7, below ca. 28; ¹⁰ gill rakers, 4 or 5 (JAM) + 14-15; ² total 21; ³ branchiostegals 7; ¹⁰ vertebrae 49.³

Proportions as times in TL: Greatest depth 6; head length 5.5.³ Proportions as percent of head length: eye 31.7; interorbital distance ca. 13.4.³

Body elongate; head pointed; upper jaw projecting; gape extended to pupil; a small barbel,⁴ about 1/3 diameter of orbit,¹² on lower jaw. Lateral line broadly arched in first half, broken in posterior half.⁴ Third dorsal filament greatly produced,² 5 times longer than next longest ray; pelvics very long, filamentous.⁴

Pigmentation: Olive black above, sides gray (JAM), belly silvery white; fins same color as back and with dusky markings on edges.⁴ In alcohol brown on back, muddy or reddish white below.³

Maximum length: Ca. 382 mm.⁴

DISTRIBUTION AND ECOLOGY

Range: South of Laurentian Channel, Newfoundland^{3,4} to off Dry Tortugas, in the Gulf of Mexico (JAM).²

Area distribution: Off New Jersey; ⁶ east of Cape Charles, Virginia, but only beyond the 183 m depth contour.⁷

Habitat and movements: Adults—bottom species found at depths of 58 to 1335 m (but usually at 366 to 457 m); ^{1,3,8,9,10} larger individuals found in deeper water.^{11,12}

Larvae—specimens up to 10.0 mm long from surface to 50 m; ^{11,12} also reported from average tow depth of 435 m.⁷

Juveniles—specimens 25¹¹ to ca. 125 mm long at surface; ¹² specimens 90 to 320 mm long between 183 and 366 m.⁵

SPAWNING

Season: Probably in fall.^{3,4}

Fecundity: No information.

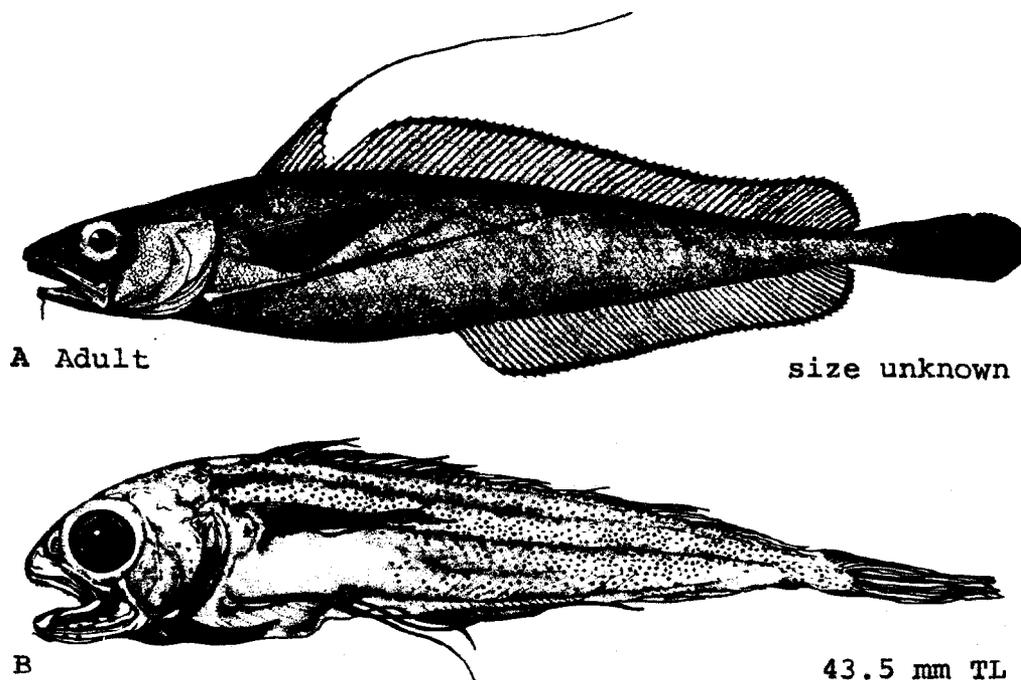


Fig. 178. *Phycis chesteri*, Longfin hake. A. Adult, size unknown. B. Juvenile, 43.5 mm TL. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 903. B, Original illustration, Elizabeth Ray Peters.)

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

JUVENILES

Size described, 43.5 mm TL.

At 43.5 mm TL, barbel formed, teeth well-developed in upper jaw (JDH).

Pigmentation: Pigment developed on both jaws, in opercular region, in two indefinite blotches on snout and top of head, and in region of cleithrum. Region of abdominal cavity grayish and apparently unpigmented; body other-

wise spotted with large, widely spaced melanophores, especially above mid-lateral line. One branch of lowermost pelvic ray with a long brown blotch; fins otherwise without pigment (JDH).

AGE AND SIZE AT MATURITY

No information.

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12. Beebe, W., 1929:17.

Pollachius virens (Linnaeus), Pollock**ADULTS**

D.₁ 21⁴⁷ (or possibly 9³²)–15⁷³ (w. Atlantic 13–14^{14,20}),
 D.₂ 17⁴³ (or possibly 14³²)–26⁴⁶ (w. Atlantic 21–22¹⁴),
 D.₃ 19^{14,47,73}–24¹² (w. Atlantic 24–28¹⁴); A.₁ 21³²–30⁷³
 (w. Atlantic 24–28¹⁴), A.₂ 17–24⁷³ (w. Atlantic 20–21¹⁴);
 P. 18 (?) or 19–22; V. 6; ³² scales 154–156; ²⁰ gill rakers
 on first arch, total 35–40,¹² lower limb 28–30; ²⁰ total
 vertebrae 53–57,⁴⁶ averages (excluding hypurals) 53.40–
 53.68,^{12,70} precaudal vertebrae 23–25, caudal vertebrae
 29–32.^{32,57}

Proportions as times in TL: Depth 4.33¹⁴–4.53, head
 3.68²⁰–4.00,¹⁴ Proportions as times in HL, eye 5.73–
 6.35.²⁰ Proportions as percent HL, interorbital space
 19.3–23.8.¹²

Body rather elongate, somewhat compressed, slightly
 deeper than thick; snout pointed; lower jaw project-
 ing;^{12,14,28} usually no barbels on chin⁶⁸ (although present
 in juveniles); gape not extended to eye.^{12,14,28} Teeth pres-
 ent on jaws and vomer; small, equal, pointed, and cardi-
 form.^{14,20} Lateral line almost straight, lacking sharp
 curve beneath origin of 2nd dorsal.¹² First dorsal tri-
 angular and originating slightly behind pectorals;⁶⁸
 caudal considerably emarginate.^{12,73}

Pigmentation: Dorsum rich olive green, brownish green,
 or grayish, paling to yellowish, smoke gray, or green on
 sides; forehead, snout, and lips blackish; belly silvery gray
 or milk white; lateral line white or very pale gray. Peri-
 toneum white. Dorsal, caudal, and anal fins olive gray
 or greenish, but anal pale at base; pectorals dark; pelvics
 white with pink or reddish tinge.^{12,14,20,47,53,68}

Maximum length: Ca. 1118 mm.²⁰

DISTRIBUTION AND ECOLOGY

Range: Along American coast from Hudson and Davis
 Straits to Cape Lookout, North Carolina.^{12,14,20,68} In the
 eastern Atlantic, shores of Europe from Bay of Biscay^{6,19}
 (records from the Mediterranean³³ questioned⁷⁷) around
 the British Isles and through the North Sea to the Bar-
 ents Sea and Novaya Zemlya. Also in the Baltic, the
 White Sea, and the Belts Sea, and around Bear Island,
 the Orkneys, the Shetlands, and the Faroes, Iceland, and
 the southern tip of Greenland.^{6,9,12,14,19,73}

Area distribution: Coast of New Jersey;²² juveniles at
 mouth of Delaware Bay and at Indian River inlet;⁴⁴ off
 Virginia at ca. 36–46 m,²³ and in Virginia waters of
 Chesapeake Bay;^{4,58} juveniles inshore along Virginia
 seaside.⁸²

Habitat and movements: Adults—a schooling spe-

cies^{34,60,68,72} found at bottom, and midwater depths as
 well as at the surface^{12,19,28} where it sometimes breaks
 water like mackerel.⁶⁵ Usually at edges of shoals and
 banks,¹ also close inshore²⁷ as in “tide rips.”²⁵ Reported
 from fjords in Greenland.⁵⁵ Typically over stony bot-
 tom.²⁸ In Bay of Fundy, 36–183 m; ¹ in Iceland down to
 ca. 200 m;^{19,30} and in Europe “over great depths” and
 down to 320 to 340 m.⁷⁵ Large fish tend to stay further
 offshore than smaller ones.⁶⁸ In American waters, few
 individuals beyond the 137 m depth contour.^{65,68} In Gulf
 of Maine, never at surface when temperatures are above
 11.1 C; minimum temperature, 0 C.⁶⁸

In American waters movements are apparently not as
 extensive as in European waters. Pollock enter sounds
 and harbors in Massachusetts later than cod and leave
 when temperatures rise to 15.6–18.3 C.¹⁶ Some fish from
 New England overwinter as far south as New Jersey. In
 the Gulf of Maine there are apparently no mass move-
 ments, although some individuals may make rather ex-
 tensive movements.⁶⁸ Pollock from Campobello and
 Grand Manan, Canada, overwinter in Cape Cod and
 return in spring.¹⁴ In European waters movements are
 considerably more extensive. There is a general move-
 ment northward in summer and southward in winter, at
 least in the latitudes of Murmansk.¹² Individuals from
 Norway migrate to Iceland, the northern North Sea, and
 the Faroes,³⁷ and pollock enter fjords bordering on the
 North Sea only in winter.⁵⁶ Prespawning concentrations
 may form 2 to 3 months before actual spawning.²⁴ In
 Norway spawning migrations may begin in September,
 October, November, or later;^{63,64} large shoals of pollock
 also form in Norway in June.³⁵ Diurnal vertical migra-
 tions of more than 100 m have been reported. Indi-
 viduals leave the seabed in large shoals at dusk, tend to
 disperse, but form midwater shoals by the middle of the
 night.⁷⁶

Larvae—usually found from shoreline¹² to 200 m line,
 but also reported over depths of up to 1550 m.^{9,57} Yolk-
 sac larvae initially float upside down.¹⁵ Stratification
 apparently takes place, with youngest larvae nearest the
 surface, but there are exceptions to this generalization.
 Specimens 30 mm long, for example, have been reported
 from both middepths and the surface.^{46,57} Maximum
 distance out at least 185 km (RRM).

Drift with current, and usually carried from spawning
 grounds;^{3,13} larger larvae, however, can direct their
 movements (RRM).

Juveniles—individuals up to 53 mm long may still be
 pelagic,^{3,13} and specimens 50 to 75 mm long have been
 collected at the surface with young of *Pollachius*
pollachius.⁴³ Typically, however, young juveniles are in-

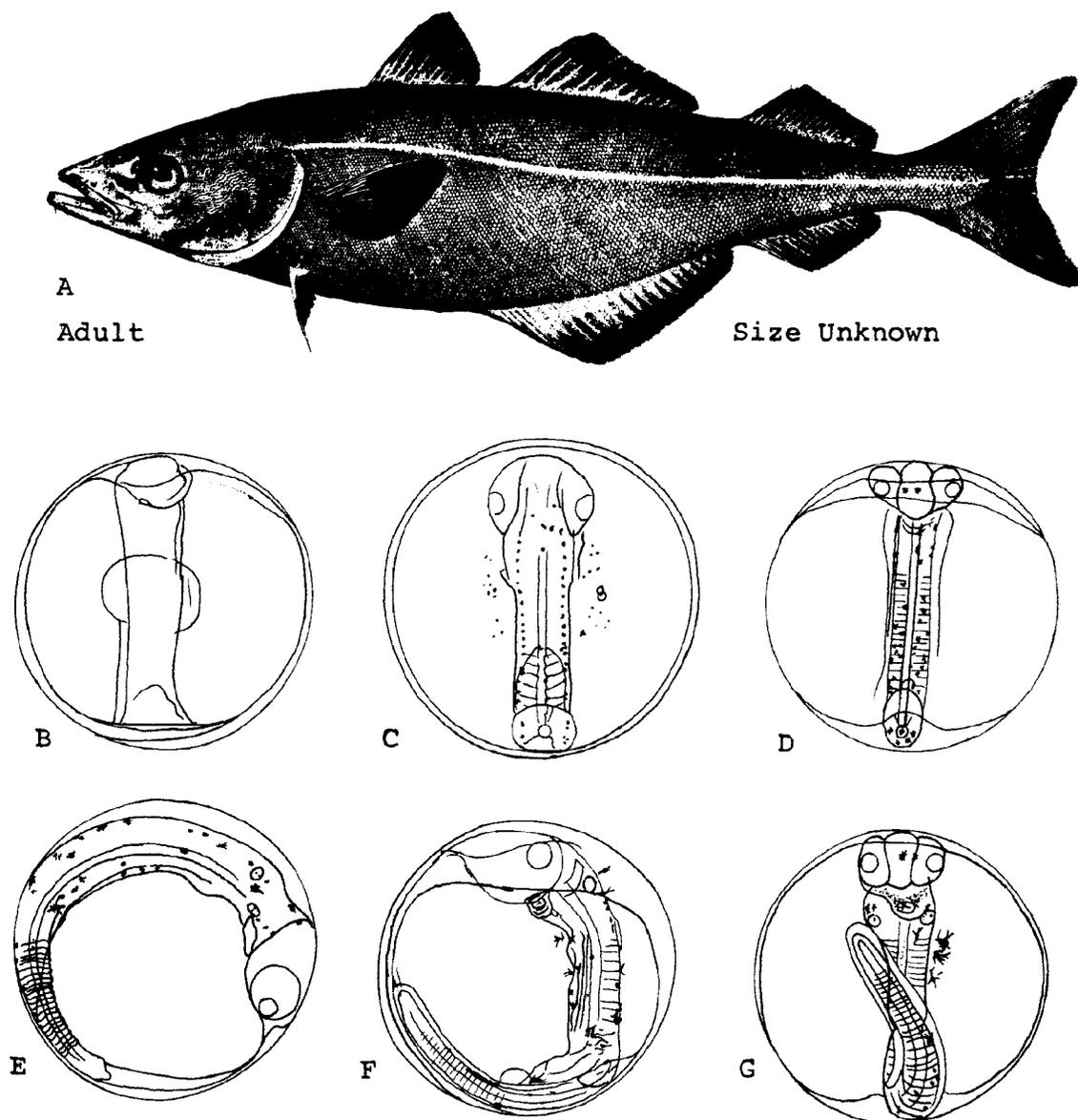


Fig. 179. *Pollachius virens*, Pollack. A. Adult, size unknown. B. Egg, 5 days after fertilization, embryo well formed. C. 6 days, pigment evident, lenses formed. D. 7 days, Kupffer's vesicle evident. E. 9 days, otocysts formed, pigment scattered over body. F. 10 days, tail elongate. G. 9 days, but specimen more advanced than previous specimen, otoliths formed. (A, Goode, G. B., 1884: pl. 60. B-G, McIntosh, W. C., 1894: pl. 2, Tamiko Karr, delineator.)

shore^{12,69} but can be found on offshore banks.^{44,45} Specimens ca. 25–50 mm long have been observed in rocky pools,⁴² along shores,⁶⁷ and in harbors where they are associated with *Ulva*.⁴³ Specimens 50 to 300 mm long are in shallow sublittoral nursery areas such as bays¹³ and are recorded variously from harbors, rocky tangle-covered ground,^{15,48} and beaches.³⁰ Juveniles of unspecified sizes are sometimes associated with jellyfish³³ and have been

observed in inlets, creeks,³⁹ estuaries,^{8,65} and tidal rock pools.¹⁵ One year olds form large inshore schools.¹² Juveniles apparently prefer rocky bottom,⁶⁶ but have also been reported from over sand and mud⁴³ and in association with aquatic vegetation.⁴³ "Fingerlings" abundant at 80 to 200 m in North Sea,⁵⁶ and specimens ca. 250 mm long in shallow water and out to 3.6 to 5.5 m in Ireland.⁴³ "Young" individuals out to and beyond the 183 m depth

contour.³¹ Specimens 38 and 40 mm long at 8.0–15.5 C.⁸² About 200 mm specimens down to 0 C, and seldom above 15.6 C.⁶⁸ Specimens 38–40 mm long at ca. 31.5 ppt.

At 25^{9,56} to 50 mm,^{28,59} swim to bottom (and apparently shoreward), but may not arrive inshore until 60 mm long.¹⁵ In American waters the bottom stage begins after 3 months or more. Although Bigelow and Schroeder believed that young pollock descend in practically the same water in which they were hatched,^{17,68,74} there is evidence to suggest an active migration in European waters toward littoral waters and away from the spawning area.^{75,48} A "run" of 25 to 37 mm specimens occurs in Massachusetts in April.¹⁶ In Europe the pelagic stage usually lasts three months, but apparently can be shorter or considerably longer;⁵⁶ and the transition stage occurs between May⁴² and September.⁵² In Iceland pelagic stage apparently occurs only in mid-June;⁵⁷ in the North Sea it continues from early summer to September;⁵² and in the Faroes from May⁵⁷ to the end of July.⁴⁶ In Murmansk juveniles move shoreward in June and July, and enter bays in large schools in July and August.^{5,73} In American waters specimens ca. 200 to 250 mm long move inshore in April, but seek deeper water in winter. Pollock first appear in the Gulf of Maine as yearlings.⁶⁸ In Iceland juveniles remain in shallow bays and firths for 2 to 3 years.^{19,39} In Ireland specimens 50 to 75 mm long move offshore into slightly deeper water during winter; and at ca. 375 mm they move into still deeper water in winter and do not return.⁴³

SPAWNING

Location: In North America primarily between Nova Scotia and Cape Cod¹² with greatest concentration apparently in vicinity of Massachusetts Bay.^{14,68} Larvae are known from as far south as Long Island, New York.¹⁵ In European waters, northern parts of the North Sea, the coast of Norway, the Shetland and Faroes Islands,²⁴ and, presumably, as far north as 66° N;^{9,56} southward possibly to the Bay of Biscay;⁴⁸ also in southern Greenland^{12,30} and Iceland.⁵⁷ Spawning apparently takes place off the bottom⁷⁷ in the vicinity of coastal slopes and banks^{48,52} and usually over broken, hard, rocky bottom,^{27,33,68} but also, sometimes, over soft bottom.^{50,73}

Depth: In North American waters ca. 42–140 m^{6,53} and possibly to 170 m.⁶⁸ In European waters 50 m⁹ (although usually considerably deeper^{24,59}) to not over 250 m,⁹ with maximum activity between 100 and 200 m.^{7,12,26,29,48,49,59} In Iceland mainly at 150 m, with very little or no activity at less than 100 m.⁵⁷

Season: In American waters September 29 or earlier⁷¹ to early March, with both extremes recorded in Massachusetts Bay where peak activity occurs from early November to mid-January.^{12,68} On Georges Bank, December to February.⁵⁴ Fish collected at Campobello Island, Canada, on June 28 were in prespawning condition.² In Europe

December^{15,56} to June⁷³ with peak activity occurring in February and March.^{9,49,50,59,77} Spawning has been observed in aquaria (in Europe) in early May.⁶⁷ In Iceland mid-February^{19,39} to early May,⁴⁰ with maximum production in April.⁷⁴

Temperature: Spawning occurs on a falling temperature, and the entire water column must cool to 8 or 9 C before spawning begins.⁶⁸ Temperature range in American waters 3 to 10 C,¹² with greatest activity estimated at ca. 4.5 to 6 C⁶⁸ and 8 to 9 C.¹² Bigelow and Schroeder have pointed out that a minimum of ca. 3.5 C is probably required for proper incubation of the eggs and a somewhat higher temperature for the maturation of the gonads.⁶⁸ Temperature range in European waters, ca. 5.5 to 10 C.^{7,12,57,73} with maximum activity at ca. 7 C.^{29,51}

Salinity: In North America 32.0 to 32.8 ppt.^{12,68} In Europe 35.10 to 35.30 ppt, with optimum at 35.15 to 35.25 ppt.⁷

Fecundity: Ca. 200,000^{6,53} to 8,260,000.¹⁰ Reported averages, 220,000,¹⁴ 222,000,²¹ 225,000,^{12,53,68} 300,000,^{405,125.}²¹

EGGS

Location: Pelagic, free floating (at least at salinities of 35 ppt or higher). Sometimes carried great distances from spawning grounds.^{6,12,14,50,52} Usually in water 50 to ca. 250 m deep.⁵⁷

Unfertilized eggs: Large clear eggs (prior to spawning) 0.9–1.8 mm in diameter⁸¹ (although upper stated limit doubted, RRM); micropyle single and resembling that of haddock.⁸¹

Fertilized eggs: Spherical;¹⁴ completely transparent.^{15,49,50} diameter 1.0^{11,14,33} to 1.22 mm;^{9,28,51,59,64} average diameter 1.15 mm;^{11,50} nonadhesive⁶ (Bean's assertion that they are adhesive after 3 days²¹ is questioned, JDH); egg membrane comparatively fragile;⁹ yolk homogeneous; oil globules lacking;^{15,59} narrow perivitelline space (RRM).

EGG DEVELOPMENT

Development at "low" temperature (M'Intosh, series 1):⁸⁰

1st and 2nd day.	Morula.
3rd day.	Embryo differentiated.
4th day.	Blastopore closed; 8 or 9 somites developed; Kupffer's vesicle evident in some specimens; minute black specks developed along body; one specimen with a single black melanophore in each eye.
6th day.	Pigment more distinct along body.

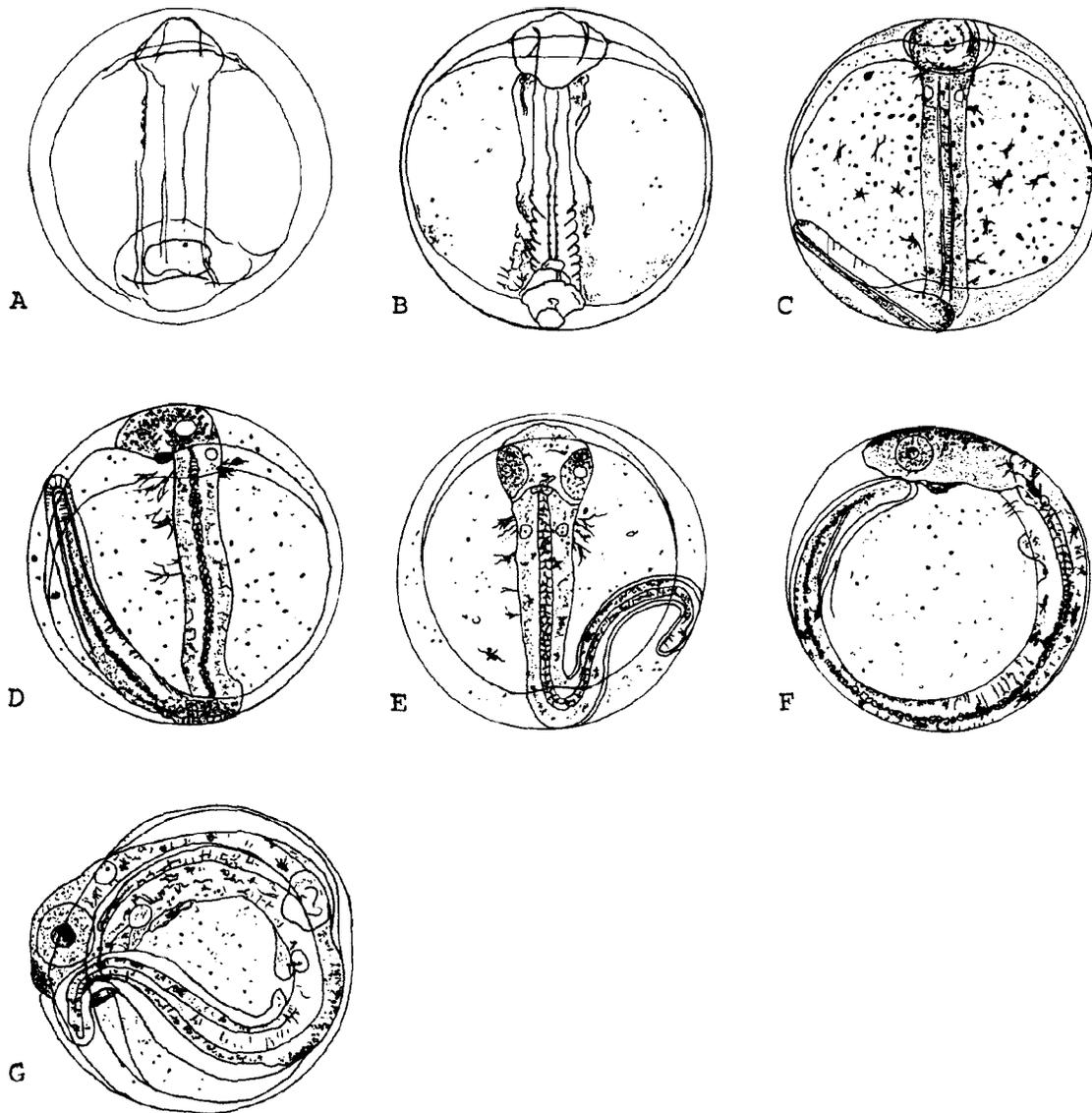


Fig. 180. *Pollachius virens*, Pollack. A. 4 days after fertilization, blastopore closing. B. 5 days, blastopore closed, somites forming. C. 7 days, dense pigmentation on yolk. D. 8 days, pigment forming on yolk. E. 8 days, showing variation in pigment, less on yolk, more on body. F. 9 days, pigment in conspicuous series on body. G. Age unknown, hatching. (A, G, McIntosh, W. C., 1893: pl. 9, Tamiko Karr, delineator.)

	some melanophores in median region behind eye.		cellular, pectoral buds evident, gut distinct.
7th day.	Number of somites increased, lenses distinct, Kupffer's vesicle still evident, entire body covered with pigment.	11th day.	Heart contractions begun, tail nearly around yolk, melanophores generally enlarged and 8 or 9 melanophores developed on head.
8th day.	Tail elongate, black pigment more distinct, some stellate chromatophores evident.	12th day.	Hatching begins. ⁸⁰
9th day.	Otoliths developed, pigment somewhat irregular.	Development at unspecified temperature (M'Intosh series 2): ⁷⁹	
10th day.	Otocysts broadly ovoid, notochord	3rd day.	Blastopore still open, but reduced;

- optic vesicles formed; perivitelline space variable within the series.
- 4th day. Blastopore closed, Kupffer's vesicle formed, myomeres evident, yolk with faintly granular appearance, pectoral buds large.
- 6th day. Melanophores over yolk, and indications of similar pigment on body.
- 7th day. Chromatophores greatly increased, but pigmentation variable.
- 8th day. Sides of body and yolk with conspicuous melanophores, tip of tail extended to head.⁷⁹
- 9th day. Hatching begun.³³

Incubation period: 5 or 6³³ to 15 days⁷³ (no temperatures given).

Incubation at various temperatures:

6.0-7.0 C.	ca. 12 days. ⁵⁰
6.1 C.	9 days. ^{52,72}
	ca. 9 days. ^{6,20}
9.4 C.	6 days. ^{52,60,72}

Comments on incubation: Eggs develop best from 3.3 to 8.9 C.⁶⁸

YOLK-SAC LARVAE

Hatching length, 3.2^{9,73} to 4.2 mm, average 4.0 mm.¹¹ Yolk absorbed at 3.5⁹ to ca. 5.3 mm.⁸⁰ Duration of stage, ca. 5 days (at 6.1 C)^{6,60,72} to at least 14 days.¹⁵ Mandible projected, mouth slightly open by 7th day or ca. 4.0 mm.⁸⁰ At time of hatching, origin of dorsal finfold about over pectoral fins.⁵⁹ Opening of anus lateral and at base of finfold.¹¹

Pigmentation: At hatching, transparent;²¹ pigment slight, scattered,^{77,80} lacking on yolk sac,⁷⁸ and in eye.^{59,77} At 3 days eye with minute black dots and silvery hue.⁸⁰ By end of stage postanal pigment grouped in specific areas but not in definite bars;¹¹ or in 2 sets of distinct bars, the dorsal 2 of which may be connected.⁵⁹ Bars sometimes evident as early as 5th day.⁸⁰

By 6th day postanal chromatophores definitely grouping into dorsal and ventral masses, conspicuous stellate chromatophores over back of head, abdomen, and pectoral fins.¹⁵

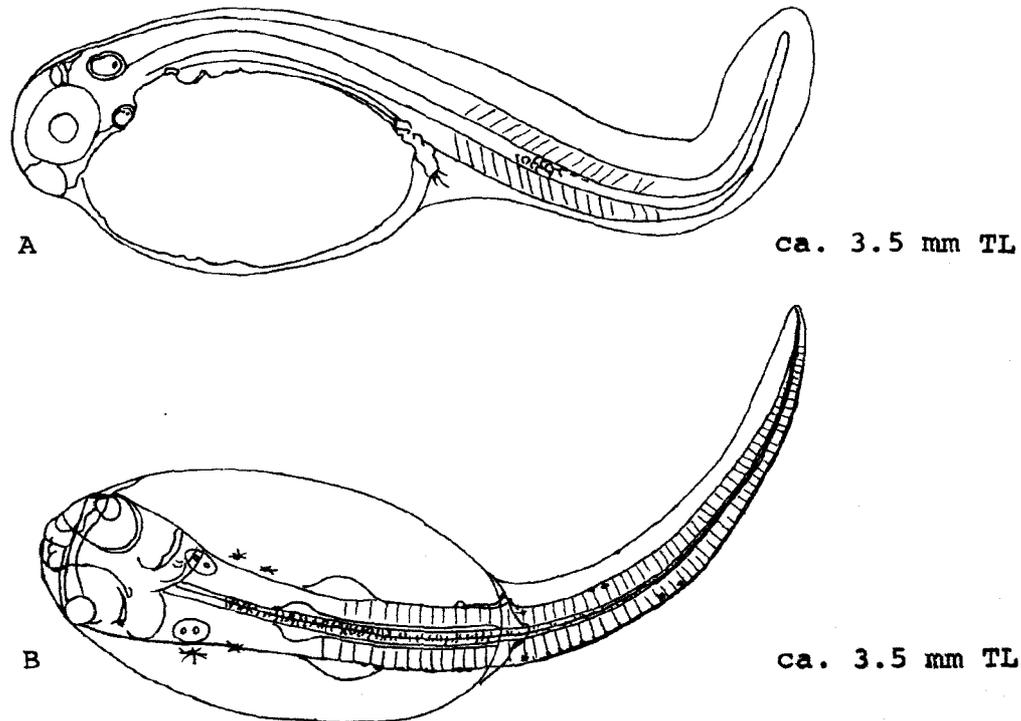


Fig. 181. *Pollachius virens*, Pollack. A. Yolk-sac larva, newly hatched, ca. 3.5 mm TL. B. Yolk-sac larva, newly hatched, ventral view, ca. 3.5 mm TL. (A, B, McIntosh, W. C., 1894: pl. 2, Tamiko Karr, delineator.)

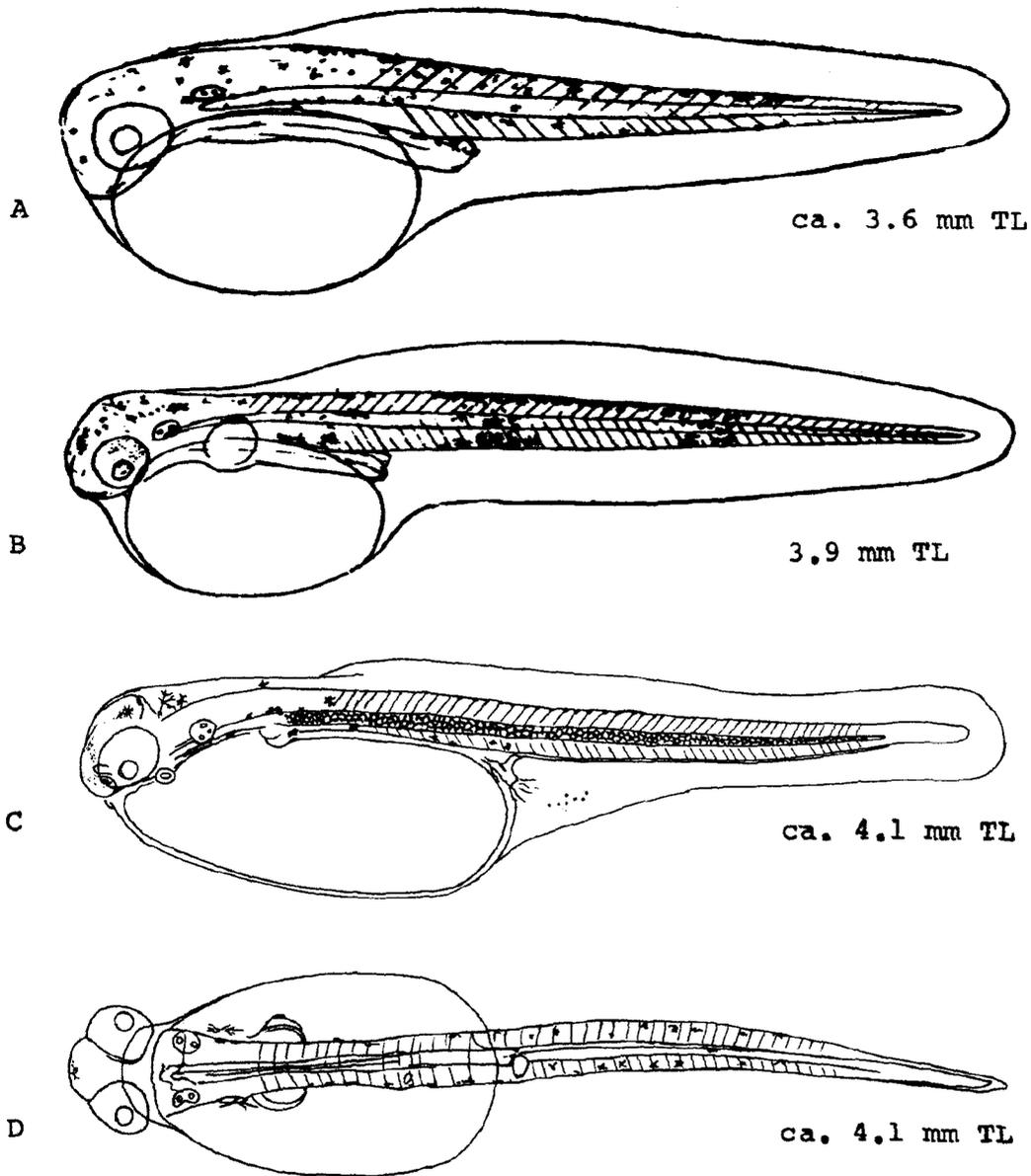


Fig. 182. *Pollachius virens*, Pollack. A. Yolk-sac larva, ca. 3.6 mm TL, pigment scattered more or less randomly over body. B. Yolk-sac larva, 3.9 mm TL, pigment forming distinct bands. C. Yolk-sac larva, ca. 4.1 mm TL, finfold becoming constricted. D. Yolk-sac larva, ca. 4.1 mm, freshly hatched, ventral view. (A, B, Ehrenbaum, E., 1909: fig. 89. C, D, McIntosh, W. C., 1894: pl. 2, Tamiko Karr, delineator.)

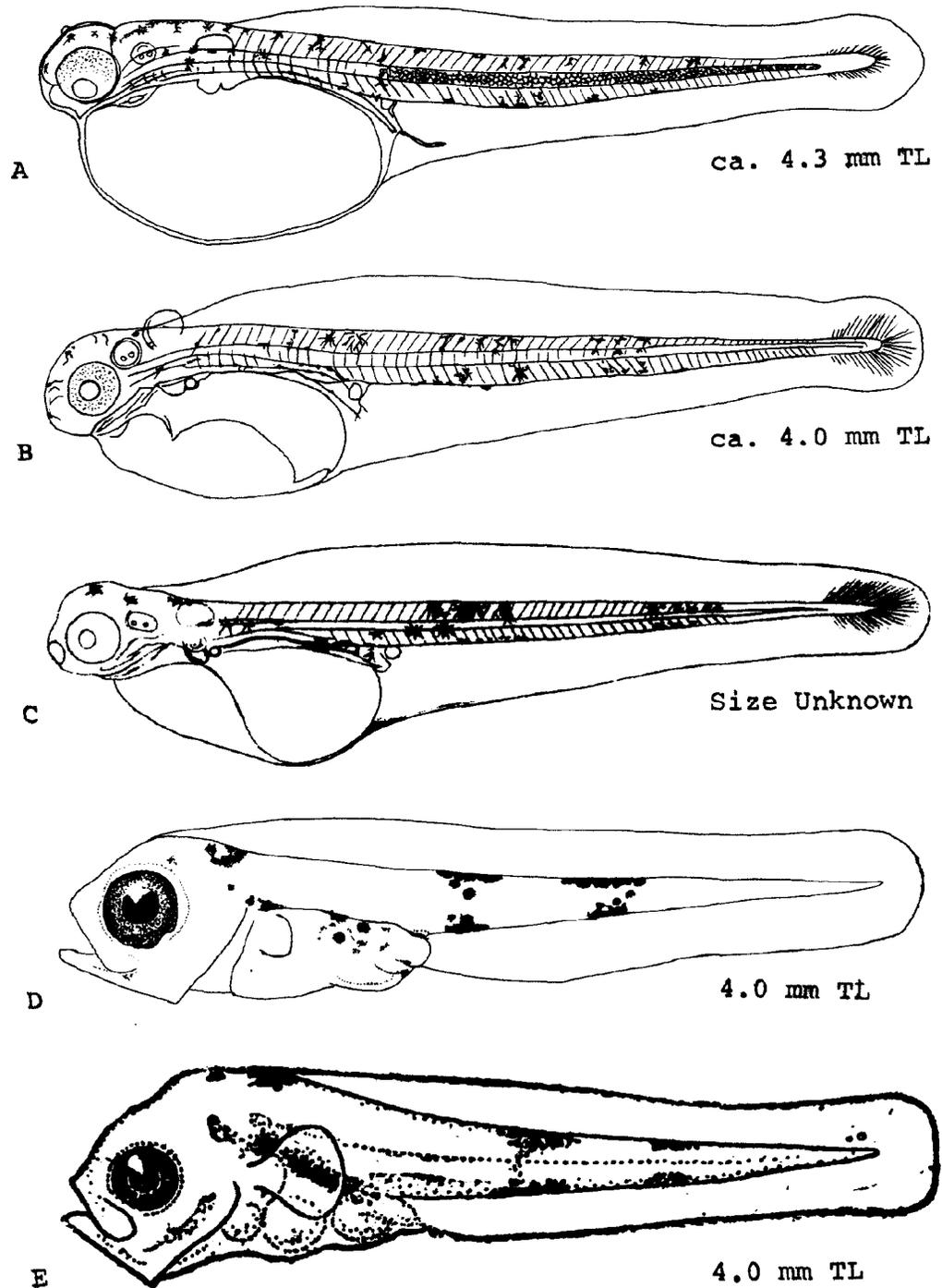


Fig. 183. *Pollachius virens*, Pollack. A. Yolk-sac larva, ca. 4.3 mm TL. In this specimen, pigment still generally scattered on body. B. Yolk-sac larva, ca. 4.0 mm, pigment consolidated in bands, pigment scattered throughout eye. C. Yolk-sac larva, size unknown, yolk reduced. D. Larva, 4.0 mm TL. E. Larva, 4.0 mm TL. (A, B, McIntosh, W. C., 1894: pl. 2, Tamiko Karr, delineator. C, McIntosh, W. C., and A. T. Masterman, 1897: 10. D, Schmidt, J., 1905: pl. 1, Tamiko Karr, delineator. E, Rass, T. S., 1949: fig. 24.)

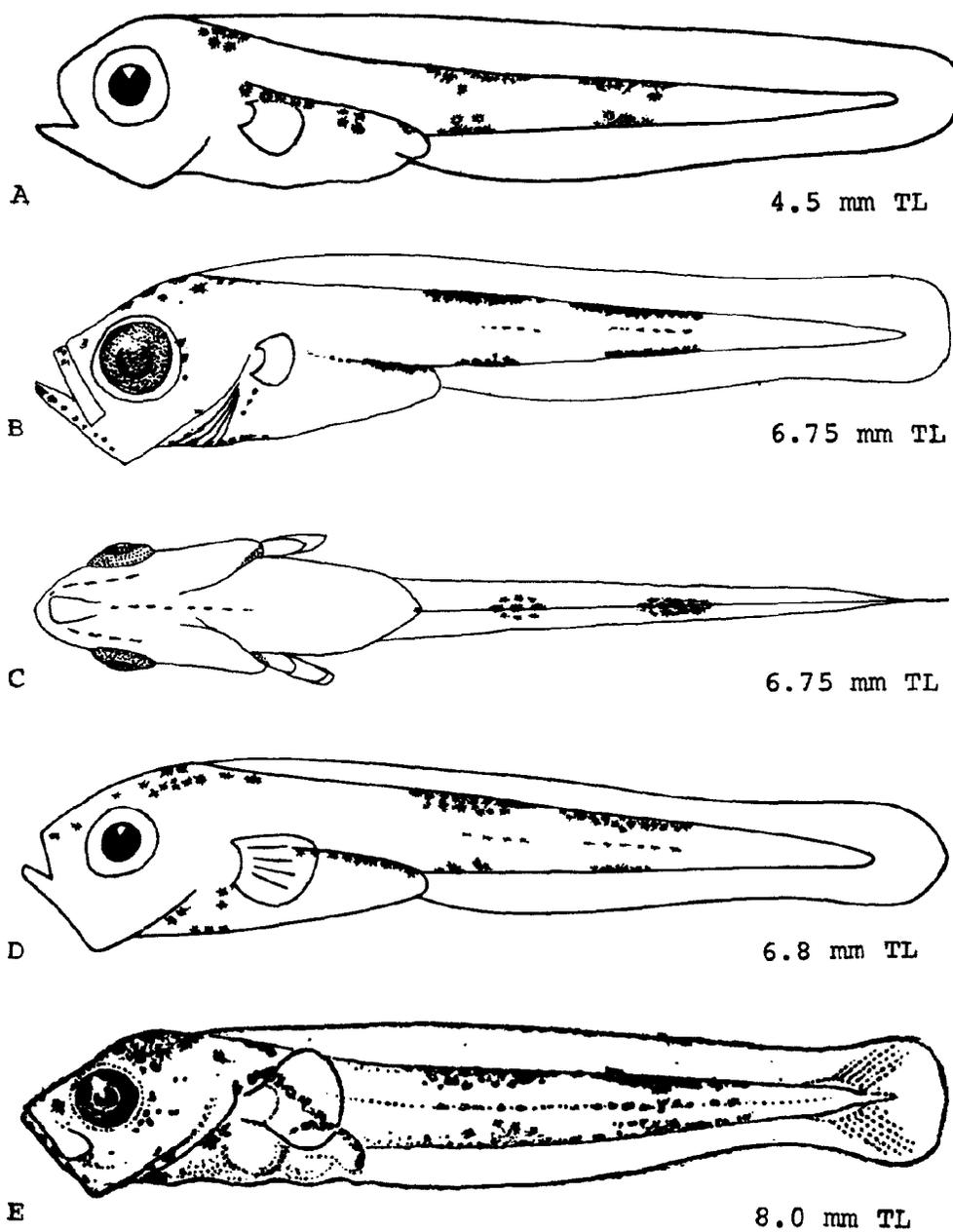


Fig. 184. *Pollachius virens*, Pollack. A. Larva, 4.5 mm TL, dorsal and ventral pigment bars well formed. B. Larva, 6.75 mm TL, ventral view. C. Ventral view of B. D. Larva, 6.8 mm TL. E. Larva, 8.0 mm TL, pigment generally increased. (A, D, Colton, J. B., Jr., and R. R. Marak, 1969: 19. B, C, Schmidt, J., 1905: pl. 1, Joan Ellis, delineator. E, Rass, T. S., 1949: fig. 24.)

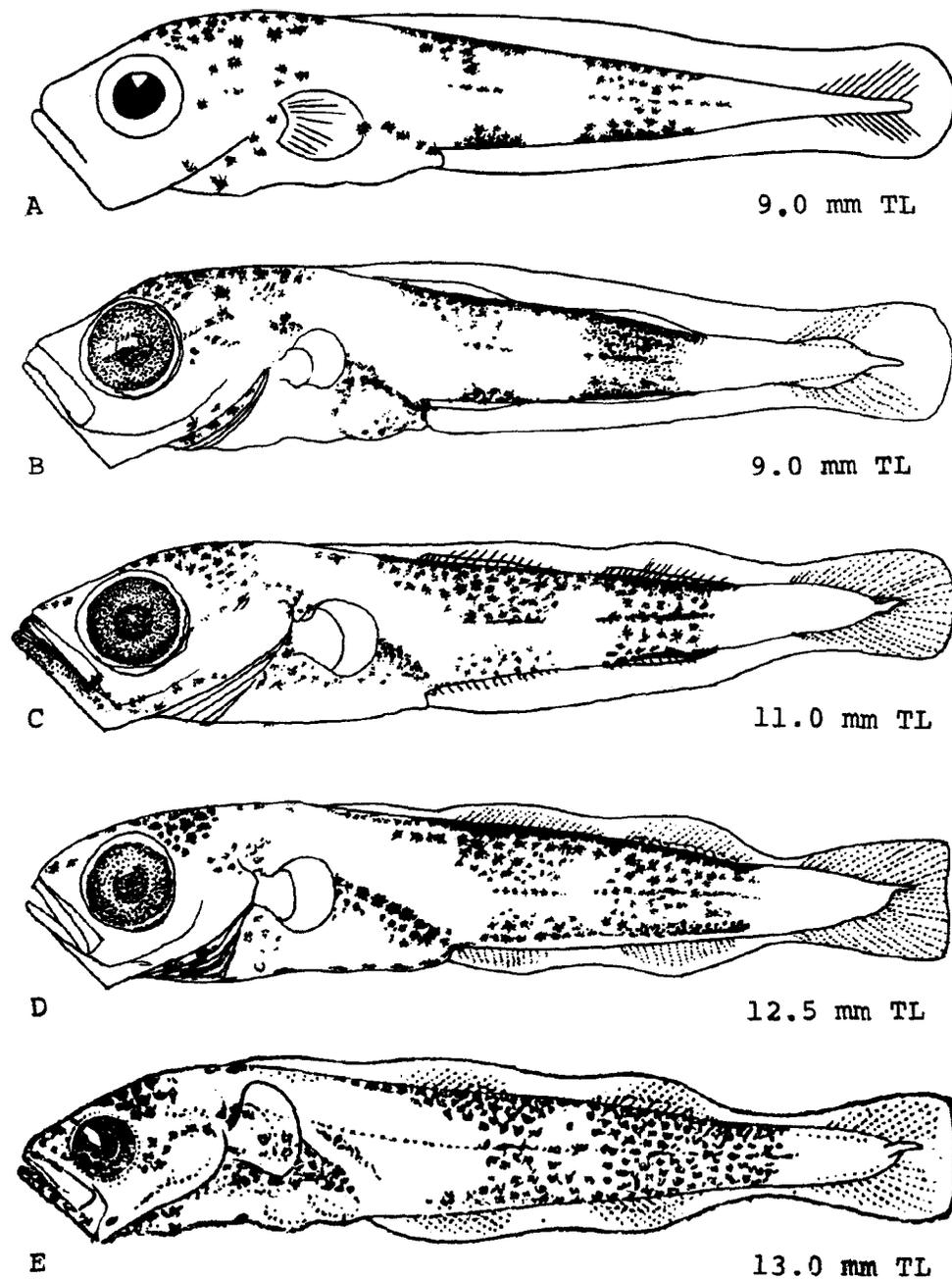


Fig. 185. *Pollachius virens*, Pollack. A. Larva, 9.0 mm TL, dorsal and anal fins not evident. B. Larva, 9.0 mm TL, anlagen of dorsal and anal fins developing. C. Larva, 11.0 mm TL, incipient rays in dorsal and anal. D. Larva, 12.5 mm TL. E. Larva, 13.0 mm TL. (A, Colton, J. B., and R. R. Marak, 1969: 19. B-D, Schmidt, J., 1905: pl. 1, Tamiko Karr, delineator. E, Rass, T. S., 1949: fig. 24.)

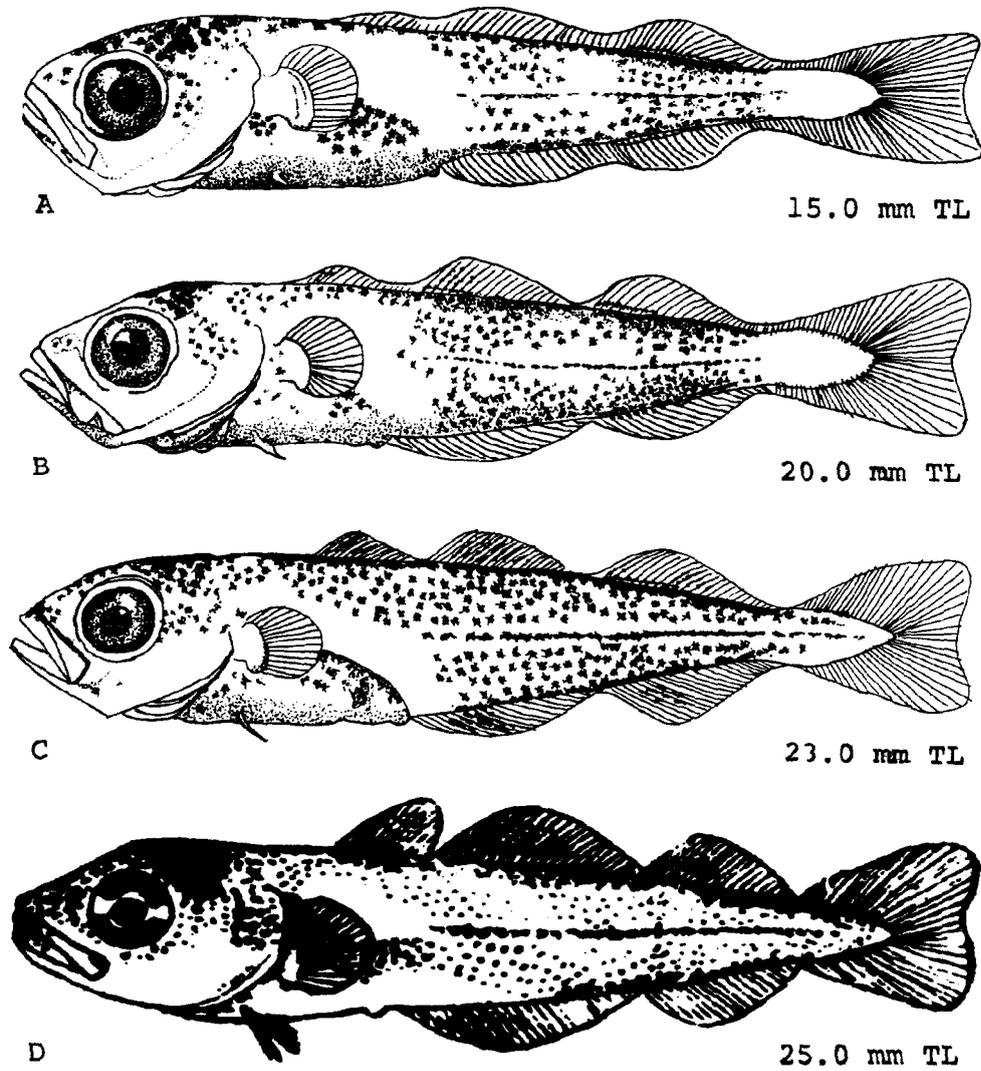


Fig. 186. *Pollachius virens*, Pollack. A. Larva, 15.0 mm TL, first dorsal fin forming. B. Larva, 20.0 mm TL, pigment developing in dorsal fins. C. Larva, 23.0 mm TL, pigment developing in anal fins. D. Juvenile, 25.0 mm TL. (A-C, Schmidt, J., 1905: pl. I, Tamiko Karr, delineator. D, Ehrenbaum, E., 1909: fig. 89, after Heincke, F., 1909.)

By 14th day yolk sac distinctly reticulated, ventral chromatophores more scattered.¹⁵

LARVAE

Size range described, 4.0 to 23.0 mm.^{41,77}

Abdominal vertebrae, 23-25, mean 23.6.¹¹

Head short, blunt (distinctly shorter than that of cod at 15.0 mm).⁴¹ Development of unpaired fins first evident at 9.0 mm.⁵⁹ Incipient rays in D_2 and D_3 , and in anal fin at 9.0-11.0 mm.^{41,77} At 20.0 mm A_1 considerably lower and clearly longer than A_2 .⁵⁹ Caudal rays apparently not evident in some specimens until 6.75 mm; at 12.5 to 30.0 mm caudal fin somewhat concave.^{6,41,57} Pelvics evident as low knobs at 12.5 mm; at 15.0 mm no longer knob-like and not quite 1/4 diameter of eye; at 20.0 mm pointed, less than 1/2 diameter of eye.⁴¹ All unpaired fins separated by 20.0 mm.⁵⁹ Urostyle straight at 9.0 mm,⁷⁷ oblique at 11.0 mm.⁴¹ Position of anus variously stated: At ca. 8.0 to 20.0 mm a little in front of D_2 ; at 20.0 mm under posterior end of D_1 ; at ca. 15.0 to 30.0 mm under posterior 3rd of D_1 .^{41,57}

Pigmentation: Living larvae with small yellow chromatophores on body.⁸³ At time of yolk absorption 2 dorsal and 2 ventral pigment bars; dorsal bars longer than ventral (opposite in cod); space between bars greater ventrally.¹¹

At 4.0 mm as above; also a weak mediolateral streak (which fails to reach anus), stellate chromatophores on occiput, few chromatophores on throat, and increased pigment in dorsal part of abdomen.^{41,77}

At 6.75 mm mediolateral streak distinct, strongest posteriorly; dorsal postanal bars beginning to fuse; pigment on occiput sharply divided from dorsal pigment.⁴¹

At 8.0 to 10.0 mm preanal pigment weak, generally not reaching anus; dorsal and ventral portions of posterior-most pigment bars short, so that unpigmented portion of end of tail proportionately long.^{36,41,57}

At 9.0 mm dorsal and sometimes ventral postanal pigment bars fused; dorsal bars more intense than ventral bars; anteriormost ventral bars weaker than posterior one; posteriorly both dorsal and ventral bars end abruptly and at same level; some dorsolateral and ventrolateral pigment developed; small yellow chromatophores on sides but not on colorless caudal area; a characteristic light spot on tail at a point where mediolateral stripe and yellow pigment are discontinuous (opposite space between original dorsal and ventral pigment bars).^{41,59,77} Yellow pigmentation lost quickly in preservation (RRM).

At 9.25 mm (identity putative) eyes bluish silvery with

black pigment along dorsal margin; abdomen with black pigment specks and tinted red from food.^{15,80}

At 11.0 mm original posterior bars no longer evident; mediolateral streak distinct, usually broken; dorsal pigment much stronger than ventral.⁴¹

At 12.5 mm ventral pigment weak; anterior part of abdomen possibly with silvery color; yellow pigment increased, now extending back as far as black pigment extends and more abundant posteriorly than anteriorly, also developed on occiput; forward part of abdomen definitely with silvery sheen.^{41,59,77}

At 15.0 mm mediolateral streak extended forward almost to beginning of D_2 backward a little beyond limits of dorsal and ventral pigment; ventral pigment weaker than dorsal.⁴¹

At 20.0 mm black pigment between rays of D_1 and D_2 ; pigment on flanks denser and extended posteriorly; lateral light area now sparsely covered with chromatophores; dorsal pigment reaches anterior part of caudal fin, but end of tail still without pigment; mediolateral line continuous; preanal pigment sparse.^{41,59,77}

At 23.0 mm pigment on all dorsal and anal fins.⁴¹

PREJUVENILES

Size range, 25.0 to 50.0 mm (based on time of descent to bottom).^{28,59}

Specimens described, 25.0 to 33.0 mm.^{20,59} At 25.0 to 30.0 mm adult-like.^{9,20}

At 33.0 mm distance from anus to tip of head about equal to distance from anus to base of caudal fin.⁵⁹

Pigmentation: Colors stated below are visible only in live or freshly preserved material (RRM). At 25.0 mm extreme caudal tip of body still pigment free, lateral clear area no longer visible, some pigment in all fins except A_2 .⁵⁹

At ca. 28.5 mm body deep green (darker than in cod); eyes with greenish tinge; fins dusky; D_1 , D_2 , D_3 , and A_1 often marked with yellow; pectorals sometimes with 2 broad arches of pigment.⁴²

At 30.0 mm pigment extended to caudal apex and dense throughout except ventrally in front of anus; mediolateral streak distinct and extended anteriorly to origin of D_2 ; yellow pigment on occiput and sides interspersed among black spots; abdomen silvery; all dorsals and anals strongly pigmented; caudal pigment weak (description based on specimen from surface, but author comments that uniform homogenous pigment changes little when individuals move to bottom).⁷⁷

At 33.0 mm pigment fairly evenly spread over body ex-

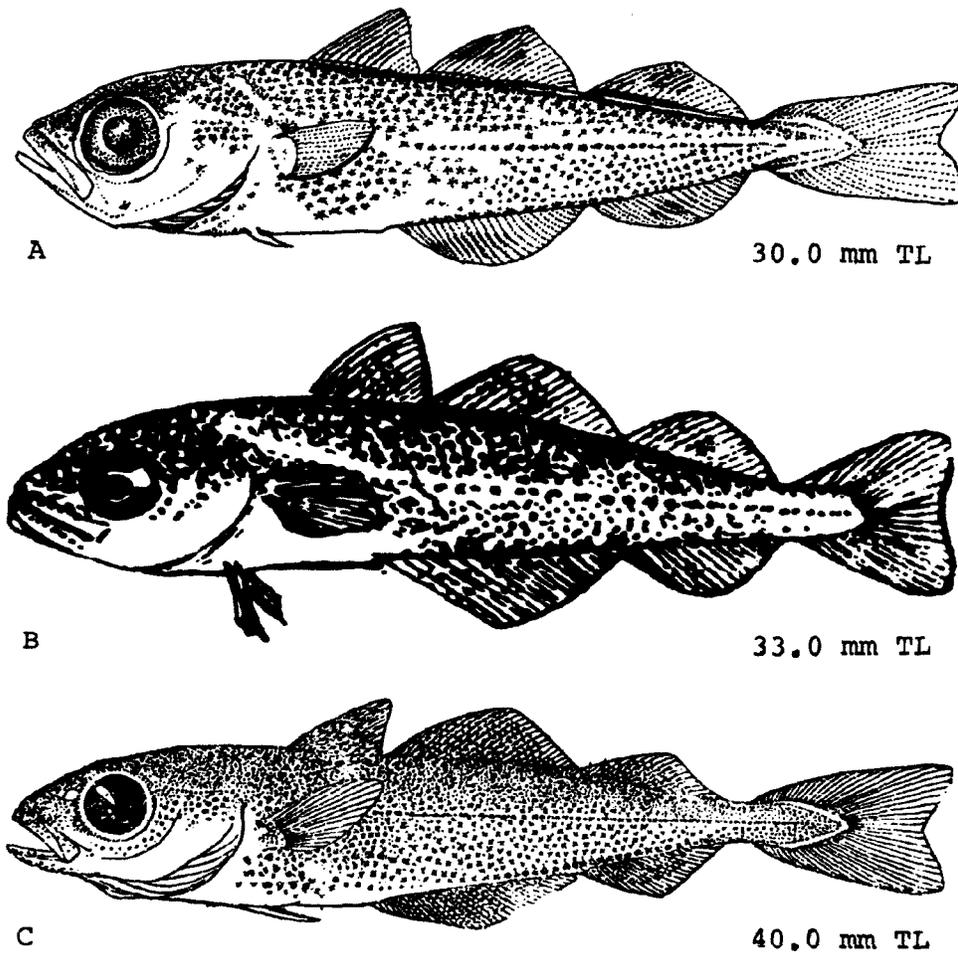


Fig. 187. *Pollachius virens*, Pollack. A. Juvenile, 30.0 mm TL, pectoral fin elongated. B. Juvenile, 33.0 mm TL. C. Juvenile, 40.0 mm TL. (A, Schmidt, J., 1905: pl. 1, Joan Ellis, delineator. B, Ehrenbaum, E., 1909: fig. 89, after Heincke, F., 1909. C, Rass, T. S., 1949: fig. 24.)

cept for preanal ventral wall; back dark; abdominal area silvery, unpaired fins, except caudal, well pigmented.⁵⁹

JUVENILES

Minimum size, 50.0 mm.^{28,59}

Juveniles apparently develop small, rudimentary chin barbels (but barbels, as a rule, absent in adult).^{28,68}

Pigmentation: Specimens up to 60.0 mm (description includes some prejuveniles) with deep green hue; abundant black pigment on fins and body; dorsal and anal fins sometimes with yellow spots; pectorals sometimes with 2 broad arches of pigment.¹⁵

Young fish darker than larger ones and sometimes tinged with yellow on sides.⁶⁸

At sizes below ca. 380 mm usually brownish green.²⁰

AGE AND SIZE AT MATURITY

Minimum 3 years^{12,68} (an implication of maturity at 2 years⁶ is questioned, JDH). Generally males at 4 to 7 years, females at 5 to 7 years,¹ most spawn for first time at five years, majority at 6 years, all by 7 years.^{12,37,39}

Mature by 340 to 700 mm^{13,39,61,62,63} (a report of ripening at ca. 172 mm⁶ is questioned, JDH). Various minimums: In Manx waters 340 mm;¹³ off Europe ca. 457 mm;⁶⁸ in Newfoundland waters 540 mm;³⁶ in Bay of Fundy males 500 to 650 mm, females 550 to 700 mm;¹ in Icelandic waters 500¹⁹ to 700 mm.³⁹ Individuals in American waters probably mature at somewhat larger sizes than those in European waters.⁶⁸

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Urophycis chuss (Walbaum), Red hake**ADULTS**

D. ₁, 9–11; ^{6,9,12} D. ₂, 53–64; A. 45–56; ^{21,45} C. 30; ⁴¹ P. 16; ⁹ V. 2; ¹⁰ scales 95–117 (reports of 110–140 include *U. tenuis*), ^{21,45} scale rows above lateral line in vicinity of first dorsal, 9; ²² total vertebrae 45–50 (including hypural), precaudal vertebrae 14–17, mode 15, ^{21,45} caudal vertebrae 33; ⁴¹ gill rakers on lower branch first arch 12–13, ¹² epibranchials of first arch 3, ^{21,45} but gill rakers also stated as 16–18.⁹

Proportions as times in TL: Depth 4.8 ¹² to 5.5; ^{6,16} head 4.25–4.5. ¹² Proportions as percent HL: eye 24.9–28.4; interorbital space 16.7–17.1.⁹

Body somewhat elongate, ¹² rounded in front of vent, somewhat compressed behind. Head more or less pointed, ¹⁰ noticeably broader than deep, depressed. ¹² Upper jaw projecting ¹⁰ maxillary bone usually to rear edge of pupil; ^{12,21,32,45} a small barbel on lower jaw. ¹⁰ Teeth on jaws and vomer, those in upper jaw in 2 indefinite rows, those on lower jaw very irregular. ¹² Third ray of first dorsal filamentous and much longer than in *Urophycis tenuis*; ³² caudal fin rounded. ¹²

Pigmentation: Sides and back reddish, muddy, olive reddish, olive brown, or, rarely, almost black; sometimes mottled. Lower sides usually washed with yellow, sometimes marked with dusky spots. Belly white, grayish, or yellowish. Unpaired fins same as back, but anal pale at base. Pelvics pale pinkish or yellowish. ^{9,32}

Maximum length: Ca. 760 mm.⁶

DISTRIBUTION AND ECOLOGY

Range: Along continental shelf from Nova Scotia to Cape Hatteras. Records from Labrador, Grand Bank, the Gulf of St. Lawrence, and the west coast of Ireland are apparently in error. ^{21,45}

Area distribution: Offshore waters of New Jersey, ^{1,7} Delaware, ²⁴ Maryland, ¹⁴ and Virginia; ¹⁵ also Sandy Hook Bay, ²⁶ lower Delaware Bay, ²⁵ Virginia waters of Chesapeake Bay including lower York River, ^{6,36} and north in Chesapeake Bay to Bloody Point, Annapolis. ¹²

Habitat and movements: Adults—a coastal species found in relatively deep water ^{2,3} as well as close inshore; ¹²

known to enter harbors. ³¹ Tend to stay close to objects on the bottom (such as sea scallops, etc.). ³⁷ Typically over soft mud or silt bottoms, less frequently over sand and shell, never over rock. ^{4,9,12,21,45} Minimum recorded depth, 35 m ⁹ (although reported from within a hundred feet of shore ¹² and from the tide line). Estimates of greatest abundance vary from 110 to 130 m, ⁹ 182 m, and 457 m, ¹⁸ but these differences may reflect seasonal movements. ^{21,45}

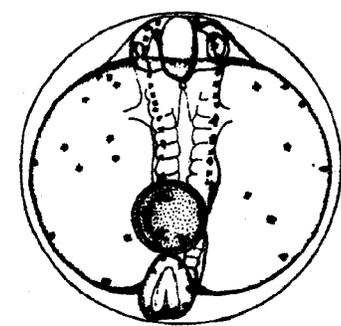
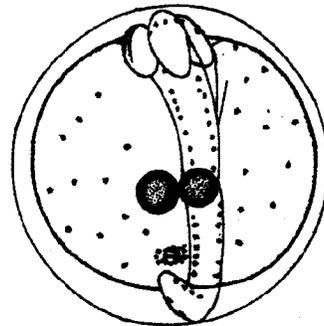
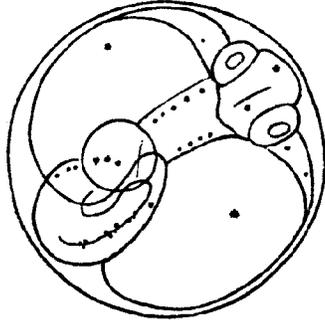
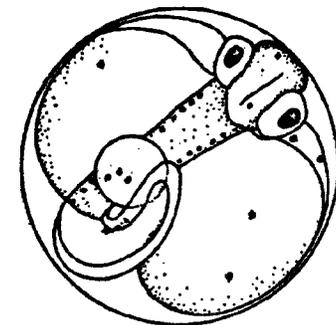
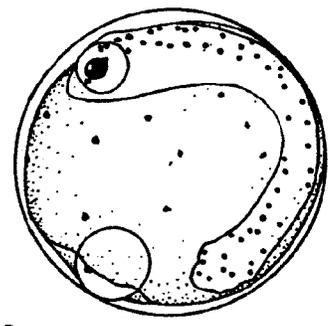
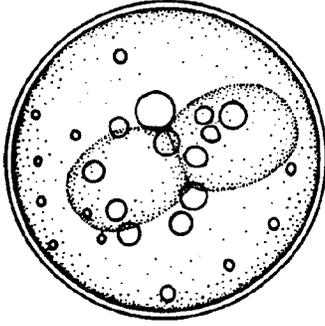
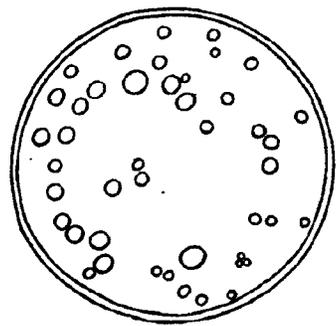
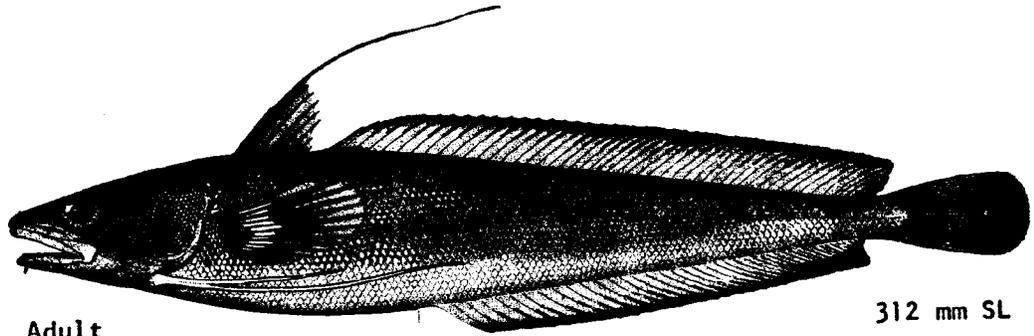
Make definite inshore-offshore movements ^{5,12} which are apparently governed by temperature (avoiding temperatures below 5 C). In New England generally inshore in April and May and again in October. ^{5,11,12,21,29,45} Offshore to edge of continental shelf in winter. ^{21,45} In Block Island Sound in spring, summer, and fall; absent in winter. ¹⁶ In Sandy Hook, New Jersey, and Long Island, New York, inshore in spring and fall, offshore in summer and winter. ^{21,30,45} Inshore at Ocean City, Maryland, from October 1 to December 10. ²³

Larvae—putative larvae drift at surface, sometimes under floating eelgrass and rockweed. ³² Larvae with mean lengths of 3.2–9.4 mm inshore along coast of Maine June through November. ⁴²

Juveniles—initially at surface, ²⁹ but primarily on bottom. Found in mantle cavity of scallops (*Placopecten megalanicus*) at lengths of 27 to 140 mm and remain in vicinity of scallop beds until 2nd year of life if temperature remains above 4 C; ^{1,4,21,45} also recorded as hiding under shells, sponges, or litter, ³⁷ associated with jellyfish, ²⁵ and, at ca. 60 to 150 mm, in eelgrass along shore; ²⁹ a specimen ca. 225 mm long was found inside the egg case of a naticid gastropod (probably the moon snail, *Lunatia heros*). ³⁴ Juveniles 11.5–38.5 mm long offshore near 180 m depth contour; ⁴⁴ specimens 68–139 mm long recorded at salinity range of 31.0–32.8 ppt, and temperature range of 4.2–7.5 C. ⁴³ Early bottom stages at 36 ¹ to 110 m according to scallop distribution; ^{21,45} “immatures” recorded from 4–6 m. ⁹

Juveniles descend to bottom at lengths of 27 to 49 mm, but primarily at 35 to 40 mm. ^{4,21,45} (A report of 50 to 100 mm ¹² is apparently in error, JDH). In northern parts of range fish in their 2nd year of life migrate inshore to within 55 m and remain until temperature drops to ca. 4 C, then move to warmer, deeper, offshore water.

Fig. 188. *Urophycis chuss*, Red hake. A. Adult, 312 mm SL. B. Egg, 1 hour after fertilization. C. 2-cell stage, 1 hour and 30 minutes. D. Early embryo, pigment established on yolk and body, 50 hours. E. Embryo, probably tail-free, 74 hours. F. Embryo, 74 hours. Probably redrawn from previous illustration, but note pigment in eye. G. Advanced embryo, 90 hours. H. Advanced embryo, showing 2 oil globules. I. Advanced embryo, ventral view. (A, Coode, G. B., 1884: pl. 62. B, F, Bigelow, H. B., and W. Welsh, 1925: figs. 224–225. C–E, G, Hildebrand, S. F., and L. E. Cable, 1938: figs. 123–126. H, I, Redrawn from Agassiz, A., and C. O. Whitman, 1885: pl. 12, Frances P. Younger, delineator.)



During the following spring they migrate inshore with adults in April, and become mature by summer.^{4,21,45} Young ca. 50 to 225 mm long in Chesapeake Bay in late fall and spring, leave for offshore waters by end of June.¹²

SPAWNING

Location: On continental shelf with concentration on southeastern Georges Bank and south of Long Island.^{21,45} Spawning has been reported as far south as New Jersey, and a female with ripening ovaries was reported from Chesapeake Bay.^{12,21,32,15}

Season: Principally in summer,^{3,12,30} but apparently prolonged, based on distended ovaries in April, eggs in late September,³² and newly hatched young in October.^{6,21,45} In New England May to August;⁷ in Georges Bank June to September;²⁷ near Long Island Sound May to September, with peak activity in late June and July;³⁵ a single ripe female in Chesapeake Bay in April.¹²

Depth: Shallower than 46.8 m to as deep as 108 m.^{17,21,29,45}

Temperature: Probably 5–10 C.^{21,45}

Fecundity: No information.

EGGS

Pelagic;^{4,13,20,45} buoyant;^{3,6} spherical;¹³ transparent; clear;^{3,6} diameter, 0.63–0.97 mm;^{8,20} stated average diameters, 0.69, 0.70,¹⁸ 0.74,⁶ 0.76 mm.^{7,20} Initially with numerous oil globules (up to 54), but these coalesce in first 26 hours; thereafter usually one large and 2–3 small oil globules. Diameter of oil globules 0.15–0.22, mean 0.19 mm.^{6,7,8,13,20,35}

EGG DEVELOPMENT

At 15.6 C:^{6,7,35}

1 1/2 hours—first cleavage.

26 hours—morula stage, oil globules coalesced.

50 hours—embryo around 1/2 yolk, eyes evident, melanophores on body and yolk.

74 hours—yolk reduced, movements evident, oil globule pigmented.

90 hours—eyes pigmented.

95 hours—chromatophores large, evident on body, yolk and oil globule; length of embryo about equal to diameter of yolk.^{6,7,35}

Pigmentation of embryo just prior to hatching: Number of melanophores on yolk and body reduced, but those of body still in two distinct rows and now large and dendritic; caudal end of body without pigment; a single large chromatophore in front of eyes and 12–15 small black dots in posterior part of eye.⁴⁰

Incubation period:

At 15.6 C, 96³⁸–98⁺ hours.³⁵

At 21.1 C, ca. 30 hours.¹⁷

YOLK-SAC LARVAE

Hatching length, 1.76^{7,17,20}–1.98 mm.⁶ Largest specimen described 2.2 mm.⁷ Duration of stage, ca. 22–38 hours (although remnant of oil globule is evident at 62 hours).¹⁷

At time of hatching yolk mass large and extending far forward under head; oil globule in posterior part of yolk sac. Dorsal finfold extended forward to head throughout stage. Pectoral bud evident in smallest specimen illustrated (ca. 1.9 mm), but otherwise not noticeable until length of 2.75 mm.⁶ Anus located laterally and at base of finfold.⁷ Sensory organs of lateral line evident as distinct but very delicate and perfectly transparent membranous extensions from body.⁴⁰

Pigmentation: At hatching melanophores present⁶ or absent from yolk sac, pigment in eye a little denser than in late embryo, a single large black spot in front of and between eyes, few yellow chromatophores on yolk sac and anterior half of body,⁴⁰ large melanophores along dorsal and ventral outline of body.⁶ At 3 hours eye lightly pigmented; 2–3 chromatophores on forehead; ca. 6 scattered on trunk; a single chromatophore on dorsal aspect of body directly above anus; about halfway along tail a pair of chromatophores, one on ventral and one on dorsal midline, these often extending out onto finfold; oil globule pigmented. At 15 hours eye more densely pigmented, a small concentration of pigment on dorsal aspect of developing gut. At 22 hours eye darkly pigmented, chromatophores on forehead moved slightly posterior, 1–2 chromatophores developed on nape, peritoneum more heavily pigmented.¹⁷ In late yolk-sac larvae pigment increased on dorsal surface of gut and in postanal region; postanal pigment highly variable.⁷

LARVAE

Size range described, 2.1¹⁷–11.0 mm.⁶

Proportions as times in SL: At ca. 7.0 mm, dorsal fin 3.6, at 9.0–11.0 mm, 4.0–4.3; at 5.0 mm, depth 3.5, distance from anus to tip of notochord 2.2.⁶

Nasal opening divided at 9.5 mm. Finfold constricted in caudal region at 2.75 mm, still evident at 5.0 mm,⁶ completely obliterated at 6.6 mm.²⁰ Second dorsal well formed at 6.6 mm.⁷ Pectorals first evident at 2.75 mm (although pectoral buds also indicated in smallest yolk-sac larva illustrated). Pelvics first evident at 2.75 mm,⁶ extended to anus at ca. 6.0 mm.²⁰ Urostyle slightly oblique at 5.0 mm.⁶

Pigmentation: Absorption of yolk is accompanied by

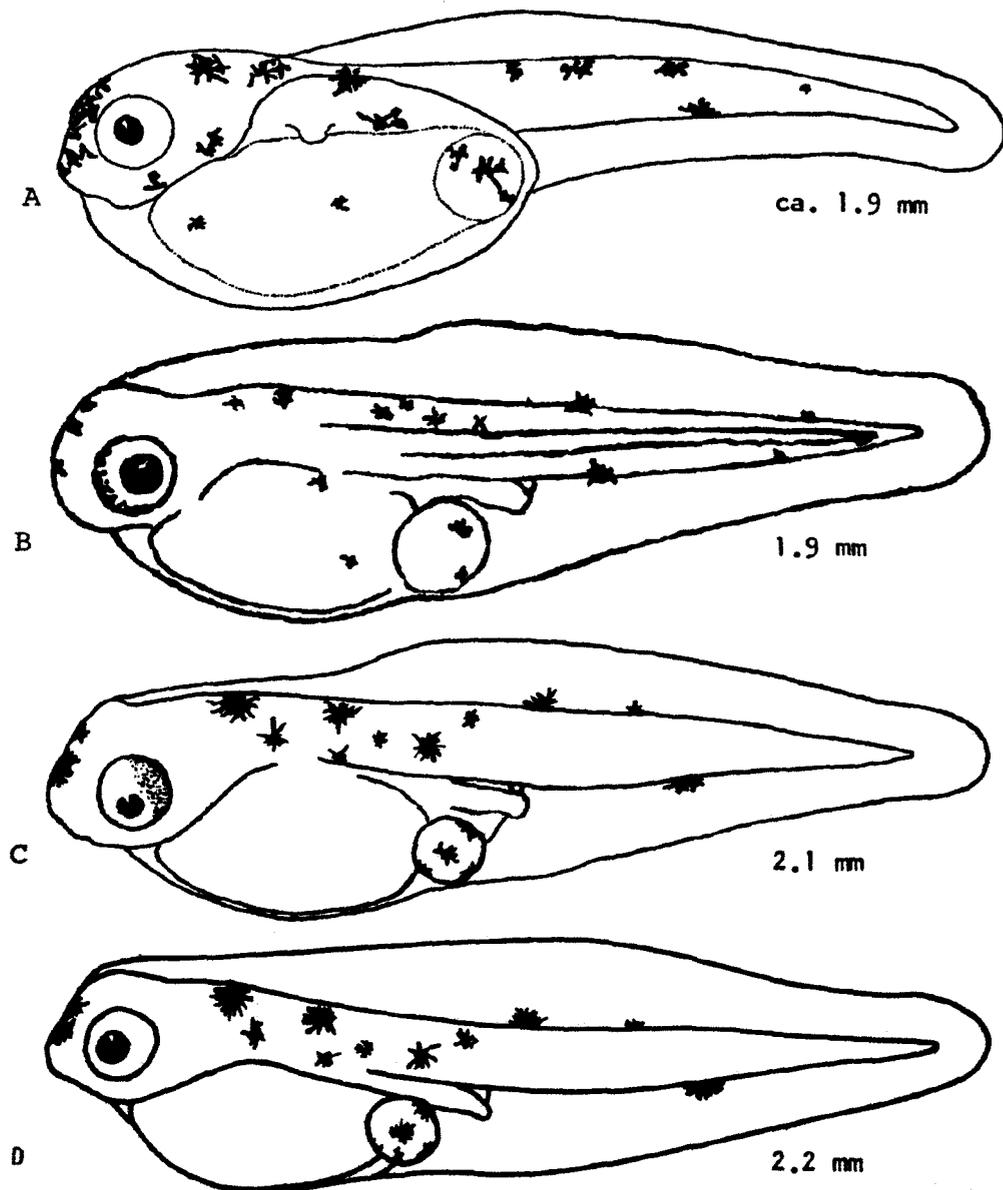


Fig. 189. *Urophycis chuss*, Red hake. A. Yolk-sac larva, newly hatched, ca. 1.9 mm. B. Yolk-sac larva, 1.9 mm. C. Yolk-sac larva, 2.1 mm, 3 hours old. D. Yolk-sac larva, 2.2 mm, yolk sac noticeably reduced. (A, Hildebrand, S. F., and L. E. Cable, 1938: fig. 127. B, Miller, D., 1958: 35. C, Miller, D., and R. R. Marak, 1959: fig. 1. D, Colton, J. B., and R. R. Marak, 1969: 20.)

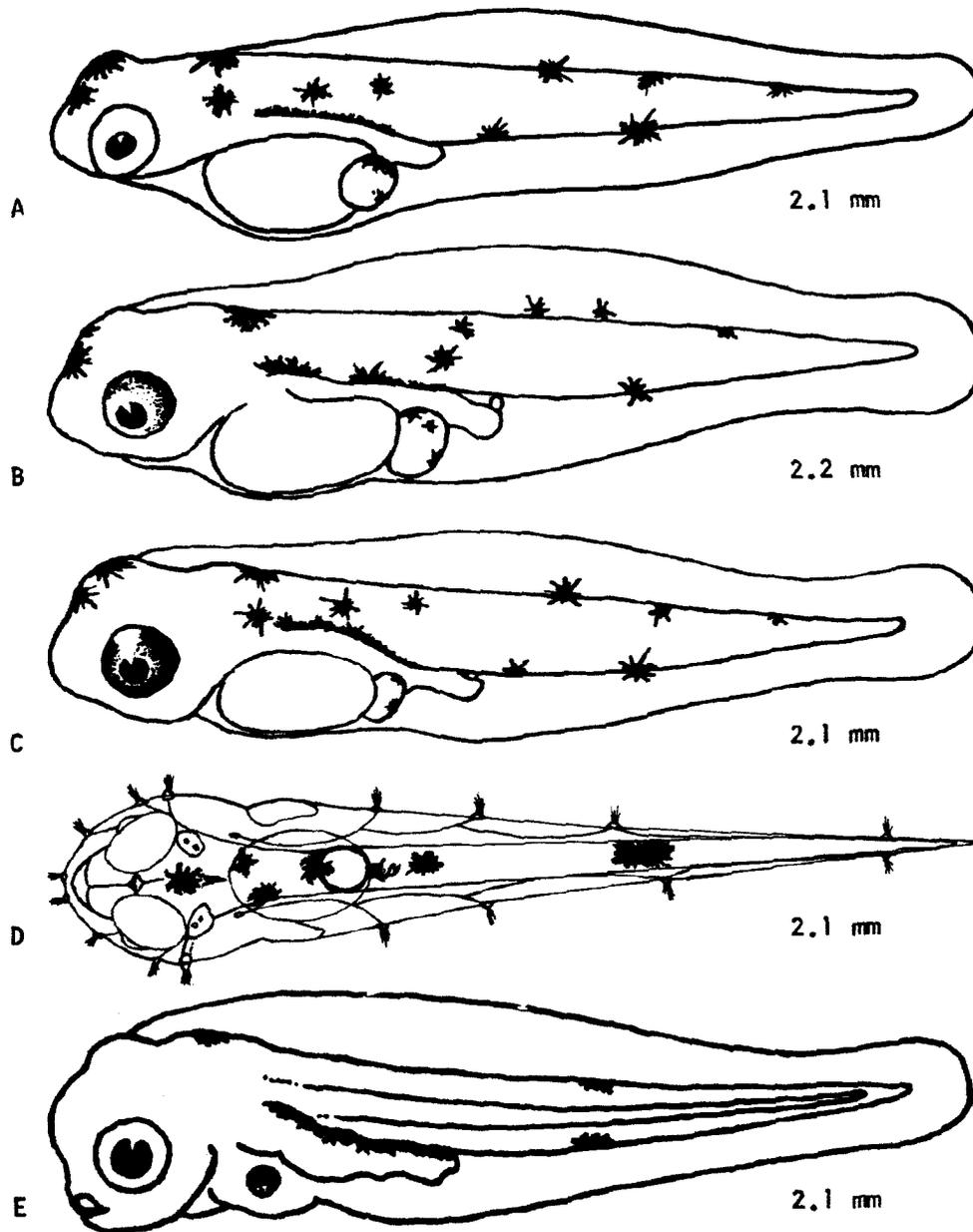


Fig. 190. *Urophycis chuss*, Red hake. A. Yolk-sac larva, 2.1 mm, pigment developed over gut. B. Yolk-sac larva, 2.2 mm. C. Yolk-sac larva, 2.1 mm. D. Yolk-sac larva, 2.1 mm, dorsal view to show development of lateral line organs. E. Yolk-sac larva, 2.1 mm, pigment on body noticeably decreased. (A, Colton, J. B., and R. R. Marak, 1969: 20. B, C, Miller, D., and R. R. Marak, 1959: figs. 2-3. D, Redrawn from Agassiz, A., and C. O. Whitman, 1885: pl. 12, Frances P. Younger, delineator. E, Miller, D., 1958: 36.)

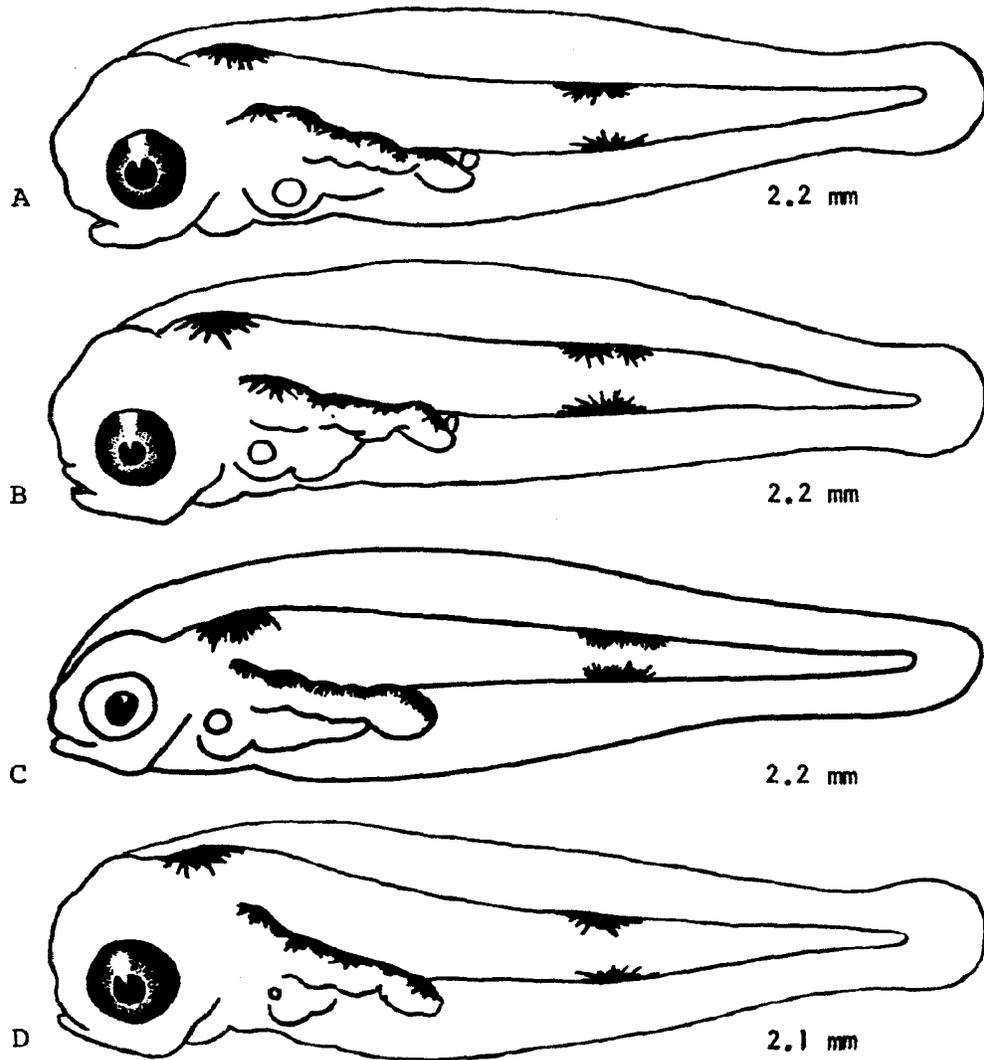


Fig. 191. *Urophycis chuss*, Red hake. A. Yolk-sac larva, 2.2 mm. B. Yolk-sac larva, 2.2 mm. C. Yolk-sac larva, 2.2 mm. D. Yolk-sac larva, 2.1 mm, oil globule greatly reduced. (A, B, Miller, D., and R. R. Marak, 1959: figs. 4-5. C, Colton, J. B., and R. R. Marak, 1969: 20. D, Miller, D., and R. R. Marak, 1959: fig. 6.)

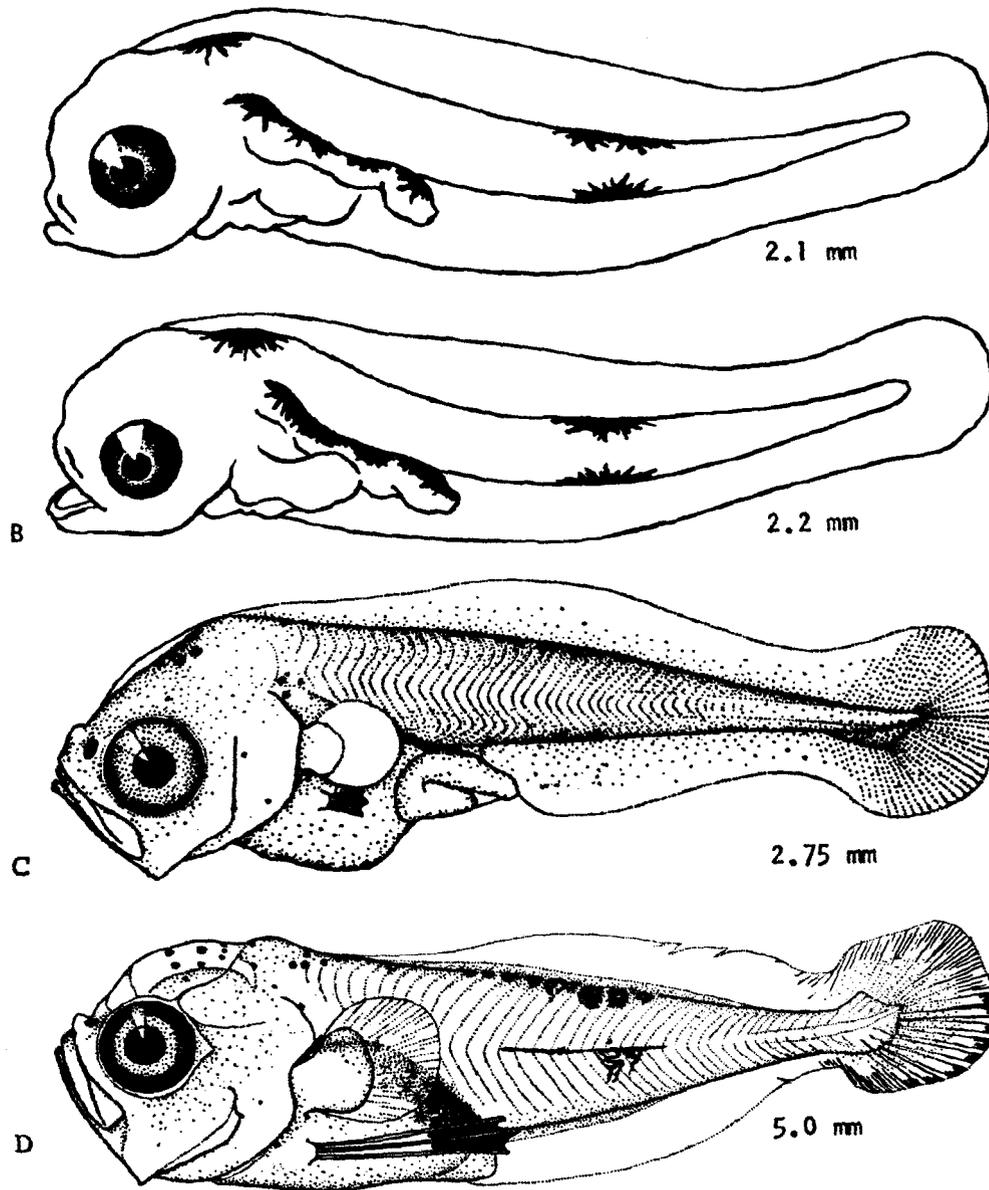


Fig. 192. *Urophycis chuss*, Red hake. A. Larva, 2.1 mm. B. Larva, 2.2 mm. C. Larva, 2.75 mm, pelvic buds evident. D. Larva, 5.0 mm, pelvic fins elongate, urostyle flexed. (A, B, Miller, D., and R. R. Marak, 1959: figs. 7-8. C, D, Hildebrand, S. F., and L. E. Cable, 1938: figs. 129, 131.)

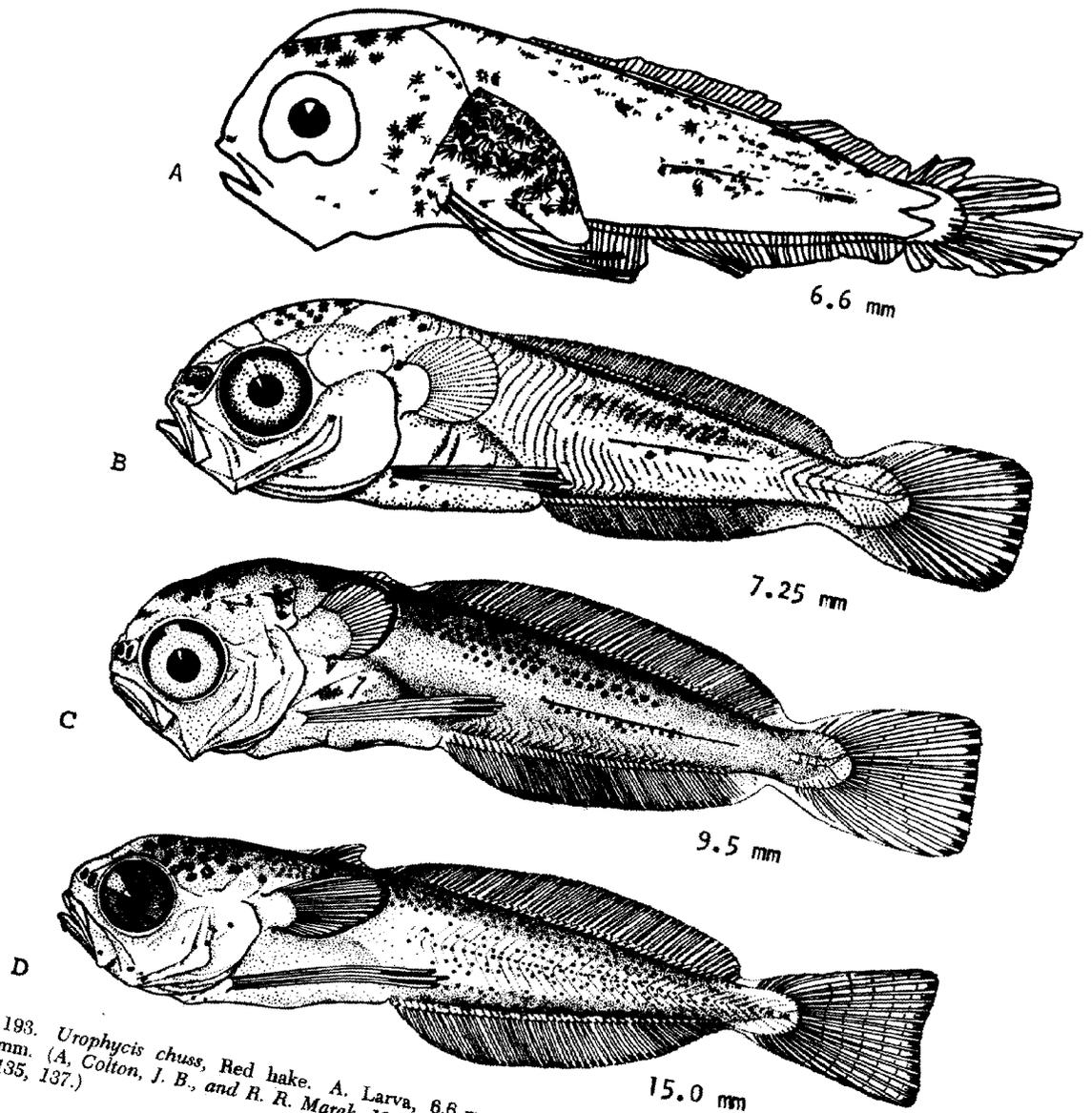


Fig. 193. *Urophycis chuss*, Red hake. A. Larva, 6.6 mm. B. Larva, 7.25 mm. C. Larva, 9.5 mm. D. Larva, 15.0 mm. (A, Colton, J. B., and R. R. Marak, 1969: 20. B-D, Hildebrand, S. F., and L. E. Cable, 1938: figs. 129, 135, 137.)

profound changes in pigmentation. At 2.2 mm (38 hours) a single large chromatophore on back of head, peritoneum over gut heavily pigmented, and one dorsal and one ventral pigment spot about halfway down tail.¹⁷ At 5.0 mm distal membrane of pelvics black.⁶ At ca. 6.0 mm pattern evident, but pigment more scattered.^{7,20} At 9–11 mm melanophores on head and back and, sometimes, on cheek, opercle, and first dorsal.⁶

PREJUVENILES

Size range described, 15⁶–49 mm.^{21,45}

Anterior nasal aperture with distinct fleshy collar at 24.5 mm.¹⁶ Chin barbel evident at ca. 15 mm.⁶ Body laterally compressed at 30–40 mm.^{21,45} Scales first evident at 25 mm, fully formed at 35–50 mm.⁶ At 24.5 mm dorsal origin posterior to pectoral origin when viewed from above.¹⁶ Caudal variable, round, straight, or slightly concave at ca. 15 mm.⁶ Pelvics well beyond anus at 24.5 mm.¹⁶

Pigmentation: At ca. 15 mm dark pigment generally increased. Black pigment at tip of pelvics lost through size range of ca. 25–40 mm.⁶ At 30–40 mm blue above, silvery on sides and belly; ^{21,45} “fry” also described as greenish on back, silvery on sides.¹²

JUVENILES

Minimum size described, 59 mm.^{21,45}

Body terete within 12 hours after becoming demersal; at 59–66 mm pelvics and head longer, body less deep than in *U. tenuis*.^{21,45}

Pigmentation: After becoming demersal, brown above, white below.^{21,45} At 80–204 mm bluish above;¹⁶ (only in pelagic specimens, JAM) lower sides more or less silvery; venter white, gray, or yellowish; pelvics and pectorals pale; other fins with dark punctulations.¹²

AGE AND SIZE AT MATURITY

Mature at 2 years; females mature by 270–330 mm, mostly at 290 mm; males 240–300 mm, mostly at 290 mm.^{4,21,45}

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Urophycis earlli (Bean), Carolina hake**ADULTS**

D. ₁ 9-10, D. ₂ 54-63; A. 49-56^{3,4} (a count of 47¹ is questioned, JDH); P. 14-16 (JAM); V. 2;⁷ scales in lateral line 148-156 (JAM), or 169;¹ oblique scale rows above lateral line 153-175;³ vertebrae 14-15 + 31-32 = 46-47 (plus urostyle); gill rakers 2 + 8-10 (JAM).

Depth 5, head 3 2/3 times in TL; ² eye 6 times in head; ⁷ barbel 1/3 as long as upper jaw ² or 2/3 to equal to orbit diameter (this character diagnostic, JAM).

Body stout,² not much compressed anteriorly; interorbital wide, convex; mouth large; maxillary to below or slightly beyond posterior margin of eye; ⁷ scales small.⁴ Caudal rounded; ⁶ dorsal without produced anterior rays; ² pelvis extended almost to anus; ⁴ origin of dorsal slightly behind vertical from base of pectoral; origin of anal about midway between snout and caudal base.⁷

Pigmentation: Brown ² to nearly black,³ with purple iridescence in life (JAM); back with light blotches; ⁶ sides with light spots ² or, sometimes pale blotches; lateral line not in a black streak and without pale spots; dorsal, anal, and caudal sometimes nearly black,³ otherwise some light spots on 2nd dorsal, and 2nd dorsal and anal margined with dark brown; ² iris dark gray-brown.¹ In general a dark, dusky fish compared to other hakes (JAM).

Maximum length: Ca. 457 mm.⁶

DISTRIBUTION AND ECOLOGY

Range: New Jersey¹ (where rare, JAM) to northern Florida.⁸

Area distribution: Known from the Norfolk Canyon, off Virginia (JAM), and from a single specimen off Ventnor, New Jersey.^{1,5}

Habitat and movements: Adults—an outer shelf, upper slope form (JAM), sometimes in harbors and close inshore among eelgrass.⁶

Larvae—no information.

Juveniles—apparently inshore at Beaufort, North Carolina.³

SPAWNING

Season: Possibly winter on coast of North Carolina³

(although young as large as 25.0 mm TL have been collected in January and February⁸).

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LARVAE

No information.

JUVENILES

Minimum size described, 37.0 mm TL.

At 37 mm chin barbel greater than one-half length of eye; mouth inferior, nearly horizontal; maxillary extended almost to posterior margin of eye.³

Pigmentation: Darker on lower sides than any other hake, melanophores cover abdominal area (JAM). At 37 mm, dark brown, including fins; caudal fin dark brown at base, rest of fin pale translucent; pectorals and pelvis brown at base, otherwise colorless. At 100 mm almost uniform dark brown, with vertical fins almost black.³

AGE AND SIZE AT MATURITY

No information.

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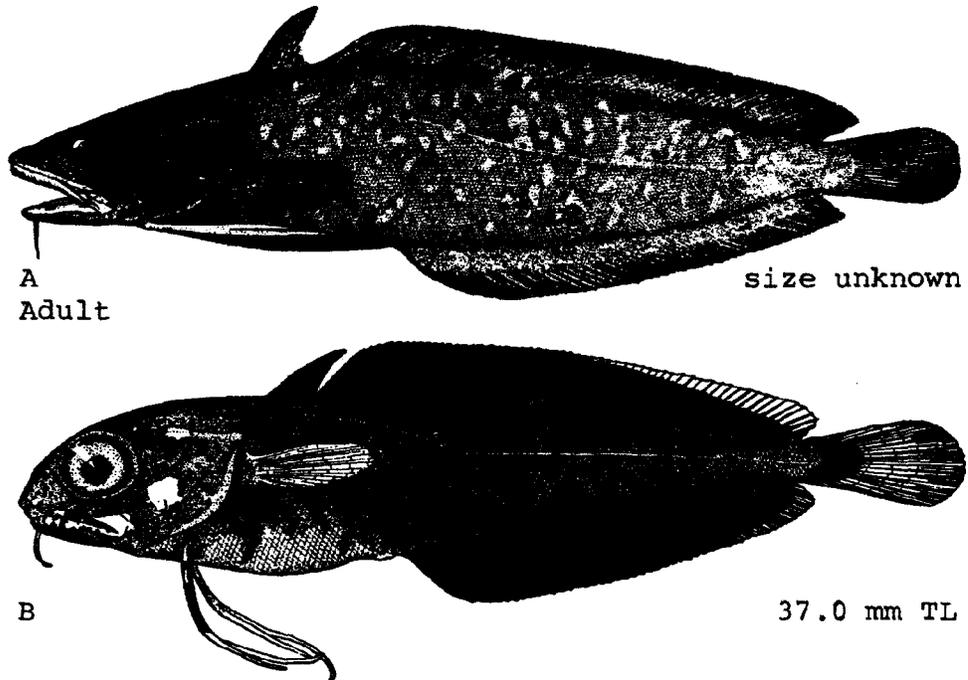


Fig. 194. *Urophycis earli*, Carolina hake. A. Adult, size unknown. B. Juvenile, 37.0 mm TL. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 900. B, Hildebrand, S. F., and L. E. Cable, 1938: fig. 139.)

Urophycis regius (Walbaum), Spotted hake**ADULTS**

D. ₁, 7–9, mostly 8; D. ₂, 43–51; A. 41–45 (JAM) or 50; ³¹ C. 30–32; P. 16; ⁷ V. 2; ⁸ scales 83 (JAM)–97; ^{6,7,11} total vertebrae 45–46; precaudal vertebrae 13–14; caudal vertebrae 31–33; ³¹ gill rakers 3 + 13–17 (usually 14–15) (JAM).

Proportions expressed as times in TL: Head 3.85–4.4, depth 3.9–5.05. Proportions as times in HL: eye 2.9–4.6.¹¹

Body rather elongate, compressed; ⁸ head scarcely depressed, its depth about equal to width; ⁶ snout blunt; mouth large, its angle extended behind eye; upper jaw slightly projected; a small barbel on lower jaw.^{8,11} First dorsal fin without prolonged rays, hardly higher than second; pectoral fins extended as far as anal origin; ^{6,27} pelvic rays filamentous.⁸

Pigmentation: Pale brownish or brown above, tinged with yellow; lateral line dark brown or black and interrupted by conspicuous pale spots; pores of mucous canal on sides of head dark. First dorsal fin black, distally margined with white; second dorsal fin olivaceous and with irregular round dark spots; pelvics and lower edge of pectorals whitish.^{6,7,8,27}

Maximum length: Ca. 417 mm.⁴

DISTRIBUTION AND ECOLOGY

Range: Coastal waters from Nova Scotia ^{4,6} and vicinity of Sable Island ^{8,27} to Texas ²⁶ (rare, however, north of southern New England); also reported from Tortugas, Florida.¹⁸

Area distribution: Coast of New Jersey; ^{12,13} Delaware Bay ²¹ and adjacent offshore waters; ^{16,27} Virginia seaside, both inshore ^{1,14,32} and offshore; ^{15,25} also 48 km up York River, Virginia; ²⁸ Maryland seaside near Ocean City; ²⁶ off Delmarva Peninsula; ¹⁶ northward in Chesapeake Bay to Kent Island and Annapolis.^{10,11,19}

Habitat and movements: Adults—a coastal bottom ^{7,24} species found over the continental shelf but also entering bays, ^{10,11,21,22} harbors, ²³ and rivers.² Associated with objects on bottom, but less so than *Urophycis chuss*.²⁵ Maximum depth, 426 m.³ Specimens 220–450 mm long reported concentrated at 164 m in Gulf of Mexico.³⁰

Inshore in fall in Massachusetts ⁹ and Sandy Hook Bay; ²² primarily south of Chesapeake Bay in winter, moving north in spring, with major concentration north of Bay in summer and fall.⁵

Larvae—a series of larvae 2.75 to 4.5 mm long which presumably included both *Urophycis regius* and *Uro-*

phycis floridanus was collected 10 to 21 km off Beaufort, North Carolina. Depth of capture not reported.⁶ Specimens as small as 8.0 mm near the 183 m depth contour.³³

Juveniles—may be found at surface at lengths of up to 40 mm, and specimens up to 27.0 mm found near 183 m depth contour.³³ At 40 mm and larger prefer muddy bottom.^{4,6,14} Burrow into bottom, lying on side.²⁹ Specimens 50 to 167 mm long in bays, inlets, and rivers.^{4,6,14} Young-of-the-year overwinter near shore. Under aquarium conditions “juveniles” burrow in sand, and specimens less than 135 mm curve their bodies around objects in the tank.²⁴ Salinity range 5.0–35.5 ppt,³⁶ although specimens 83–245 mm long (including some adults) recorded at maximum of 38.2 ppt; ³⁴ specimens 73–141 mm long recorded at salinities of 15.0–19.9 ppt.³⁵ Temperature range 6.7 ²⁸–27.0 C.³⁴ Descend to bottom after one to several months, presumably at length of ca. 40 mm, and move inshore at lengths of 50 to 150 mm,^{6,24} arriving inshore (at least in tributaries of lower Chesapeake Bay) at an age of 6 to 7 months. Specimens 62 to 299 mm long (all regarded as young of the year and immature) enter the lower Chesapeake Bay and the York River, which they penetrate for 48 km, mainly in March (with few individuals, however, apparently arriving in fall or winter) and remain until June. Peak abundance in the York River occurs in April and May. Spring movement into the Chesapeake Bay and its tributaries is a part of a general shoreward movement along the Atlantic coast.^{17,24,28} Inshore in North Carolina from February to June; ⁶ specimens 50 to 210 mm long inshore at Ocean City, Maryland, September to June 20.

SPAWNING

Location: Offshore waters.²⁸

Season: In Chesapeake Bay region probably as early as September (or earlier since near spawning fish have been recorded in late August) to February or March; peak activity in October and most fish spent by late November.^{24,26} Off the Carolinas probably November to February.^{4,6}

Depth: Running ripe adults at 120 m.²⁶

Fecundity: Unknown.

EGGS

Location: Buoyant,²⁶ probably hatch at surface; ⁶ under laboratory conditions settle to bottom ca. 44 hours after fertilization, become suspended with increased aeration.²⁶

Fertilized eggs: Spherical, diameter 0.67–0.81 mm (mean

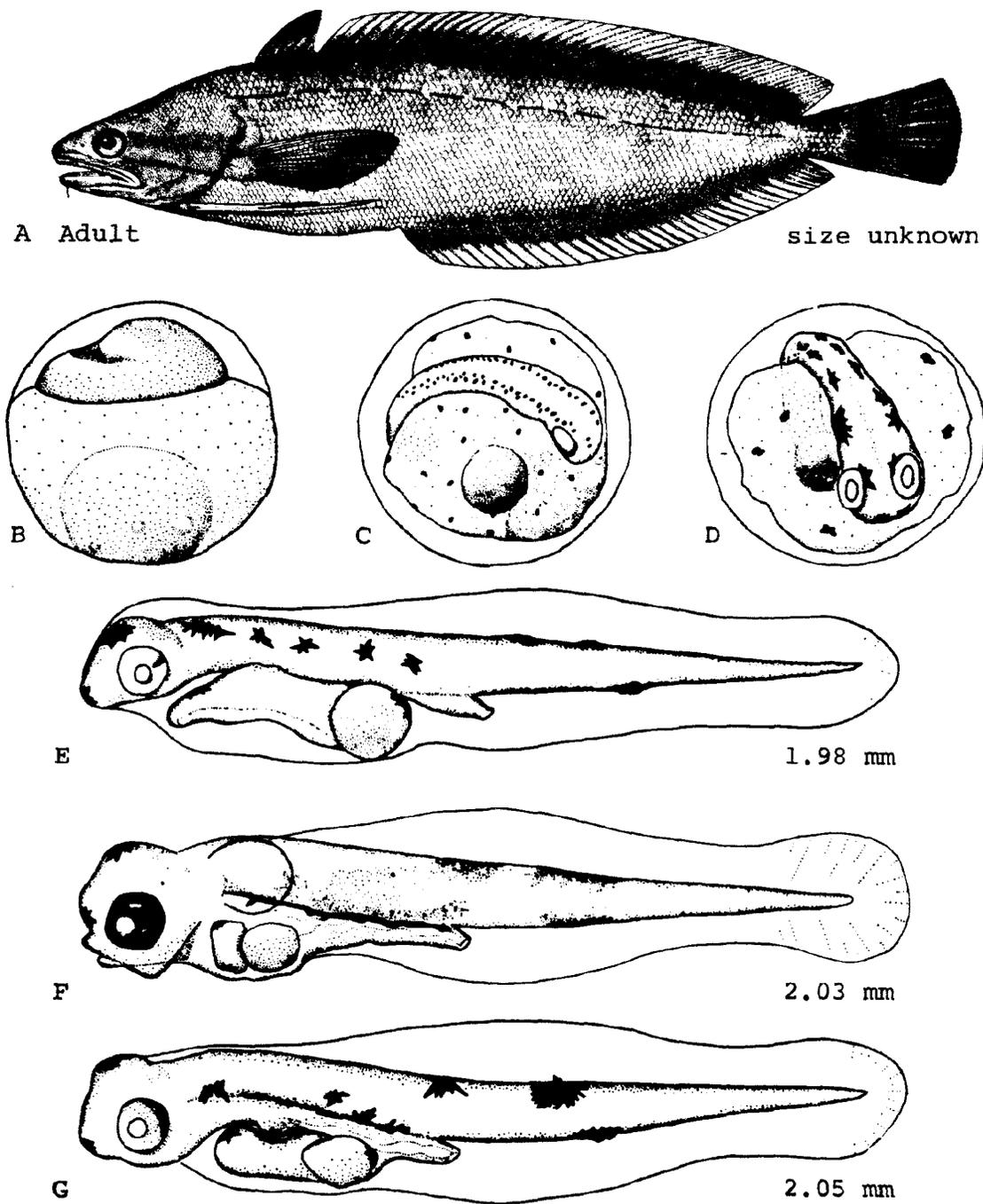


Fig. 195. *Urophycis regius*, Spotted hake. A. Adult, size unknown. B. Egg 12 hours after fertilization. C. 24 hours, eye forming, no lense, pigment developed on body and yolk. D. 36 hours, pigment coalesced in large patch. E. Yolk-sac larva, just hatched, 1.98 mm. F. Yolk-sac larva, 2.03 mm. G. Yolk-sac larva, 2.05 mm. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: pl. 364. B-G, Barans, C. A., and A. C. Barans, 1972: figs. 1-6.)

0.73) when recently fertilized. Oil globules vary during development: at 12 hours a single large oval globule, diameter 0.34–0.45 mm (mean 0.40 mm); at 18 hours a cluster of small accessory oil globules; at 24 hours size of large oil globule 0.14–0.22 mm (mean 0.18 mm), diameter of cluster of accessory globules ca. 0.40 mm. Perivitelline space ca. 0.05 mm wide directly above blastodisc at 18 hours, decreasing in thickness between yolk and egg capsule toward vegetal pole; at 24 hours, sometimes up to 0.10 mm wide.²⁶

EGG DEVELOPMENT

At 22–23 C:

After 12 hours—blastodisc well-developed and opposite oil globule.

After 18 hours—all eggs with distinct oil globule, large irregular cluster of accessory globules; embryo slightly less than 1/2 circumference of yolk; numerous small melanophores on embryo and yolk sac.

After 24 hours—melanophores in irregular row along each side of dorsal ridge of embryo.

After 30 hours—oil globule located in posterior section of yolk sac; a single row of melanophores on each side of dorsal ridge along entire length of embryo except above area of eyes; 2 or 3 pairs of melanophores anterior to eyes; eye lenses formed.

After 36 hours—tail free; oil globule in posterior section of yolk sac; melanophores on embryo and yolk sac larger and fewer with single pair on tip of head; a single stellate melanophore just posterior to each eye; 6–8 pairs of melanophores dorsolaterally on trunk; 3 dorsal and 2 ventral melanophores on tail region; eyes unpigmented.

After 42 hours—a single melanophore directly posterior to each eye and one at anterior tip of head; pattern of melanophores on body variable with 5–7 pairs dorsolaterally along trunk axis, one or two large melanophores on dorsal surface midway between trunk and posterior tip of tail and one ventrally and slightly posterior to them.

After 48 hours—tail tip overlaps eye, oil globule directly under center of embryo and pigmented on posterior dorsal surface.

After 54 hours—tip of tail well beyond eyes; eyes with small wedge of pigment in dorsal posterior quarter.²⁶

Incubation period: At 22–23 C, mostly 54–60 hours.²⁶

YOLK-SAC LARVAE

Size range described, 1.57–2.05 mm.

Jaws “poorly developed” at 2.05 mm (36 hours). Oil globule located posteriorly during at least first 18 hours, still present, but reduced, at 36 hours. Pectoral fins first evident between 18 and 36 hours (2.03–2.05 mm); incipient caudal rays at 36 hours; dorsal finfold forward to tip of head during first 18 hours; anal opening lateral and at base of ventral finfold.²⁶

Pigmentation: A prominent melanophore on anterior tip of head throughout stage. In recently hatched specimens postorbital melanophores now shifted in position and located slightly above eyes; 5–6 pairs of melanophores dorsolaterally from nape to vent, 1 or 2 on dorsal surface posterior to vent, and a single large melanophore on ventral surface slightly posterior to them. At ca. 12 hours melanophores above eyes migrate to crown of head and form a single large pigment spot. At ca. 18 hours pigment developed along dorsal surface of alimentary canal. At 26 hours (2.05 mm) diffuse pigment over much of body, eye fully pigmented.²⁶

LARVAE

Size range described, ca. 4.0–15.0 mm.

Proportions as times in SL: Depth at ca. 5.0 mm ca. 2.8; at 7.0 mm 3.4; at 9.0–11.0 mm dorsal fin 3.8–3.9. At 5.0 mm eye 2.75 times in head.⁶

Mouth strongly oblique at ca. 5.0 mm, much less so at 9.0–11.0 mm. Barbel first evident at ca. 15 mm. Second dorsal and anal developing at ca. 7.0 mm; first dorsal partly formed at 9.0–11.0 mm; dorsal and anal incomplete at 15.0 mm; pelvics evident at 4.0 mm; pelvics with 3 rays at 15 mm; pelvic rays hair-like and extended well beyond vent at ca. 5.0 mm.

Urostyle oblique at ca. 5.0 mm.⁶

Pigmentation: At ca. 4.0 mm usually plain, sometimes with melanophores above anal base. At ca. 5.0 mm melanophores on upper surface of head, on back below anterior half of dorsal; occasionally 1–2 chromatophores at base of anal; a dark lateral stripe, variable in length, above anterior half of anal; a dusky area upward and forward from vent; sometimes a dusky area at upper angle of gill opening; fins plain. At 9.0–11.0 mm pigment variable, some specimens with black dots on cheek and opercle, some with variable lateral stripe, some with dark specks in first dorsal. At 15.0 mm scattered chromatophores along back and on lateral surfaces.⁶

PREJUVENILES

Size range described, 25.0–50.0 mm (based on color pattern).

Body quite slender, compressed at 25.0 mm. Maxillary initially to or a little beyond posterior margin of pupil:

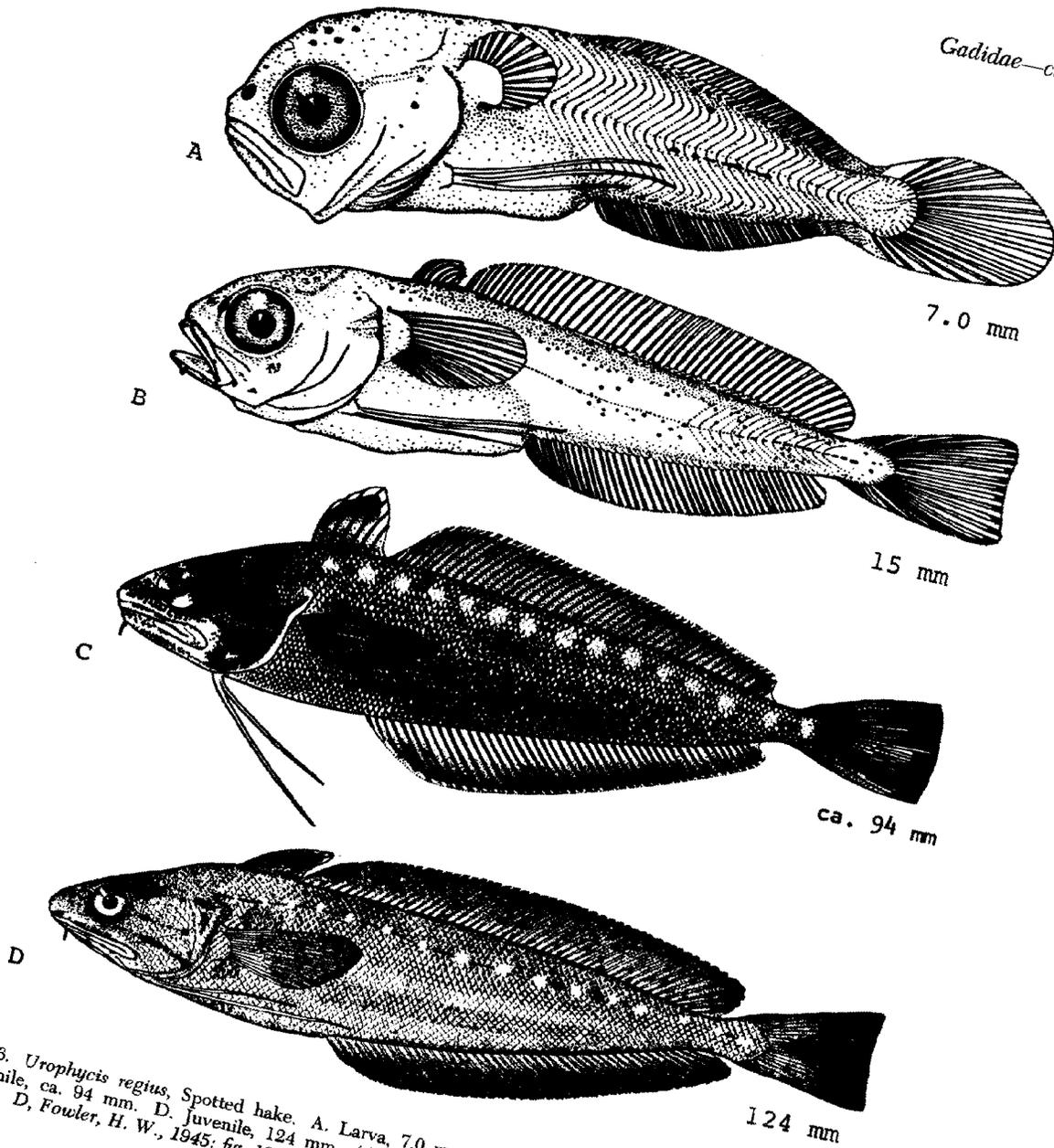


Fig. 196. *Urophycis regius*, Spotted hake. A. Larva, 7.0 mm. B. Larva, 15 mm, first dorsal not fully formed. C. Juvenile, ca. 94 mm. D. Juvenile, 124 mm. (A, B, C, Hildebrand, S. F., and L. E. Cable, 1938: fig. 132, 136, 140. D, Fowler, H. W., 1945: fig. 182.)

at 35.0–50.0 mm maxillary broad posteriorly; barbel scarcely half as long as eye diameter by end of stage.⁶

Proportions as times in TL (at ca. 25.0 mm), depth 4.0–4.6, head 3.3–4.0. Proportions as times in head, snout ca. 4.0–4.4, eye 3.3–3.6.⁶

Pectoral origin beyond anal origin at 35–50 mm. Scales present at 25 mm.⁶

Pigmentation: At 35–50 mm bright green to bluish above; a black area surrounded by white on distal end of first dorsal.⁶

JUVENILES

Minimum size described, 60.0 mm.

At ca. 100 mm eye narrower than interorbital distance, 5.1–6.5 times in HL.⁶

Pigmentation: At 60 mm four black dots in a vertical row sometimes present behind eye, also a spot over eye, another posterior to nostril, and 3 on opercle; dark lateral stripe containing roundish pale spots sometimes present, although often not evident until much larger size.⁶

At ca. 94 mm a series of 15 prominent light spots along developing lateral line from region above pectoral fin to caudal base; several dark lines on opercle radiating from eye.²⁹

At 153 mm brownish above, white below; white spots along lateral line connected by thin black line; first dorsal edged with white and with a prominent jet black spot; 2nd dorsal uniformly dark; anal white or pinkish at base, bluish at center, edged with black; pelvics white; pectorals pale dusky, edged with light yellow.¹¹

At ca. 150 mm body gray, mottled with brown; belly glistening white; 14–16 light lateral line spots; top of head with pale diamond-shaped mark; a dark band across nape and another behind each eye; first dorsal jet black, almost entirely surrounded by narrow pure white margin; 2nd dorsal gray with round dark spots; caudal dusky gray with dark edge; pectoral dusky with white margin; pelvics glistening white.²³

AGE AND SIZE AT MATURITY

Females 310 mm, males 210 mm.²⁶

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Urophycis tenuis (Mitchill), White hake**ADULTS**

D.₁ 9–10;^{7,22} D.₂ 50^{14,26}–59;⁷ A. variously stated, 41–52^{14,26} and 53–57 (based on juveniles 84–115 mm long);²⁴ P. 16;⁷ scales 119–148;^{14,26} scale rows between lateral line and region of first dorsal, ca. 12;¹⁶ total vertebral counts variously stated, 47–50 (excluding hypural),^{14,26} also 56–57²⁴ (but probably in error, JAM); precaudal vertebrae 13–17;^{14,26} caudal 42;²⁴ gill rakers 15–16, on epibranchial of first arch, 2.^{7,21}

Proportions as times in TL: Depth 5.5.²² As percent head length: eye 19.0–24.1, interorbital distance 18.3–18.6.⁷

Body rounded in front of anus, laterally compressed beyond; upper jaw projected beyond lower; gape extended to below eye; a small barbel on chin. First dorsal fin much longer than second, triangular, and with 3rd ray projected as a filament; pelvics in front of pectorals and consisting of a single elongate two-branched ray.²²

Pigmentation: Variable. Brown, purplish brown, reddish brown, or slate above; sides sometimes bronzy; belly dirty or yellowish, with or without numerous small black dots; dorsal fin same color as back; anal fin same color as belly; pelvics with yellowish tinge; all fins with black edges.^{7,22}

Maximum length: Ca. 1220 mm.³

DISTRIBUTION AND ECOLOGY

Range: Continental shelf and slope from Labrador and Grand Bank, Newfoundland, to Cape Hatteras, North Carolina; may also occur off Iceland and as far south as Florida.^{1,5,7,14} Records from Icelandic waters have not been confirmed.^{1,14,26}

Area distribution: Coast of Maryland;¹⁰ off Delaware, apparently within the 182 m depth contour;¹⁷ off New Jersey.²²

Habitat and movements: Adults—found in deep water as well as in harbors⁵ and coastal ponds.⁸ Typically over muddy,^{1,13,18,26} sandy, or silty bottoms; rarely over shelly or gravelly bottom.^{1,14,26} Maximum depth 1000 m¹⁵ off southern New England; in summer, rare or absent shallower than 182 m; in winter, usually deeper than 182 m but present at one station 110–181 m.^{1,26} Typically between 0.6 and 5.5 C; tend to avoid 0 C;²² maximum reported, 15 C.^{1,26}

Apparently resident year-round in southern Gulf of St. Lawrence.²³ In northern Gulf of Maine, inshore in summer, disperse in fall, move into deeper areas in winter.

Abundant at Woods Hole in October and November; absent in Block Island Sound in winter;^{14,26} apparently inshore April to November in Rhode Island;¹⁹ inshore at Orient, Long Island in spring.^{14,26}

Larvae—pelagic;¹ putative larvae 17–22 mm long at surface off Long Island; also shallow enough to be washed ashore.⁵ Apparently dispersed by current: Thus most larvae of New England population probably dispersed from Scotian shelf.^{14,26}

Juveniles—young of unspecified size (but presumably juveniles) under floating or attached vegetation, and sometimes associated with jellyfish.^{14,26} (Reports of young in shells of *Pecten tenuicostatus*¹⁹ in error, JAM.) When inshore, demersal, but occasionally foraging to mid- and upper layers in shallow water environment.^{14,26} Prejuveniles ca. 25 mm and longer sometimes associated with pollock in spring, often at surface under gulf weed and eelgrass;⁸ specimens specifically within the size range of 13–71 mm recorded at surface.^{6,12,21} Juveniles ca. 75–100 mm long recorded inshore in water ca. 1 meter deep, sometimes lying on sides in sand with head projecting;⁴ specimens 150–320 mm long in harbors,⁵ estuaries,¹⁶ mouths of rivers,^{14,26} and tributary inlets of bays,² as well as offshore;¹⁶ at 90–500 mm frequently recorded in water deeper than 180 m. Temperature range, 2–15 C, with some seasonal variation; temperature of greatest abundance 4–10 C.^{14,26} A transition to bottom occurs in May and June at lengths of 72–80 mm (although silvery color begins to disappear as early as 67 mm), and this transition is accompanied by an active inshore migration, but the fish again move into deeper water as size increases. Young have also been reported to move inshore with smelt in fall, and specimens 150–320 mm long enter tributary inlets in Malpeque Bay, Canada, in autumn.^{2,5,14,26}

SPAWNING

Location: Spawning habitat unknown. Fish in spawning condition have been observed in the Gulf of St. Lawrence^{14,26} and in Grand Bank, Newfoundland, the St. Pierre Bank, and Banquereau,⁹ and a female with “large row” was captured off New Jersey.²² Spawning is fortuitous and occasional in New England, and most individuals in this area were probably spawned on the Scotian shelf.^{14,26}

Season: Highly variable, depending on location. Larvae have been observed in September,¹¹ a ripening male on May 15,²² ripe eggs in July,^{5,20} and recently spent fish in August.²⁵ In Newfoundland February to April;⁹ on Scotian Bank late fall and winter; in the Gulf of St.

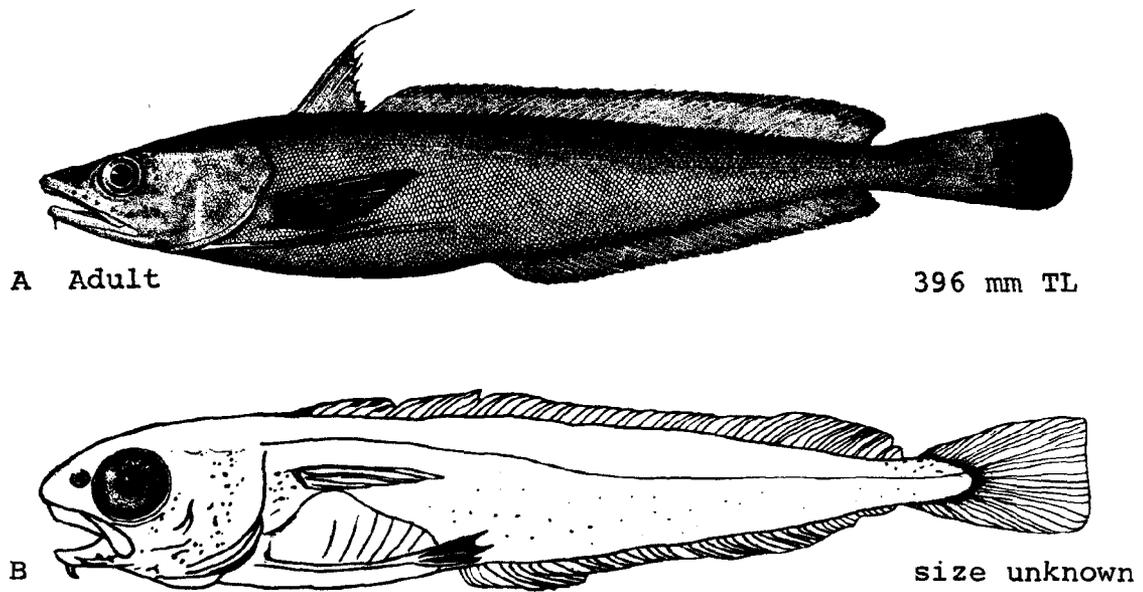


Fig. 197. *Urophycis tenuis*, White hake. A. Adult, 396 mm TL. B. Larva, size unknown, barbel developed, first dorsal incomplete. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 901. B, Original drawing, artist unknown, Virginia Institute of Marine Science.)

Lawrence spawning aggregations in June.^{14,26}

Depth: A female with "large row" at 160 m.²²

Fecundity: No information.

EGGS

Pelagic.^{1,26}

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LARVAE

No information.

PREJUVENILES

Size range described, 23.5¹¹-80 m (based on maximum size at time of descent to bottom).^{14,26}

At 23.5-27.0 mm a flap of skin extended from anterior to posterior nasal aperture, origin of dorsal at level of insertion of pectorals, pelvics not extended to anus¹¹ (but

apparently none of these characters specifically diagnostic of young of this species). At 59-66 mm pelvics shorter, body deeper, and head relatively larger than in similar-sized specimens of *Urophycis chuss*.^{14,26}

Pigmentation: Back dark, otherwise bright silvery, iris silvery with decidedly blue tinge,⁵ interradiation membrane of pelvics black.^{14,26} Remain silvery to 67-76 mm TL.⁵

JUVENILES

Minimum size described, ca. 200 mm.

Pigmentation: At ca. 200 mm brown⁶ to purplish gray (JAM) above; sides brassy tinged with purple; belly and pelvics contrastingly white; iris dark brown; 2nd dorsal and anal dark gray narrowly edged with dusky; caudal a little browner; 1st dorsal black, its filament pale; a dark streak bordered on each side by pinkish white extending below eye from center of upper jaw.⁵

AGE AND SIZE AT MATURITY

Mature at 4 years;¹⁴ mature by 500 mm; ¹ males by 400 mm, females 480 mm.^{14,26}

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Merluccius albidus
Merluccius bilinearis

merlucciid hakes
Merlucciidae

FAMILY MERLUCCIIDAE

Merlucciid hakes, of which there are two subfamilies (Macruraninae and Merlucciinae), five genera, and about 13 species, occur in the Atlantic and eastern Pacific oceans as well as in Tasmania and New Zealand. These fishes have one or two dorsal fins and one anal fin; the first complete dorsal ray is a flexible spine. Teeth are present on the vomer; the mouth is large and terminal; and the jaws are equipped with long teeth, some of which, in the subfamily Macruraninae, may be fang-like. Chin barbels and pyloric caecae are lacking. Members of the subfamily Merlucciinae, to which both regional merlucciids belong, lack fang-like teeth. The caudal fin is truncate and not continuous with the dorsal and anal fins; the pelvic fins are well in advance of the pectoral fins.

The merlucciid fishes spawn in marine waters, and at least some of them undertake definite spawning migrations. Eggs of both regional species, *M. albidus* and *M. bilinearis*, have been illustrated. These species produce relatively small pelagic eggs (diameter 0.7–1.11 mm) with a conspicuous single oil globule. As in the gadids, the anal opening of larvae of the merlucciid hakes is at the side rather than at the edge of the finfold. Development of the pelvic fins is precocious, although not as strikingly so as in certain members of the gadid subfamily Lotinae. In the Lotinae only three pelvic rays develop, while in the Merlucciinae there are typically more than three pelvic rays. Larvae of the regional merlucciid species can be distinguished from larvae of most Mid-Atlantic Bight gadids by their high preanal myomere counts (25–28). They are further distinguishable by the presence of two conspicuous, widely separated pigment patches on the tail posterior to the anus.

For more detailed descriptions and methods of distinguishing eggs and larvae of merlucciid hakes from those of gadids, see the tables and keys to identification of eggs and larvae of gadoid fishes in the introduction to Gadidae.

Merluccius albidus (Mitchill), Offshore hake**ADULTS**

D.₁ 10-13; D.₂ 35-41; A. 35-42; P. 12-17,⁹ mode 15; ^{1,2,9} V. 7; ^{1,2} C. 34; ⁷ scales 129-148; gill rakers 1-3+8-9,^{2,3} total 8-12; total vertebrae 50-56,⁹ precaudal vertebrae 25, caudal vertebrae 26-27.⁸

Proportions as percent SL: Head 26.4-32.9; eye 4.6-8.4; ⁹ 1st dorsal base 9.1-12.3; ¹ pectoral length 13.7-21.7; ⁹ pelvic length 12.1-17.6. Proportions as percent HL: eye 17.7-21.0, snout 28.2-36.3.¹ Eye as thousandths of SL (at 323-626 mm SL), 48-60.²

Cheek, preopercle, and interopercle almost wholly scaled; lateral aspect of snout naked or with lengthwise stripe of scales.² Base of tongue with teeth. Lower jaw extended beyond upper jaw. Barbels absent.⁷

Pigmentation: Dorsum dusky blackish blue (JAM) or

brown with brassy hue; sides and belly white or silvery; iris yellow; pupil black; ⁷ peritoneum uniform dark brown or black in larger specimens, stippled with dots of darker in younger specimens.²

Maximum length: 691 mm SL.²

DISTRIBUTION AND ECOLOGY

Range: North to southeastern slope of Georges Bank (lat. 40° 46', long. 66° 48' W) ³ south to off Surinam.⁹

Area distribution: Recorded at 91-100 m off Delaware.¹

Habitat and movements: Adults—probably on or close to bottom. Evidence of diel vertical migrations (JAM). Depth 91 ¹-1170 m ² and deeper in Caribbean (JAM).

Larvae—no information.

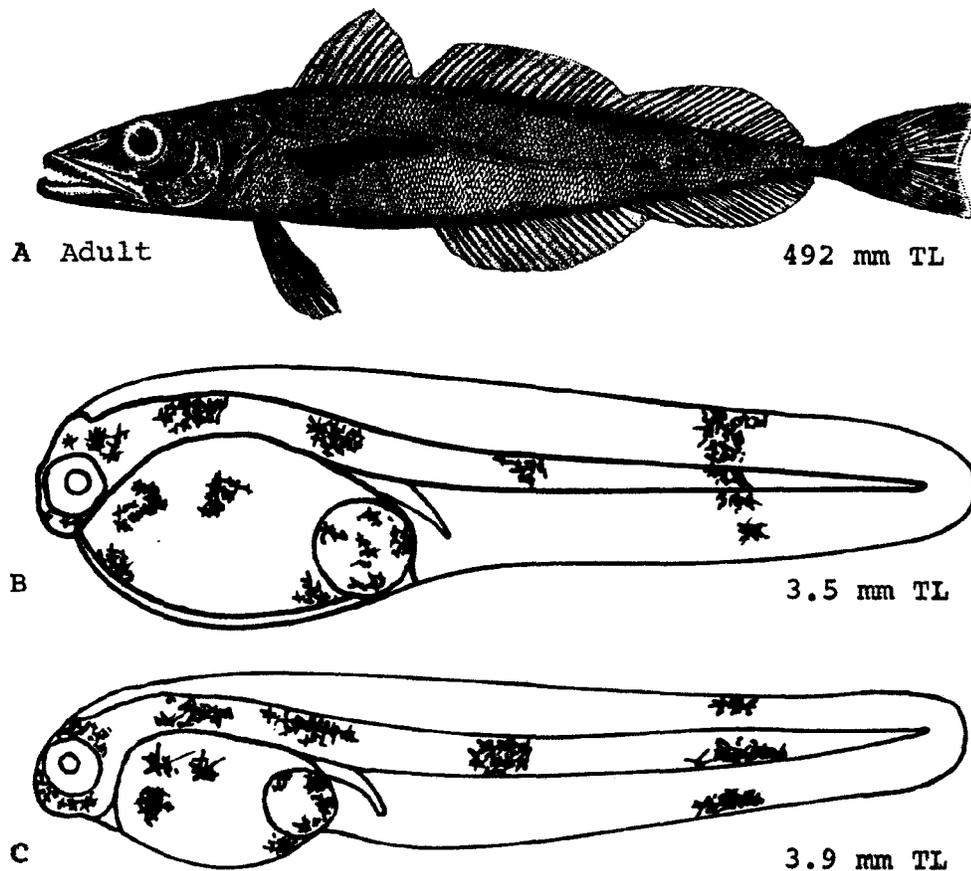


Fig. 198. *Merluccius albidus*, Offshore hake. A. Adult, 492 mm. B. Yolk-sac larva, just hatched, 3.5 mm. C. Yolk-sac larva, 3.9 mm. (A, Ginsburg, I., 1954: fig. 1. B-C, Marak, R. R., 1967: figs. 1, 2.)

Juveniles—specimens 33–66 mm at 106–122 m off Long Island.^{1,4}

SPAWNING

Location: Ripe or near ripe females from Martha's Vineyard to Virginia.^{1,4}

Season: April 26⁴ to July 7.¹

EGGS

Pelagic; spherical; transparent; diameter 0.99–1.18 mm, mean 1.10 mm. Oil globule single, diameter 0.29–0.36 mm, mean 0.32 mm. Perivitelline space narrow.⁴

EGG DEVELOPMENT

Eggs and developing embryos remain colorless until after tail-free stage at which time small stellate melanophores appear on body, yolk mass, and oil globule. Melanophores coalesce into patches as embryo develops.⁴

Incubation: At 8.9–10.6 C, 6–8 days.⁴

YOLK-SAC LARVAE

Hatching length: 3.05–3.75 mm, mean 3.54 mm.^{4,6}

Oil globule in posterior part of yolk sac; anus opened laterally near middle of ventral finfold a short distance beyond yolk throughout size range described.⁴

Pigmentation: At hatching a group of melanophores in jaw region and on posterior part of head. Body with four distinct concentrations of pigment: dorsal to yolk sac, over vent, at midpoint of trunk, and 2/3 distance to end of tail. Posteriormost concentration extended onto

dorsal and ventral finfolds. Large melanophores also present on anterior part of yolk mass and scattered on oil globule. Pigment remains about the same during first 84 hours of development.^{4,6}

LARVAE

No information.

JUVENILES

Depth at origin of 1st dorsal as thousandths of SL at 75–91 mm, 175–180. Eye as thousandths of SL at 75–91 mm, 78–84.²

Caudal possibly rounded at 115 mm, generally truncate at ca. 125 mm SL, emarginated at ca. 240 mm SL (although sometimes remaining truncate to at least ca. 295 mm SL).²

AGE AND SIZE AT MATURITY

No information.

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Merluccius bilinearis (Mitchill), Silver hake**ADULTS**

D. ₁ 11–14; D. ₂ 36–42; A. 37–42; ^{4,9,13,32} C. 32–36; ⁴⁰ P. 13–17, mode 15; ^{4,9} V. 7; ^{14,40} scales 100^{9,25}–130^{4,10} (but counts vary widely, thus 100–110^{9,25} and 112–130⁴); vertebrae 54–56 (but averages stated as 53.90–54.02),^{30,32} precaudal vertebrae 27–28, caudal vertebrae 26–27; ⁴⁸ gill rakers on first arch 2–6⁴ + 10⁹–17, total 15–22; ⁴ branchiostegals 15–20.³²

Proportions as times in TL: Head 3.55¹³–4.0,¹⁰ depth 4.6¹³–6.5.¹⁰ Proportions as percent HL, eye 19.8–21.5.⁹

Body moderately elongate, rounded to vent, slightly compressed posteriorly; head elongate, pointed, depressed, flat above and with rather prominent W-shaped ridges; mouth terminal, the lower jaw projecting; maxillary to or a little beyond middle of eye; ^{10,13} no chin barbels.¹⁴ Teeth sharp, recurved, and in 2 or more rows on jaws; similar teeth on vomer.^{10,13} Lateral line prominent, double in appearance.¹⁰ Second dorsal fin longer than first; ¹⁴ caudal fin weakly concave, square-tipped when spread.¹⁴

Pigmentation: In life (at bottom) general color brownish; 5 to 7 irregular darker vertical bars; all fins, especially 2nd dorsal, with light greenish border.⁴⁶ Silvery iridescent when fresh from water.¹⁰ Otherwise described as dark gray, brownish, or golden above^{9,13} and highly iridescent (silvery or with golden reflections); ¹⁴ lower sides and belly silvery; axil and edge of pectoral fin blackish.^{9,10} Inside of mouth dusky blue; ¹⁴ peritoneum brownish, stippled with black⁴ or blackish throughout.¹⁴

Maximum length: Ca. 760 mm.^{10,14}

DISTRIBUTION AND ECOLOGY

Range: Continental shelf of North America from the Gulf of St. Lawrence and Belle Island Strait eastward to Grand Bank and south to Charlestown, South Carolina. Also recorded from Florida and the Bahamas, but records from south of South Carolina are questioned,^{1,2,3,9,10,14} and are probably attributable to *M. albidus* (JAM).

Area distribution: New Jersey; ^{14,17,18,39} lower Delaware Bay and adjacent offshore waters; ^{10,29,31} coast of Maryland; ^{19,28} coastal waters of Virginia at 36 to 164 m^{13,46} as well as at Chincoteague inlet; ^{19,28} also lower York River, Virginia; ⁴⁴ north in Chesapeake Bay to vicinity of Barren Island and Solomons Island.^{12,13,28}

Habitat and movements: Adults—essentially a benthopelagic (JAM), schooling species,¹⁹ observed from deep sea research vessel during the day within 2 m or so of the bottom and resting in shallow depressions; ⁴⁶ also

found in midwater (sometimes as far out as outer edge of the continental slope)²⁵ as well as near surface.⁹ Known to become stranded on beaches, particularly when pursuing food at night.^{2,10,14,26} Usually over sandy, pebbly,² or gravelly bottom,⁹ seldom around rocks.¹⁴ Sometimes in water not over 50 mm deep²¹ at upper tide line; ¹⁴ out to over 914 m; ¹⁰ at 183 to 549 m in summer.³⁴ Reported from 3.3–17.8 C.¹⁴

Make inshore-offshore and, apparently, north-south movements.^{5,6,9,10} Arrive at Cape Cod as early as March, Georges Bank late April; leave coastal waters in late autumn and offshore banks by December.³⁸ Inshore in New England primarily from May to October with peak abundance in July.³⁰ In more southern parts of range inshore during colder months. In New Jersey fall to spring¹⁷ and at Chincoteague from September to May.¹⁹ Overwinter in warm layers at depths of ca. 200 meters or more off southern New England.^{10,40}

Movements to surface occur primarily at night while pursuing prey pelagically.¹⁰

Larvae—drift at surface or in undercurrents.^{25,45} Larvae 3.2 mm inshore in Maine in August and September.⁴⁹ Specimens 4.0–9.0 mm at bottom in Block Island Sound; ²⁰ specimens ca. 12 mm at 274–549 m in Gulf Stream; ^{25,35,41} in Gulf of Maine larvae of unspecified size at 40 m or deeper.⁴⁵ Apparently drift southwardly, but apparently do not drift passively for long distances.⁴⁰

Juveniles—juveniles less than 75 mm in Gulf Stream;^{25,35,41} at 90–160 mm in coastal bays; ^{19,27} small specimens inside mouths of rivers; ²¹ yearlings just above mud in Gulf of Maine.³³ Young sometimes associated with jellyfish.²³ One year olds overwinter in deep depressions.¹⁴ At ca. 25–75 mm at 274–549 m.^{14,25,35,41} Yearlings, young, and young of the year variously reported from 24 to 165 m^{14,22,33,36} although specimens 110–130 mm long are reported from 5.5 to 8 m.³⁹ 23.4–29.5 ppt in Delaware Bay,³¹ up to salinities greater than 34 ppt on continental slope (JAM). Descend to bottom at lengths of ca. 25 to 75 mm during autumn.^{2,5,14,38} Juveniles 200 to 275 mm inshore at Ocean City, Maryland, in May and October, apparently as stragglers.²⁸

SPAWNING

Location: Spawning may apparently occur at various depths¹⁴ in both inshore^{5,14} and offshore waters (with eggs sometimes occurring outside the continental shelf).¹⁰ Main spawning areas lie between Nova Scotia and Cape Cod,^{9,14} on the southeastern and southern slope of Grand Bank, and in the shallows of Sable Island.⁴⁰

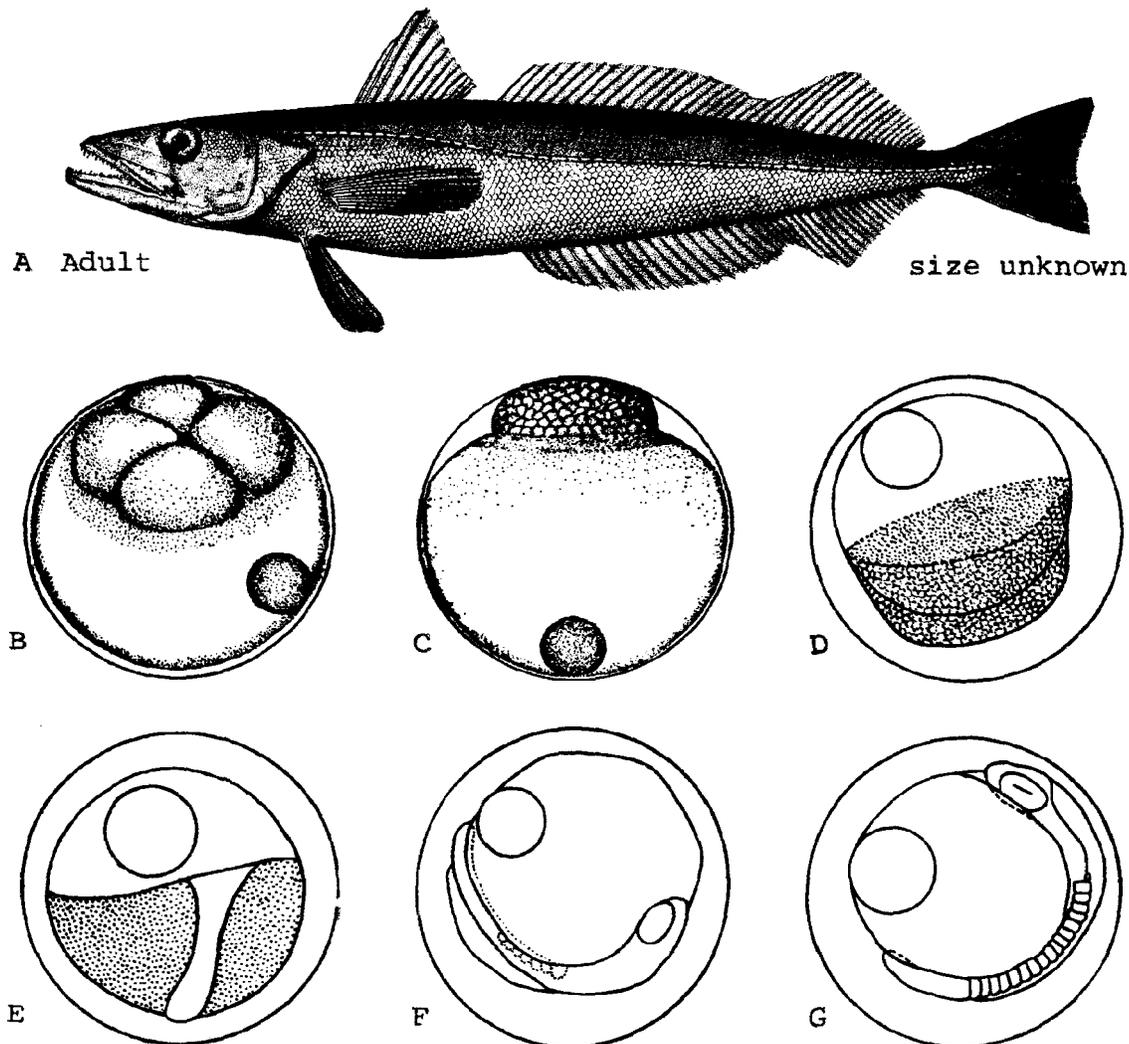


Fig. 199. *Merluccius bilinearis*, Silver hake. A. Adult, size unknown. B. Egg, 4-cell stage. C. Morula. D. Blastoderm nearly to equator of egg. E. Embryo developing. F. Eye, 7 somites formed. G. 17 somites, pigment barely evident on body (although not shown in drawing). (A, Goode, G. B., 1884: pl. 65. B, C, Kuntz, A., and L. Radcliffe, 1918: figs. 50-51. D-G, Sauskan, V. I., and V. P. Serebryakov, 1968: fig. 5.)

Southward spawning has been reported off Long Island, the offings of Cape May,¹⁴ and at the mouth of Delaware Bay. Reports of spawning in the Gulf of St. Lawrence and the Bay of Fundy are apparently in error.¹⁰

Depth: Ripe and possibly spawning fish have been recorded at all depths from surface to bottom and at depths as great as 890 m.^{9,13,14,35,41} Spawning recorded from shore to 91 m in Gulf of Maine and southeastern Nova Scotia.⁴³

Bottom: Over sloping, sandy bottom.¹⁴

Season: Generally May^{7,24} (although a single egg has been collected in April)⁴⁰ to October^{14,15} with peak activity estimated in June and July,⁴⁰ July,² July and August,^{5,8,13,14,43} and August and September, depending on locality. Spawning time (and grounds) may be slightly altered from year to year. For specific localities: on slope regions of Georges Bank, May to September; between Halifax and Sable Island and in Rhode Island, July to October;^{35,40,47} off Sandy Hook, ripe adults in May and June.² Apparently three batches of eggs are deposited in a single season.⁴⁰

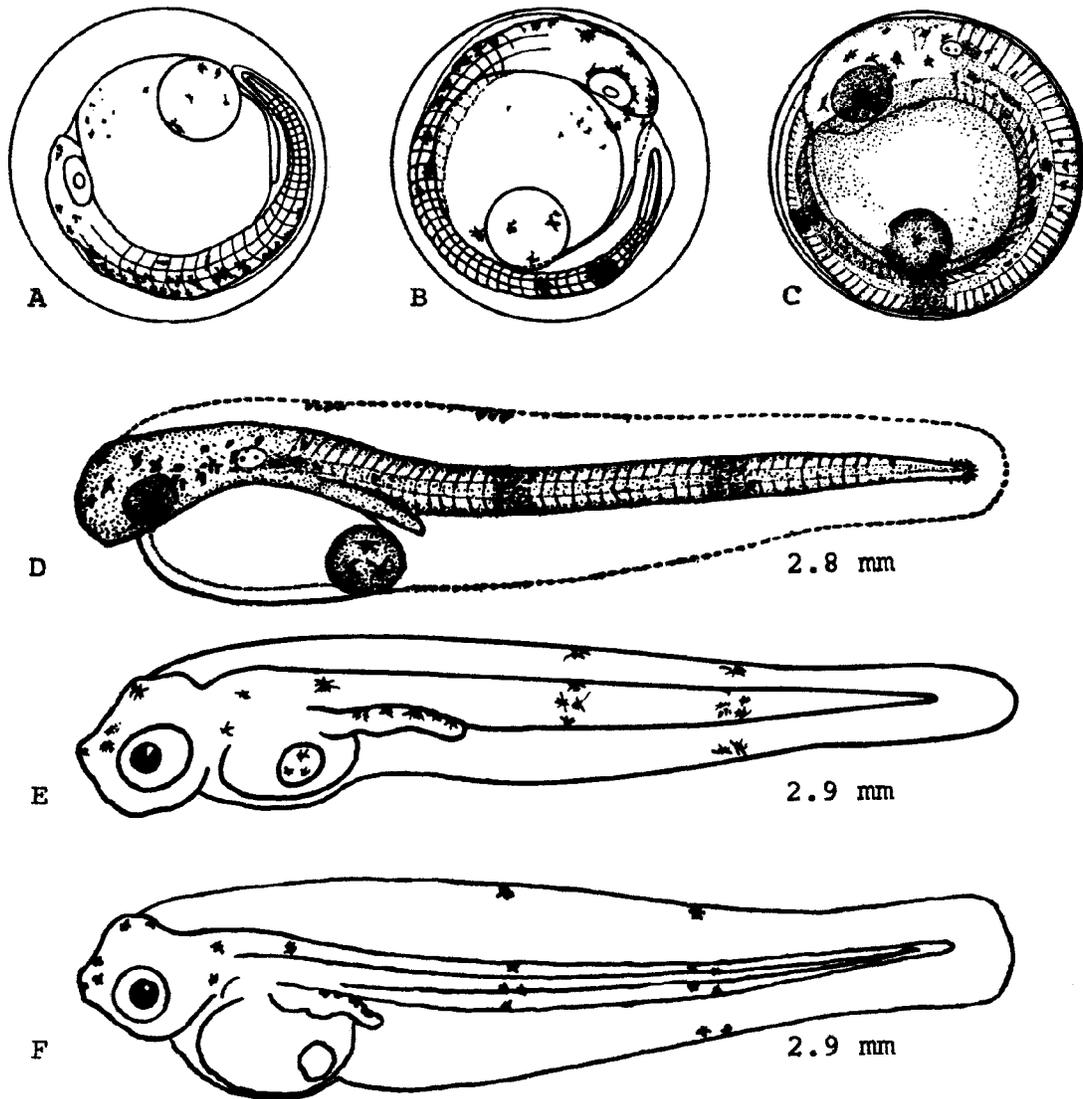


Fig. 200. *Merluccius bilinearis*, Silver hake. A. Embryo extended around 3/4 yolk, 34 somites, lens formed, pigment on head, body, and yolk sac. B. A more advanced embryo, showing characteristic pigment patches developing on posterior part of body. C. Late embryo, otoliths formed, eye pigmented (but identity of specimen questioned on basis of high somite count). D. Yolk-sac larva, newly hatched, 2.8 mm. E. Yolk-sac larva, 2.9 mm. F. Yolk-sac larva, 2.9 mm, pigment no longer present on oil globule. (A, B, Sauskan, V. I., and V. P. Serebryakov, 1968: fig. 5. C, D, Kuntz, A., and L. Radcliffe, 1918: figs. 53-54. E, Colton, J. B., and R. R. Marak, 1968: 18. F, Miller, D., 1958: 46.)

Temperature: Spawn on rising temperature, and not until water column is slightly above 5.5 C.¹⁴ Limits 5 or 7 to 12 or 15 C,⁹ but mostly at ca. 7 to 13 C¹⁴ (although eggs apparently need ca. 13 to 15 C to develop normally).⁴⁰

Salinity: 3.15-32.5 ppt.⁹ (Brinley's record¹⁶ of eggs in freshwater is probably in error, JDH).

Fecundity: Total eggs, 343,000 in specimens 250-300 mm long, 391,700 at 300-350 mm.⁴⁰

EGGS

Location: Pelagic,^{16,24,40} floating at surface^{2,13} and carried with current for distances of up to ca. 110 km.

Usually in water less than 91 m deep, but in some areas such as southern New England and off Nova Scotia over much deeper water.^{38,40}

Ovarian eggs: Three groups of eggs develop in the ovary simultaneously.⁴⁰

Ovulated eggs: Transparent, nucleus shifted toward micropyle.⁴⁰

Fertilized eggs: Spherical; highly transparent; diameter 0.70–1.11, stated averages 0.85,⁴⁰ 0.91.⁷ Egg membrane described as smooth⁴⁰ and thin and horny.^{8,16} Yolk light yellow, homogeneous, semitransparent, diameter 0.60–0.90.⁴⁰ A single, large,² relatively yellowish or brownish oil globule,^{7,8,14,24} diameter 0.15–0.43 mm,¹⁵ mean 0.26.^{7,35} Perivitelline space 0.09–0.12 mm.⁴⁰

EGG DEVELOPMENT

Development at unspecified temperature:

Soon after closure of blastopore—Embryo ca. 1/2 around yolk; black chromatophores sparsely scattered over embryo and oil globule; extra-embryonic blastoderm free of pigment.⁸

Several hours later—Auditory vesicle, otoliths formed, tail free. As time of hatching approaches⁸ (although identity of figure on which this is based has been questioned)⁴² yellow pigment back of eye, back of otocyst, in series along lateral surface of anterior region of trunk, and in two vertical bands on posterior half of body. Anteriorly black pigment remains as in earlier stages, posteriorly melanophores aggregate in two vertical bands.⁸

Development at unspecified temperature:

At time of gastrulation—Blastoderm near equator of egg, germ layer formed, oil globule at vegetal pole, animal pole oriented downward.

7-somite stage—eyes forming.

17-somite stage—embryo around slightly more than 1/2 of yolk, pigment forming on embryo (although not shown in figure).

34-somite stage—embryo around 3/4 yolk; tail free; lens formed; embryo, yolk sac, and oil globule pigmented; 2–4 melanophores in front of eye, 3–5 above and behind eye; body heavily pigmented in region of 7th and 8th somites.

Advanced embryo—embryo completely encompasses yolk. Pigment concentrated on head and around eyes, between 2nd and 7th somites, on 10th to 13th somites, at level of 27th somite, and between anus and tip of tail. Pigment on yolk mainly in head region; melanophores on oil globule larger than those on yolk.⁴⁰

Incubation period: At ca. 20⁴⁰ to 22 C, ca. 48 hours;^{2,11} normally develop at 12.2–15.6 C¹³ or, possibly at 9–22 C⁴⁰ although development is apparently not normal at less than 10.0 C or above 18.3–21.1 C.¹⁴ Eggs are killed by a change in temperature of over 20 C in less than 24 hours.³⁷

YOLK-SAC LARVAE

Size at hatching 2.64–3.52 mm, mean 3.02 mm.^{7,24} Maximum length reported, 4.42 mm.⁴⁰

Body relatively slender, head slightly deflected over anterior end of yolk sac.^{2,8} Oil globule evident to at least 3.3 mm.⁷ At 4.42 mm jaw apparatus rudimentary.⁴⁰ At hatching depth of dorsal and ventral finfolds greater than body depth posterior to vent; conspicuously more slender by end of stage.^{7,8} Incipient caudal rays evident at 3.3 mm⁷ (although apparently lacking in a specimen 4.42 mm long). Rudiments of epurals and hypurals evident as enlargements in caudal portion of trunk at 4.42 mm. Pectoral buds evident, but lacking rays by end of stage.⁴⁰ Anus immediately behind yolk sac and lateral to base of finfold.^{2,7,8}

Pigmentation: At hatching or in early yolk-sac larvae, melanophores sparsely scattered over head, anterior trunk region, oil globule, and gut; a small yellow area just posterior to otocyst. Caudal region marked with two vertical bands of yellow and black, the second of which is somewhat more than half the distance from vent to posterior end of body.^{7,8,14,24} At 4.42 mm eye pigmented, 2–3 pigment cells above head, 3–4 in occipital region, 1 on gill cover, 3–4 on undersurface of yolk sac, ca. 10 in peritoneal cluster, 1 at beginning of tail at level of lateral line, 1 midway along tail, and 1 at end of notochord.⁴⁰

LARVAE

Size range 3.5²⁴–22.5 mm⁴⁰ (but smallest described 6.5 mm).⁸

Total myomeres, ca. 50 at 9.93 mm.⁴⁰

Proportions expressed as percent of body length: At 12.1 mm depth 19.5, predorsal distance 38.5; at 15.3 mm, depth 17.5, predorsal distance 38.0; at 22.5 mm, depth 17.0, predorsal distance 37.0.⁴⁰

At 6.5 mm body tapers gradually toward posterior end; at 6.5–11.0 head relatively large.⁸ A single row of conical teeth at ca. 7.5 mm.^{7,24} Finfold continuous at 6.5 mm,⁸ essentially lost throughout remainder of stage, although evident between 1st and 2nd dorsal in specimens up to 12.1 mm.⁴⁰ Median fins with well-developed rays at 7.5 mm.⁷ Appearance of pectoral rays highly variable: Evident in one specimen at 6.5 mm,⁸ absent in another

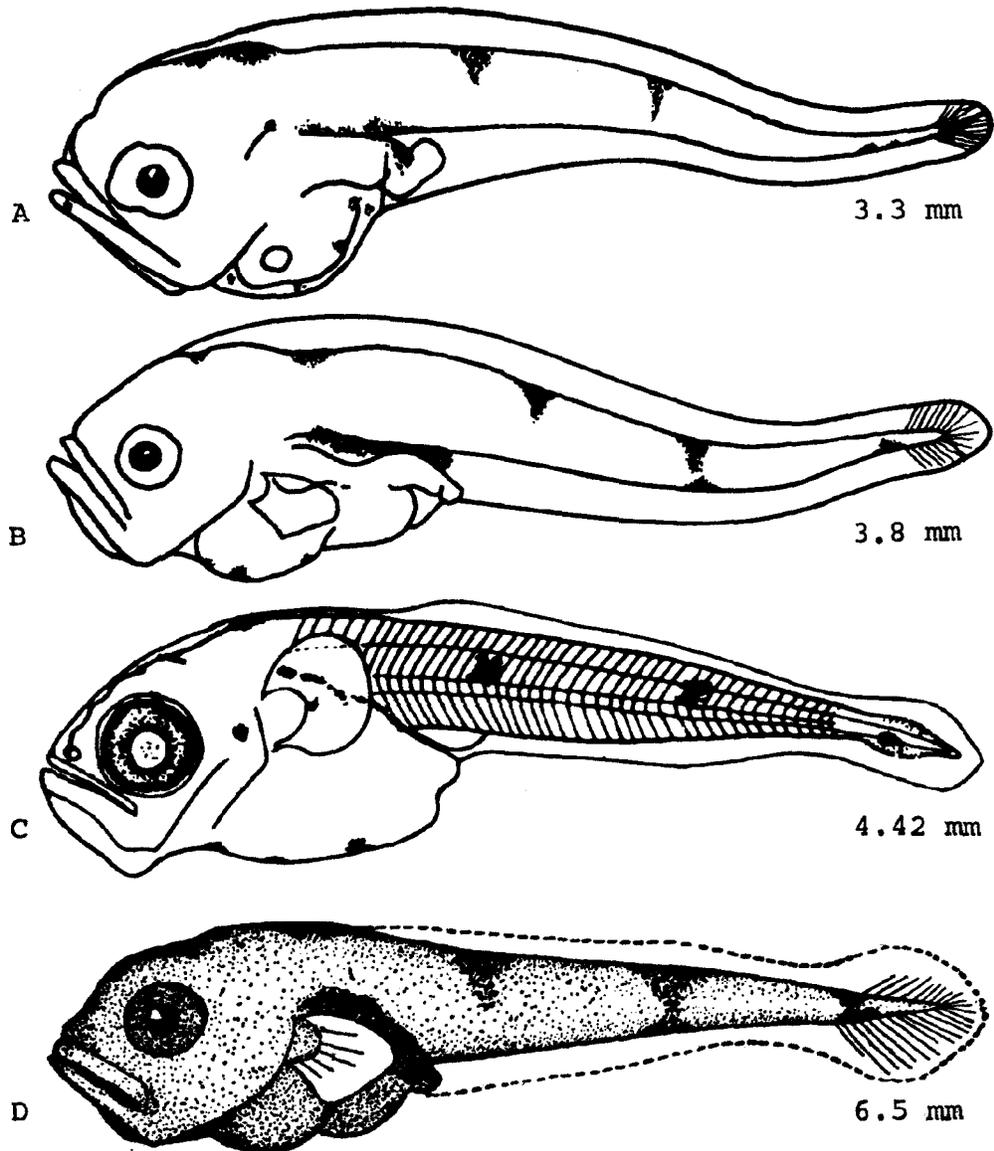


Fig. 201. *Merluccius bilinearis*, Silver hake. A. Yolk-sac larva, 3.3 mm, incipient caudal rays formed. B. Yolk-sac larva, 3.8 mm, oil globule no longer evident. C. Yolk-sac larva, 4.42 mm. Note atypical pattern, lack of caudal rays, and advanced development of pectoral fin. D. Larva, 6.5 mm. (A, B, Miller, D., 1958: 46-47. C, Sauskan, V. I., and V. P. Serebryakov, 1968: fig. 6. D, Kuntz, A., and L. Radcliffe, 1918: fig. 55.)

21.1, and incompletely formed at 22.5 mm. Pelvics formed and with rays at 9.93 mm, reaching anus at 15.3 mm. Notochord oblique at 9.93 mm.⁴⁰

Pigmentation: Three postanal pigment bands, typical of yolk-sac larvae, evident at ca. 11 mm.^{7,24} At 4.0-9.0 mm these bands fail to merge over the back, thus appearing, in dorsal view, as pairs of pigmented areas (a character which separates them from larvae of *Centropristis striata*).²⁰ At 6.5 mm dorsal region of abdominal cavity

heavily pigmented, large black melanophores on dorsal aspect of head and anterior region of trunk.⁸ At 9.93 mm additional pigment in front of eyes, beneath pectorals, near dorsal fin, and near end of tail.⁴⁰ At 11.0 mm dorsal region of abdominal cavity heavily pigmented, large melanophores along entire dorsum except in caudal region.⁸ At 12.1 mm pigment appears on both jaws, caudal and dorsal melanophores increase, and melanophore developing at base of caudal rays. At 15.3 mm

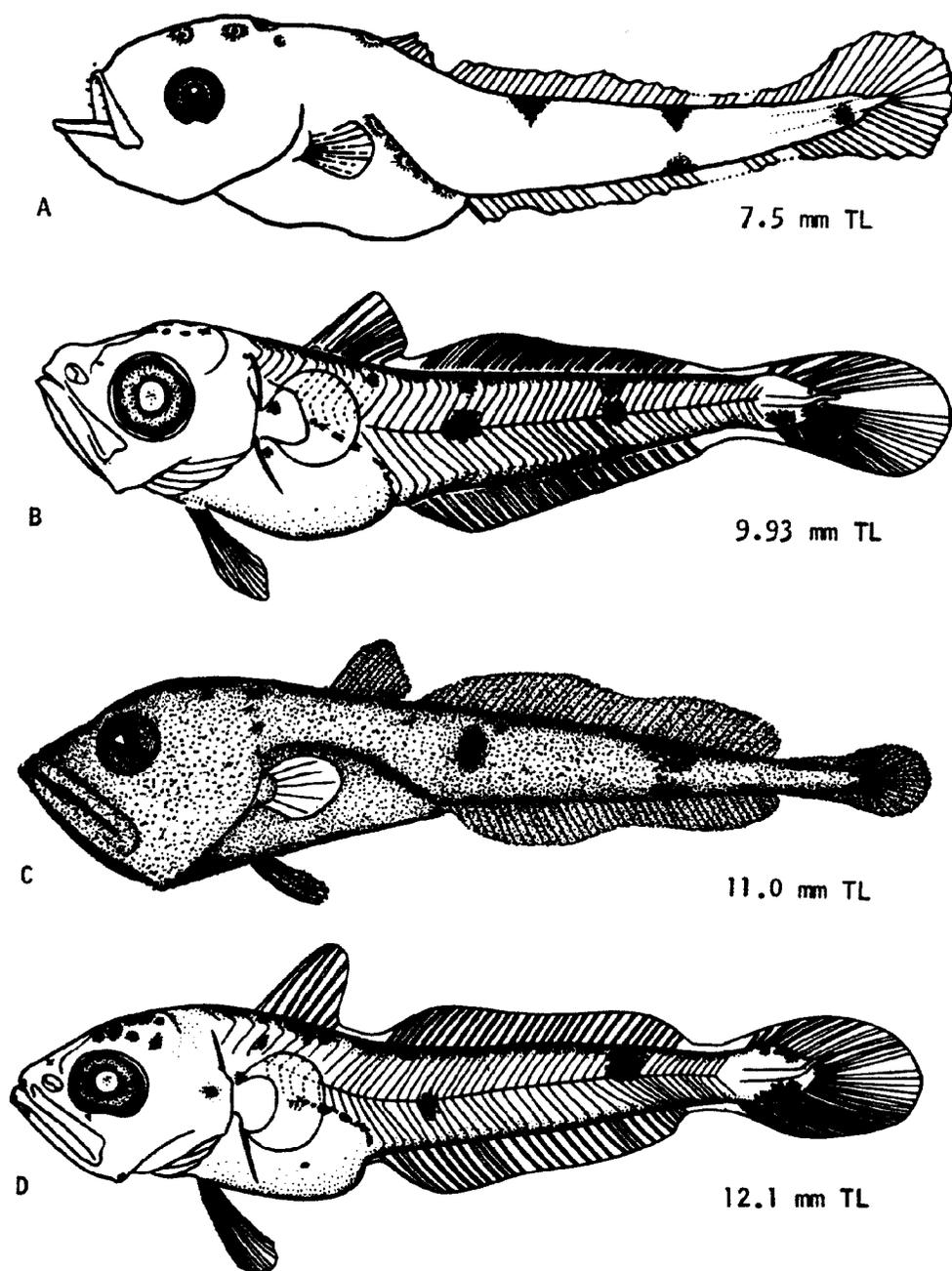


Fig. 202. *Merluccius bilinearis*, Silver hake. A. Larva, 7.5 mm TL, teeth developing. B. Larva, 9.93 mm TL. C. Larva, 11.0 mm TL. D. Larva, 12.1 mm TL. (A, Colton, J. B., and R. R. Marak, 1968: 18. B, D, Sauskan, V. I., and V. P. Serebryakov, 1968: fig. 6. C, Kuntz, A., and L. Radcliffe, 1918: fig. 56.)

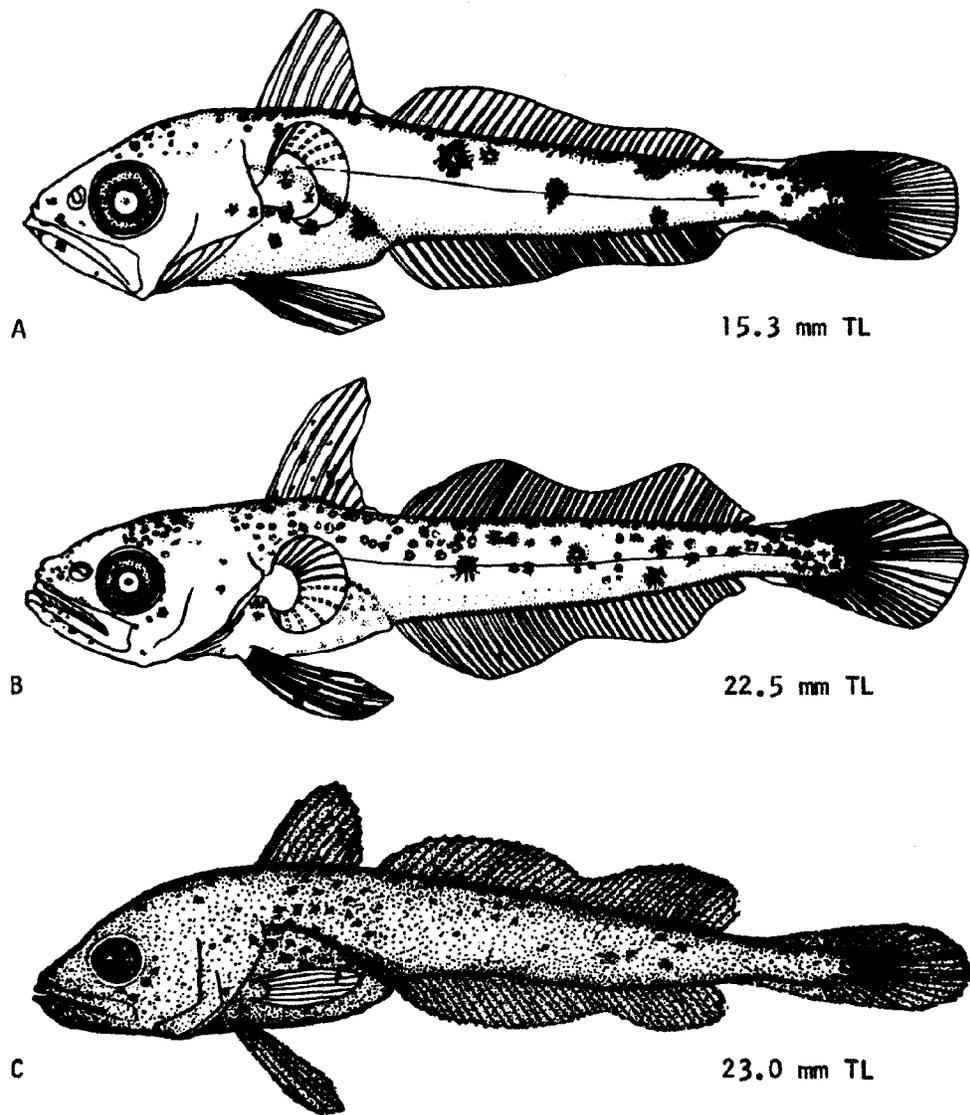


Fig. 203. *Merluccius bilinearis*, Silver hake. A. Larva, 15.3 mm TL. B. Larva, 22.5 mm TL. C. Prejuvenile, 23.0 mm TL. (A, B, Sauskan, V. I., and V. P. Sevebryakov, 1968: fig. 6. C, Kuntz, A., and L. Radcliffe, 1918: fig. 57.)

pigment increased on jaws, beneath pectoral fins, and on peritoneum. A cluster of melanophores at base of caudal, and 2 large melanophores on last 3rd of 2nd dorsal and anal. At 22.5 mm dorsal and dorsolateral aspects of body with scattered melanophores, pigment developed on first dorsal, caudal, and pelvics.¹⁰

PREJUVENILES

Size range, ca. 20 (based on comment adult characters may be developed at this size)^{10,17}–75 mm (based on maximum length at time of descent to bottom).^{2,5,14,38}

Pigmentation: At 20–25 mm dorsal and dorsolateral aspects of body lightly and more or less uniformly pigmented.⁸

JUVENILES

Undescribed, except for comment that, on the average, caudal fin becomes emarginate at 260 mm SL.⁴

AGE AND SIZE AT MATURITY

Probably mature at 2 years;³⁸ and at ca. 300 mm² (although smallest female with countable eggs 250 mm⁴⁰).

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Apeltes quadracus
Gasterosteus aculeatus

sticklebacks
Gasterosteidae

FAMILY GASTEROSTEIDAE

This family is found throughout most of the northern hemisphere, occurring approximately between the 30th parallel and the Arctic Circle. Its various members occur collectively in fresh, brackish, and marine waters, and several species are anadromous. Typical habitats include streams, creeks, ponds, lakes, marshes, estuaries, tide pools, and the open ocean. The family consists of five genera and about eight species.

The three-spined stickleback, *Gasterosteus aculeatus*, one of the two regional members of the family, appears to consist of two distinct forms, apparently reproductively isolated: the migratory marine form (*trachurus*) and the non-migratory freshwater form (*leirus*). The status of these two populations is still unclear. In the present review both populations are considered part of the "aculeatus-complex" as defined by Nelson (1971). This complex may, in fact, include a number of geographically and/or reproductively isolated species.

In the sticklebacks the caudal peduncle is typically long and the body laterally compressed. Bony lateral scutes may be present or absent. The teeth are small but well-developed. The circumorbital ring is incomplete posteriorly. Sticklebacks have three branchiostegal rays, and a series of up to 16 well-developed isolated dorsal spines in advance of the soft dorsal fin. The caudal fin is round or very slightly forked. One pelvic spine is present (although in some populations the pelvic fins are entirely lacking), and there are 27 to 42 vertebrae. Complex nesting behavior and parental care of the eggs and young are important characteristics of the family.

Male sticklebacks construct elaborate nests of aquatic vegetation, which are held together by a thread-like material secreted by the kidney. In *Gasterosteus aculeatus* the nest is on the bottom, sometimes over a shallow excavation. In all other species, the nests are generally off the bottom. After courtship and spawning the male remains with the eggs to aerate them and protect them from predators. Aeration may be accomplished either by fanning or by blowing water through the nest. A male *Apeltes quadracus* may guard up to four nests simultaneously. In this species, if eggs fall from the nest during spawning they are immediately recovered by the male. Males of *Gasterosteus aculeatus* remove dead eggs from the nest.

In the regional sticklebacks the eggs are demersal, vary from 1.0 to 2.0 mm in diameter, and have a number of oil globules of various sizes. In both species the perivitelline space is relatively narrow. *Apeltes quadracus* eggs are reported to have adhesive threads on the chorion, while the chorion is smooth in *Gasterosteus aculeatus*. Eggs of *G. aculeatus* adhere to one another, but their adhesiveness to other objects is apparently variable. The eggs of this species may have significantly more oil globules than the somewhat smaller eggs of *Apeltes quadracus*.

Larvae of *Gasterosteus aculeatus* hatch at 3.0 to 7.0 mm; those of *Apeltes quadracus* at 4.2 to 4.5 mm. In larvae of both species the mouth is open at the time of hatching; the pectoral buds are well-developed; the yolk sac is large, oval, and has a well defined vitelline circulation pattern. The finfold is relatively low and not extended forward to the head. Pigment is present at least on the body. Throughout the larval period the anus lies at a point between two-fifths and three-fifths of the distance to the tail.

Apeltes quadracus (Mitchill), Fourspine stickleback**ADULTS**

D. II to VI, 9-14⁵ (3 or 4 isolated spines + 1 at beginning of soft dorsal⁴²); A. I,²⁷ 7-11; C. 13; P. 11²⁴⁻¹²; ⁴² V. I, 2; ²⁶ vertebrae 29⁴²⁻³⁴; ²⁶ branchiostegal rays, 3.⁴²

Proportions expressed as times in TL: Head 3.4^{19-4.5},²⁶ depth 3.6^{27-6.0}.²⁶ Eye 25.0-33.3% HL.⁴²

Body fusiform,¹² elongate, compressed, triangular, flat-bottomed in cross-section; back elevated at beginning of rayed dorsal; caudal peduncle long, slender; head rather long; snout pointed; mouth small, slightly oblique, nearly terminal; maxillary failing to reach eye. Teeth slender, small, in single series.^{16,19,27,28} Scales absent. Innominate bones not joined, no bony plate between pelvics.^{12,14,26} Dorsal and anal rounded in outline, exactly opposite.²⁸

Pigmentation: Brownish olive or greenish above,^{26,28,29} white¹² or silvery below;^{16,27,33} flanks with dark mottlings or blotches¹⁹ alternating, below lateral line, with upward extensions of ventral coloring;^{28,29} back with ca. 4-5 obscure saddle blotches; a dark streak from tip of snout to orbit, and 2 similar streaks behind eye on sides of head;¹⁹ often with an indefinite pale streak along side;²⁷ iris brownish with olive reflections.¹⁹ Fins plain translucent²⁷ to pale amber or brownish.¹⁹ Males much darker than females,^{28,29} sometimes almost black.⁴⁵ Spawning males almost black,^{14,16} pelvic spine and membrane scarlet red.^{7,12,26,33}

Maximum length: 65.0 mm.²⁷

DISTRIBUTION AND ECOLOGY

Range: Labrador²⁰ and Newfoundland³⁹ to Virginia;²⁶ also Sable Island, 290 km off coast of Nova Scotia.²⁷

Area distribution: Maryland,¹⁴ Virginia,^{15,27} Delaware River estuary,²⁵ New Jersey;^{4,19} north in Chesapeake Bay to vicinity of Havre de Grace.^{27,32,37}

Habitat and movements: Adults—found in salt, brackish, and fresh water¹⁰ in grassy bays,^{23,27} lagoons, tide pools,²⁰ salt marshes;^{12,31} brackish and freshwater ponds,^{5,26,34} lakes, streams,^{2,12,30} and ditches;¹² near mouths of creeks²⁰ and rivers³¹ and along grassy shores;²⁷ also considerable distances up rivers from brackish water;²⁶ rarely along open sandy beaches²⁷ and in open sea.²⁰ Recorded in freshwater over bottoms of mud and leaf, or mud and rock.⁴⁰ Usually associated with eelgrass,⁶ *Elodea*, *Potamogeton*,⁴⁰ or other aquatic vegetation.^{8,19} Maximum distance up rivers, 24-32 km.²⁶ Maximum depth, 31 m.²⁷ Salinity range 0.00⁹-35.0 ppt;²⁴ often run up into fresh water.^{12,28} In Chesapeake Bay retire to deeper water (up to 31 m) during winter.²⁷

Larvae—in relatively shallow water near mouth of Patuxent River, Maryland (WLD); various localities in Mystic River, Connecticut, having average annual salinities of 3.0-ca. 22.0 ppt.³⁸

Juveniles—abundant in upper Mystic River, Connecticut, in summer;³⁸ probably restricted to place of origin, although young reported from tidal currents at Woods Hole, Massachusetts;²¹ in surface collections in vicinity of Woods Hole.²² From various localities with average annual salinities of 3.0-ca. 30 ppt.³⁸

SPAWNING

Location: In nest¹² in brackish waters¹⁷ of weedy shallows,²¹ swamps,¹¹ and ditches.¹⁸ Eggs collected from localities having average annual salinities of 3.0-ca. 17.0 ppt.³⁸ Nest conical, constructed of plant material cemented together by substance secreted by male kidney,^{8,12,18} 12.7 mm high and 9.5 mm in diameter or slightly larger,^{17,18,28} built on plants above substrate,⁷ and having a single opening at top.^{17,18,28} (A single male may build and maintain up to 4 nests simultaneously.)¹¹

Season: Last half of April to early May in Chesapeake Bay²⁷ or April 1 to May 10;¹³ May, June, and July in New York;¹⁷ April³¹ to end of July in New England.^{21,28,35,38}

Temperatures: 23-24 C in laboratory.⁷

Fecundity: 42-5624.¹³

EGGS

Description: Demersal;^{3,17} deposited in nest in clumps of ca. 15-40.^{1,13,18,28,29,30,31,42}

Unfertilized eggs: Somewhat irregular in shape when freshly stripped;³⁰ average diameters vary from 1.5-1.8 mm.³⁵

Fertilized eggs: Spherical¹⁷ (although contacting areas of adjacent eggs sometimes slightly flattened³⁰); diameter 1.5³-ca. 2.0 mm;^{8,18} yellowish^{17,28} to deep brownish amber, the yolk more opaque than that of *Gasterosteus aculeatus*;³⁶ egg membrane equipped with adhesive threads;³ at one pole a number of button shaped appendages attached by pedicels; zona radiata perforated by numerous pore canals; oil globules few, small, unequal, and either widely scattered or closely aggregated.^{8,18,30}

EGG DEVELOPMENT

Development at unspecified temperature:

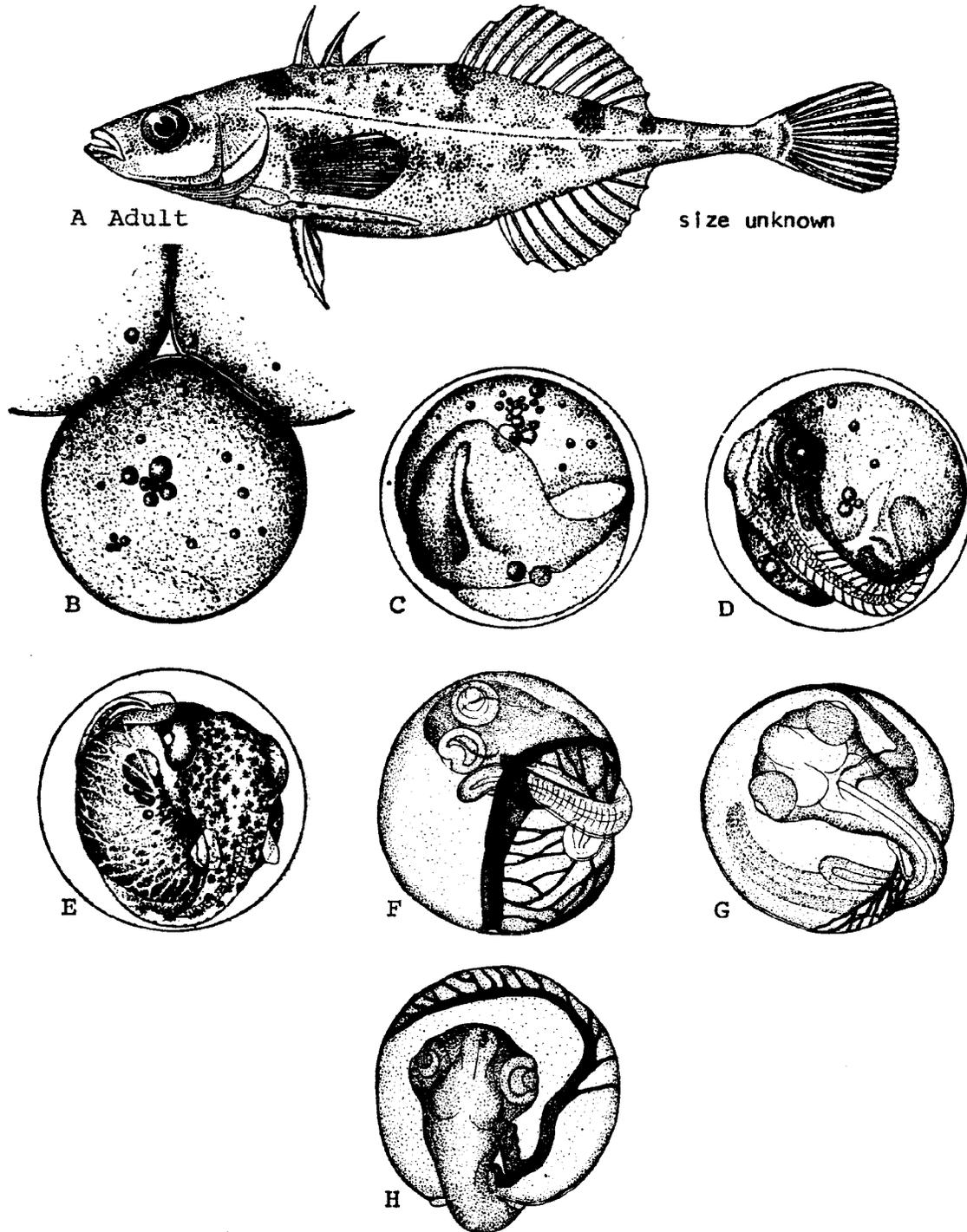


Fig. 204. *Apeltes quadracus*, Fourspine stickleback. A. Adult, size unknown. B. Unfertilized egg. C. Development of egg, diameter ca. 1.6 ca. 2.0 mm. D. Germ ring, embryonic shield. E. Myomeres formed, otoliths evident, 48 hours. F. Tail apparently free, pigment on embryo and yolk, pectoral fins evident, 96 hours. G-H. A somewhat less advanced 96 hour embryo, eye incomplete, pigment lacking. (A, Jordan, D. S., and B. W. Evermann, 1896-1900: fig. 322. B-E, Kuntz, A., and L. Radcliffe, 1918: figs. 122-125. F-H, Ryder, J. A., 1887: figs. 22-24.)

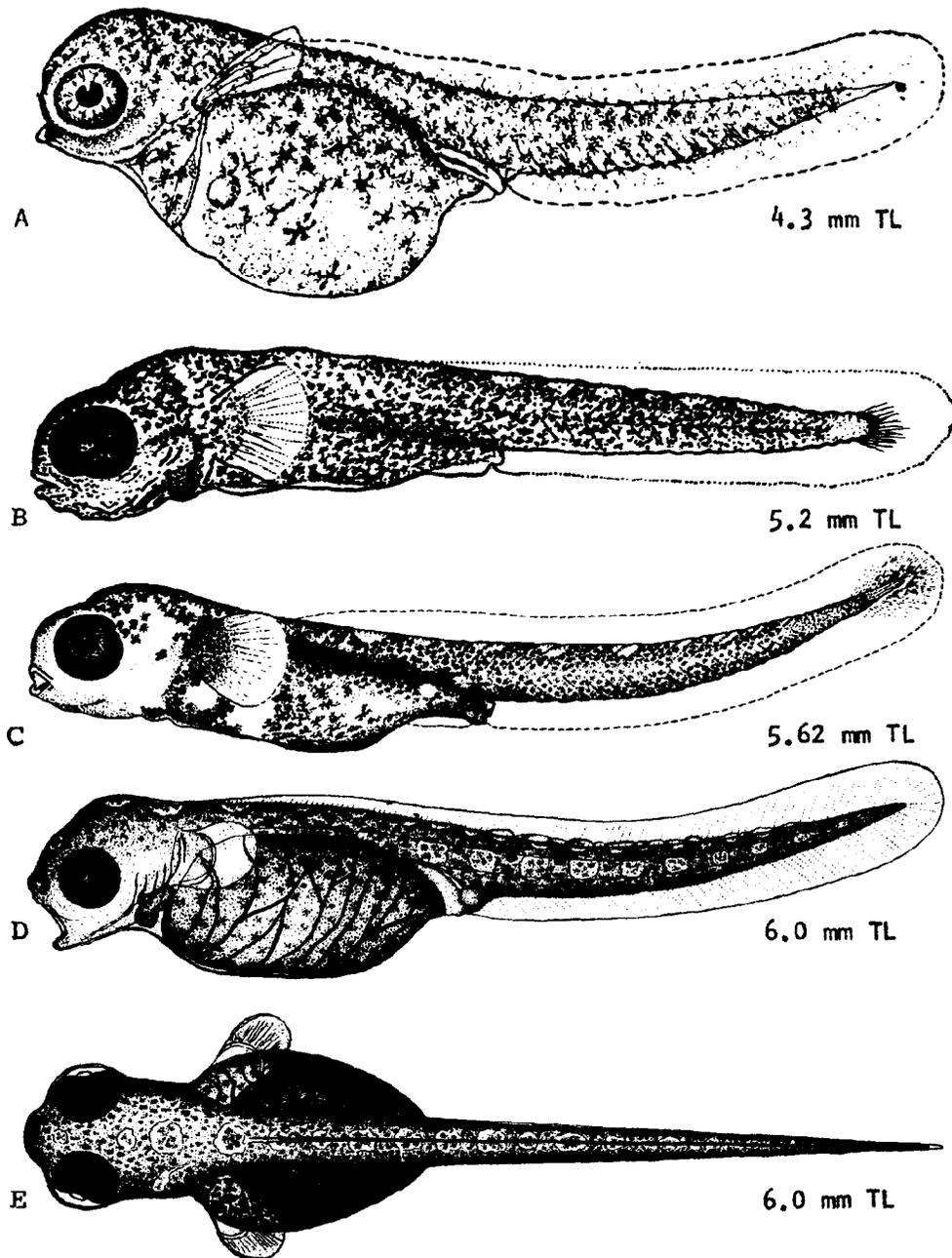


Fig. 205. *Apeltes quadracus*, Fourspine stickleback. A. Yolk-sac larva, 4.3 mm TL, just hatched. B. Yolk-sac larva, 5.2 mm TL, yolk reduced, pattern of regular dorsal light areas developing. C. Yolk-sac larva, 5.62 mm TL, incipient caudal rays developing. D, E. Yolk-sac larva, 6.0 mm TL, recently hatched, yolk still enlarged, prominent dorsal and lateral blotches. (A, Kuntz, A., and L. Radcliffe, 1918: fig. 126. B-C, Original drawings, William L. Dovel. D-E, Ryder, J. A., 1887: figs. 25-26.)

48 hours—tail tip rounded, body segmented, auditory vesicles and otoliths formed.

4 days—large black melanophores over entire surface of embryo and in adjacent extra-embryonic blastoderm; small yellow chromatophores on embryo; ³⁰ heart a simple spherical sinus.

4th or 5th day—primary divisions of brain, cerebral vesicles, optic cups, and pectoral buds formed.

7 days—heart pulsating.

Just before hatching—sides blotched with large brown melanophores, intestine greenish.^{8,18}

Incubation period: 6 days at 22 C.¹⁷

YOLK-SAC LARVAE

Hatching length 4.2–4.5 mm^{17,30} (although a specimen of 6.0 mm TL is described as recently hatched⁸); average 4.3.³⁵ Maximum size described 8.4 mm (WLD).

Body deep, stout (WLD); at 4.3 mm mouth open; yolk initially oval,³⁰ elongate at 5.2 mm; choroid fissure still evident at 5.2 mm, gill rakers at 7.3 mm (WLD). At hatching, reported to have 10–12 lateral sensory organs surmounted by transparent cells and projecting from general level of body. Pectorals well-developed at hatching; ¹⁶ incipient caudal rays at 5.2 mm; preanal finfold obliterated, urostyle oblique at 7.3 mm (WLD). Anus slightly more than one-half length of body from anterior end.³⁰

Pigmentation: Similar to *Gasterosteus aculeatus*, but more heavily pigmented.^{17,28} At hatching (4.3 mm) ground color dark brown, large black chromatophores over entire surface of body and upper half of yolk, yellow chromatophores sparsely scattered over body³⁰ (newly hatched larvae of 6.0 mm are also reported with large brown blotches along dorsal line and on sides⁸). At 5.2–7.3 mm ground color dark olive brown to black with 10 or 11 clear blotches along mid-dorsal line between head and tail (WLD).

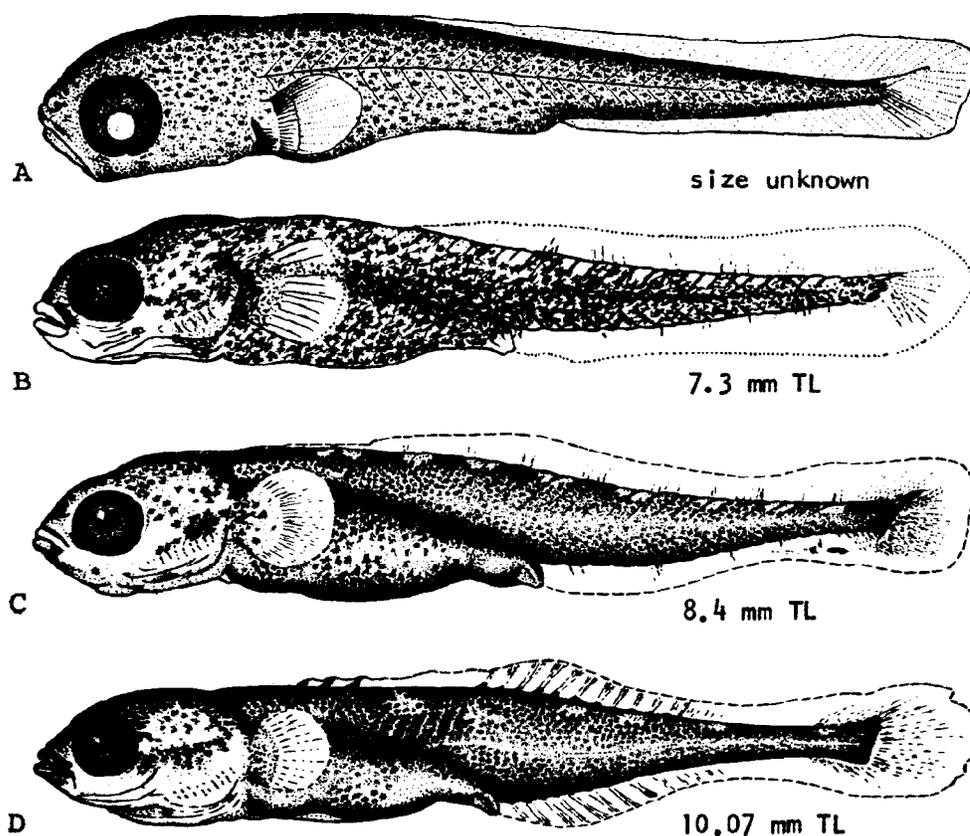


Fig. 206. *Apeltes quadracus*, Fourspine stickleback. A. Yolk-sac larva, size unknown. B. Yolk-sac larva, 7.3 mm TL. C. Yolk-sac larva, 8.4 mm TL, urostyle oblique. D. Yolk-sac larva, 10.07 mm TL, incipient rays and spines in median fins. (A, Agassiz, A., 1887: fig. 27. B-D, Original drawings, William L. Dovel.)

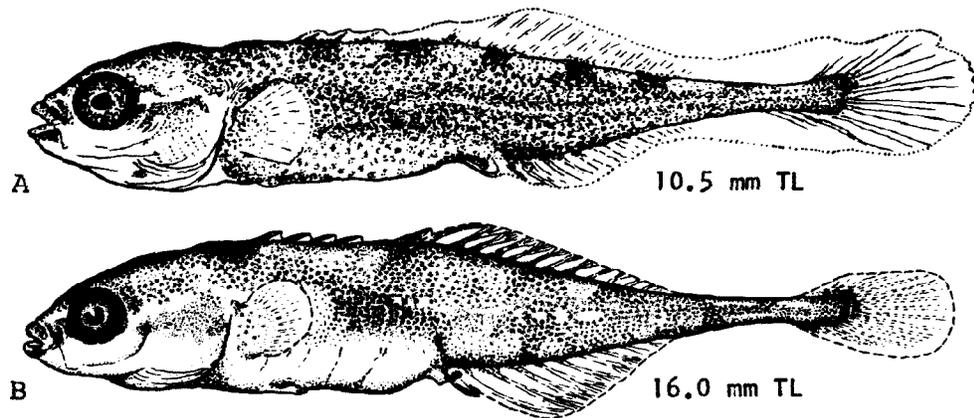


Fig. 207. *Apeltes quadracus*, Fourspine stickleback. A. Larva, 10.5 TL, pelvic buds evident. B. Larva, 16.0 mm TL. (A, B, Original drawings, William L. Dovel.)

LARVAE

Specimens described, 10.5–16.0 mm (WLD) and one of unknown size 1 week old.⁸

At 10.5 mm incipient spines in dorsal, and incipient rays in dorsal and caudal (WLD); at one week tail heterocercal;⁸ pelvis incomplete, other fins complete at 16.0 mm (WLD).

Pigmentation: At 10.5 mm dark olive drab, 7–8 light blotches along mid-dorsal line, guanophores over abdomen (WLD).

JUVENILES

Minimum length, unknown.

Pigmentation: Young with 4–5 transverse bands of brown color.^{12,24}

AGE AND SIZE AT MATURITY

Probably mature at end of first year; males 27 mm, females 33 mm.³⁵

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Gasterosteus aculeatus Linnaeus, Threespine stickleback**ADULTS**

D. II to V,⁸⁰ 6–13; ²⁹ A. I,^{42,75} 6¹²–13 (minimum of 4 experimentally); ¹⁷ C. 5–7 + 6–7; ²⁹ P. 9–11^{61,89} (8 experimentally); ¹⁷ V. I,^{42,75} lateral plates 0⁴⁴–37; ¹⁰³ vertebrae 29⁶¹–33; branchiostegal rays 3–4; ²² gill rakers 12⁷⁷–25; ⁴⁴ average number of gill rakers on first arch (various populations), outer 19.46–20.59, inner 14.86–16.35.⁶¹

Proportions expressed as times in TL: Depth 4.0⁹⁶–5.0,⁹⁵ head 3.3⁹⁸–4.2.⁹⁵

Body moderately slender, spindle-like, tapering to slender caudal peduncle,^{12,34} deeper in females than males; ⁶⁶ head short; ¹⁰⁸ snout somewhat pointed.¹² Mouth rather small, oblique, slightly superior; maxillary failing to reach eye.^{96,108} Teeth in both jaws sharp, relatively large; ^{95,101} opercle finely serrate; ¹⁰⁸ innominate bones united, forming lanceolate plate on middle of abdomen between and behind pelvises.^{43,95} Pelvises sometimes absent;^{2,6} spines erectile; ³⁴ anal spine small, detached; ⁹⁷ posterior edge of dorsal and ventral spines serrated; ⁴² anal origin well back of dorsal origin; tail moderately forked.^{12,97}

Pigmentation: Olive green,⁷⁵ greenish brown,⁹⁷ brown,¹² dark grayish,¹⁰⁸ silver,^{103,122,134} silver-white,⁸⁰ blue,⁹⁷ bluish black,^{38,108} or black¹⁰³ above; top of head and back sometimes finely punctuated with black; ¹⁰⁵ white,¹⁰⁹ silvery white,³⁸ silver^{96,108} or light below; ¹² sides paler than dorsum, silvery or yellowish.^{62,78} Dorsum and sides plain¹⁰³ or with indefinite brown cross bars and transverse blotches; ^{12,96} sometimes with irregular greenish blue stripes or bands.³⁸ Fins generally pale, but with pectoral rays outlined by small black dots,¹² base of caudal sometimes with black bar,^{96,108} and anal fin membranes sometimes red.⁹⁵ Color of both sexes modified during spawning.⁷⁹ Spawning males bluish white,⁴ blue,⁵ greenish blue,⁸⁶ green,¹⁰² gray or creamy brown above; bright vermilion or scarlet red^{38,88,109,124,129} to yellowish salmon¹² below, or red tinted over with yellow;⁸² rarely jet black throughout.¹¹⁹ Ventral nuptial pigmentation first developed in region of branchiostegals,³⁸ variable in extent, sometimes limited to throat⁸⁶ (possibly, however, outside spawning season⁸⁸), and at other times in mouth cavity, on throat, cheeks, opercles, pelvic plate, belly, and sides up to and sometimes beyond lateral line.^{63,80} Venter sometimes with large indefinite greenish blue iridescent spots over gonads.⁸² Iris iridescent blue-green,^{12,13} emerald,⁸⁸ sky blue,^{81,121} or silver-blue. Black pigment in dorsal and anal fins.⁸⁶ Nonspawning females brownish green above, white below.⁸⁵ Spawning females reddish throughout except for top of head, or brownish above with transverse spots or bands and copper yellow or brassy reflections.^{80,95,97}

Maximum length: 110 mm or larger,^{80,117} with size diminishing southward.⁷

DISTRIBUTION AND ECOLOGY

Range: Fresh and salt waters of northern hemisphere.²⁶ In eastern North America, the Strait of Belle Island, Newfoundland,⁹⁷ and the Hudson Bay region,^{34,58} west along the Arctic Islands of Canada;¹¹⁵ south through Manitoba⁵⁸ to vicinity of Lake Ontario and Atlantic coast to lower Chesapeake Bay^{34,97} or, possibly Cape Hatteras;^{80,83} in western North America from western Alaskan Peninsula south to Rio Tijuana, Mexico.⁸³ Greenland^{52,76} and Iceland.⁵⁵ In Europe, northern Norway and Sweden; the Baltic and North Seas; England and Ireland; the Hebrides, Orkneys, and Shetland Islands; Faroe Islands; all of central Europe except the Alps;^{30,83,102} south to Spain and Portugal; along the Mediterranean to Sardinia, Italy,⁸³ Turkey,⁵⁷ and Syria; the Black Sea and Sea of Azov;⁸³ along Arctic Ocean from Murmansk and Novaya Zemlya⁵³ to Bering Straits.⁸⁰ In North Africa once recorded from Algiers, but this population no longer extant and possibly based on introduction.^{76,89} In western Pacific and Asia from Aleutian Islands and islands of central Bering Sea to Kamchatka, the Juril Islands, Japan, Korea^{66,83} and western China.²⁶

Area distribution: Maryland;⁴³ Virginia;⁹⁶ Delaware;^{25,107} the Delaware River estuary;⁹² seaside of Maryland and Virginia;^{15,96,131} north in Chesapeake Bay to Cape Charles City and Hampton, Virginia.⁹⁶

Habitat and movements: Adults—occupy a wide variety of habitats from the open sea to inland waters up to at least 700 km from coast,^{3,32,97,98} and with different populations apparently occupying different habitats.^{125,134} Usually in shallow water.¹² In freshwater in rivers, brooks,^{38,61,75} streams (at elevations of up to 183 m),^{92,75} canals,⁴⁸ ditches,⁷⁰ landlocked lakes,^{8,76} ponds,²⁴ open glades covered with duckweed,¹⁵ paddy fields,⁶⁶ warm springs, peat evacuations (to which eggs were probably carried by flooding), and artesian wells to depths of up to 128 m.^{23,80} Sometimes stranded in large numbers in temporary forest pools.⁶⁰ In streams in dense vegetation over mud bottom or in moderate current over sand and silt.^{77,90} In coastal areas found in creeks and ditches of tidal marshes; brackish ponds; lagoons;^{75,97} inlets;⁸⁸ tide pools;⁸⁴ *Ulva* beds;⁷⁷ rock pools;¹²⁶ and along densely vegetated shores.^{53,97,98} May live pelagically in “neighborhood of land,”¹¹⁰ or be “truly pelagic” as in White Sea.⁸⁰ Recorded in open sea associated with floating eelgrass or rockweed.^{97,105} Maximum distance from shore, 6.4 km.¹⁰⁵ Maximum depth, 24 m.¹² Maxi-

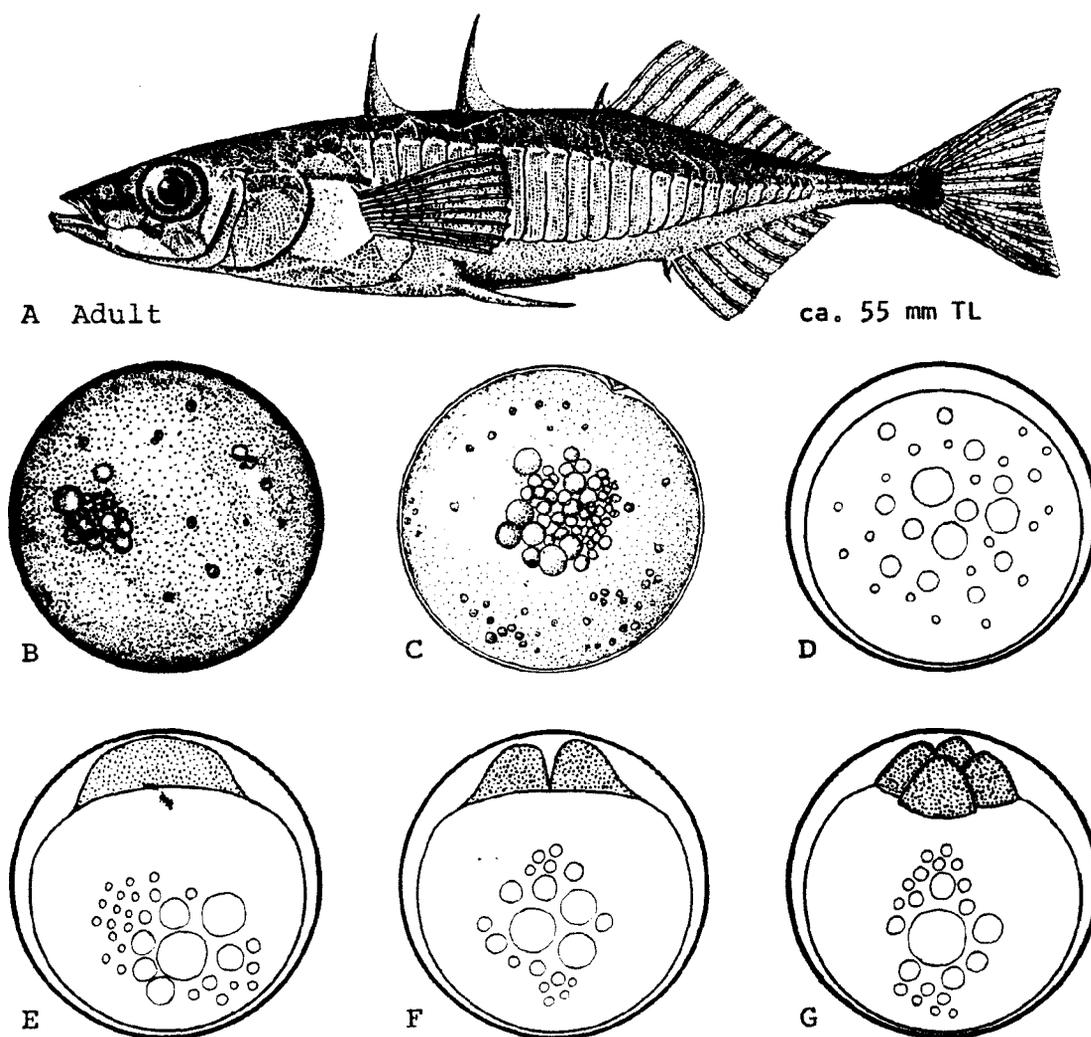


Fig. 208. *Gasterosteus aculeatus*, Threespine stickleback. A. Adult, ca. 55 mm TL. B, C. Mature unfertilized eggs. Note variation in number of oil globules, and micropyle in figure C. D. Egg immediately after fertilization, perivitelline space formed. E. Blastodisc formed, 1 hour and 45 minutes. F. 2-cell stage, 2 hours and 30 minutes. G. 4-cell stage, 3 hours. (A, Hildebrand, S. F., and W. C. Schroeder, 1928: fig. 92. B, Vrat, V., 1949: fig. 1. C, Kuntz, A., and L. Radcliffe, 1918: fig. 113. D-G, Swarup, H., 1958: figs. 1-4.)

imum salinity, experimentally survived 80 ppt for several days,⁸⁷ extremely euryhaline and capable of withstanding wide salinity changes.⁵⁰ There is tendency for northern populations to be more marine,⁷ southern populations to be more fluvial.¹ At least some populations make definite anadromous or inshore migrations in late winter or spring from coastal waters to rivers;^{46,48,76,91,123} from rivers to streams;³⁶ or from deeper to more shallow waters, as in the White Sea.⁸⁰ In Holland upstream in late January to late May, downstream before October or possibly as late as November;⁴⁹ in Germany upstream in March, April, and May, downstream in September;⁸³ in Oslofjord upstream in May;²¹ in White Sea inshore

first of June, offshore middle of July to early August;⁸⁰ in England upstream late April to early May, downstream during or before July^{49,78} or as late as autumn,⁷⁹ in Japan upstream in February or end of March.^{83,89,86} Migrations may take place one month prior to spawning;⁴⁹ males may precede females;⁷⁸ and individuals may return to specific spawning stream. There is high post-spawning mortality in some populations,^{48,70,77} apparently none in others.^{40,76} Mass invasions of *Gasterosteus* have been reported in lakes in Poland.⁶¹ Large schools form in late autumn or early winter¹⁰⁴ and may remain together in deeper water during winter, possibly in estuaries, inlets, canals, or ditches.^{78,97,104}

Larvae—during first 2 hours lie on side, but capable of swimming toward surface; after 2 hours can remain upright.^{13,16} Remain in nest for 1⁷²–2 days, and herded by mouth by male parent.^{4,78,82,94,106,124} Positively phototrophic.¹³³

Juveniles—in schools soon after leaving nest and while still under influence of male parent.⁷⁸ Young reported from weed beds in rivers;⁵ also in streams, lakes, and paddy fields among aquatic vegetation;^{38,134} and in brackish water ditches;⁴⁸ freshwater lagoons,¹²⁷ and coastal rockpools.¹²⁶ Specimens with average SL of 16 mm in 2.4 m of water 0.2 km from nearest vegetation.⁴⁷ Schools of up to 500 individuals reported in canals and ditches.^{82,106} In salt water remain in pelagic schools until 25 mm long, then near bottom among aquatic vegetation.⁸⁶ In Japan (and other areas) juveniles assemble in large schools in summer and early fall and migrate toward sea; in at least some Japanese populations the seaward migration follows scute formation at 22–27 mm TL; ¹¹⁸ remain in estuaries or spread out along coast during winter; ^{76,91} downstream movement of young begins at length of 18 mm in Elbe River.⁸³

SPAWNING

Location: Both brackish and freshwater,^{8,86,97} on or near bottom ^{56,77,81} in water 100 to ca. 500 mm deep, ^{4,52,77,100} in coves, bays, rivermouths,⁷⁰ rivers, small streams,^{13,77} ditches,^{48,49} lakes,¹² paddy fields,³⁸ and possibly flooded meadows ⁷⁷ over bottoms of sand ⁸¹ or mud.⁷⁷ Often in open water, but usually near or among aquatic plants, such as *Oenanthe*, *Eleoidea*, *Potamogeton*, *Nuphor* and *Carex* and possibly *Zostera*, or stones in standing water or in moderate current (up to 6 cm/second).^{52,77,94,128} Spawning activity has been observed in polluted water.⁵¹ Maximum recorded salinity, 7.8 ppt,⁴⁸ but nest building without spawning has been observed in the North Sea, and eggs have been produced in “Nordseewasser” (although whether in nature or under laboratory conditions is not clear), but hatching may not have occurred.⁷⁰

Nest: Built and guarded by male; variable in shape, tubular, circular, or flat,^{3,46,81,93} usually built over pit ⁶⁴ and varying in size from 80–ca. 100 mm long, 30–50 mm wide and 10–20 mm deep ^{35,81} or possibly smaller; ¹⁰⁹ equipped with single entrance ⁴ or both entrance and exit opening; ¹³ some made of weeds (preferably thread algae),⁴ others of a mixture of plant fibre, sand, and gravel; ⁸³ and others exclusively of sand grains; building material held together by substance secreted by male kidney; ^{4,13,132} nest sometimes weighted down with pebbles ⁸⁷ and sometimes partially buried in substrate.⁸⁸ In one Canadian study the mean inter-nest distance was 730 mm.¹³⁰ Egg laying without nest building has been observed over aquatic plants, among rocky crevices and other “craggy spots,”⁵² and in holes in sand.¹²

Season: Late February through September throughout range. Mystic River, Connecticut, ripe adults May to July in upper river, June and July in lower; ¹¹³ Woods Hole, Massachusetts, May to end of July; ^{47,97,99} Canada, late February or March to September ^{77,128} (April to September in British Columbia ³⁴); California, breeding colors and maturing eggs in late February, nest activity as early as February 13, eggs available until middle of August; ¹³ Alaska (Kodiak Island), ripe females May 23 to August 3; ¹² Greenland, June to July; ¹³ Ireland, continues to mid-September; ⁷⁵ England, maturation begins August or September,³⁶ ripe testes in January,³¹ spawning April to mid-August; ^{24,29,36,65} (Note, however, that in England some males have well-developed testes and red throats throughout year ¹²⁰); Scandinavia, March to July or later; ^{13,86} Netherlands, April to July,⁴⁹ with two spawning peaks; ⁴⁵ France, mid-March to end of July.^{38,69} Male gonads may be ripe throughout year in some populations, but nesting behavior will not occur in nature outside normal spawning period; ⁴⁹ can be induced to spawn almost throughout year under laboratory conditions.¹⁶ Natural spawning period lasts average of 3–4 months.⁵²

Temperature: 20 C in experimental tanks; ⁴⁶ nuptial colors at 17–20 C; ⁸⁵ nest building experimentally induced at 5 C; gonads developed at minimum of 4 C.⁴⁸

Time: Not definitely stated. Nest building observed during daylight hours (by implication),⁵³ spawning possibly at night.²⁸

Frequency: 5–6 times during 60–90 day period.^{82,117}

Fecundity: Mature eggs 50⁴–292⁷⁷ (a minimum of 3⁸⁴ is questioned, JDH); averages “usually less than 100,”²⁶ 105, and 241, varying from population to population.⁷⁷ Ovarian eggs 177–567, mean 320.²⁷ One female may produce 400–500 eggs (presumably mature) in 20 days.⁸²

EGGS

Location: Demersal,^{11,14} deposited in adherent clusters in nests, holes in sand, or rocky crevices, or scattered at random over aquatic plants; ^{17,52} 20⁹⁰–1100⁸² eggs per nest; eggs definitely adhere to one another, but may or may not adhere to nest or foreign objects; ^{13,97} egg masses surrounded by mucus.¹⁶

Ovarian eggs: Yolk formation evident at diameter of 0.18 mm; ²⁴ diameter at maturity 1.03¹⁸–1.50 mm; ⁹⁰ micropyle single.¹⁶

Freshly stripped unfertilized eggs: Irregular in form; ⁸⁹ diameter 1.10¹³–1.76 mm, mean 1.65; ²⁷ color varies, presumably with diet or physiological state of female; in fresh caught fish, light orange, in captive females which have been fed tubifex worms, colorless.¹⁶

Fertilized eggs: Spherical, but somewhat flattened at

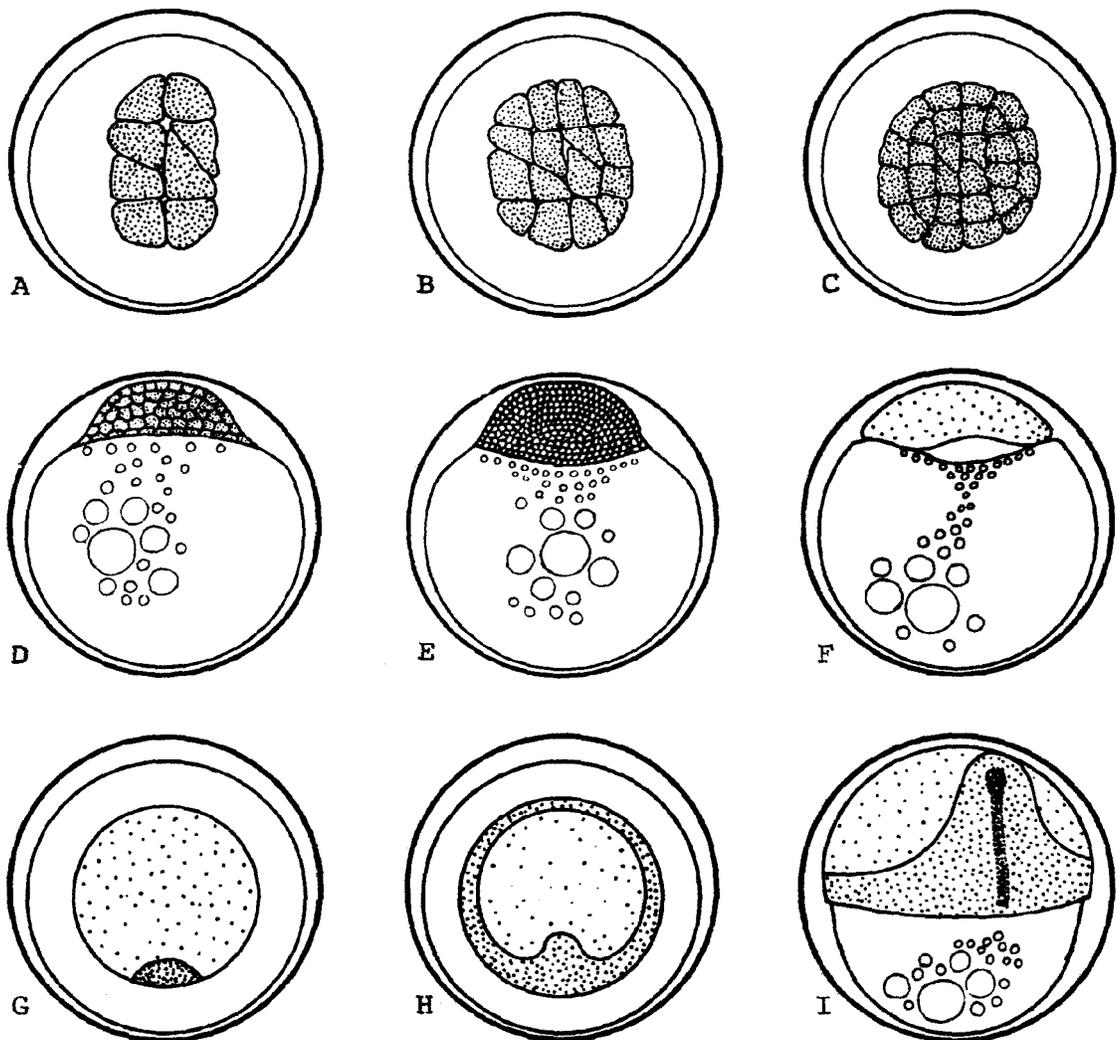
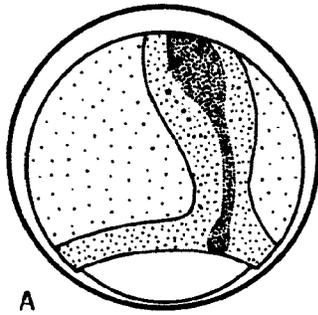
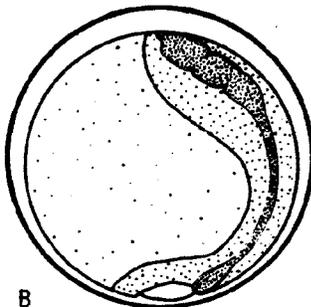


Fig. 209. *Gasterosteus aculeatus*, Threespine stickleback. A. 8-cell stage. B. 16-cell stage, 3 hours and 45 minutes. C. 32-cell stage, 4 hours. D. Early morula, 6 hours. E. Late morula, 10 hours, periblast formed. F. Blastula, 15 hours, blastocoele formed. G. Beginning of invagination (viewed from above), 22 hours. H. Germ ring formation (viewed from above), 26 hours. I. Germ ring one half over yolk, 30 hours. (A-H, Swarup, H., 1958: figs. 5-13.)

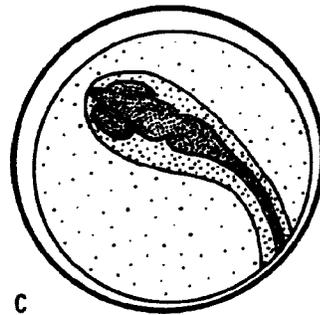
Fig. 210. *Gasterosteus aculeatus*, Threespine stickleback. A. Germ ring over 3/4 egg, neural plate formed, 36 hours. B. Small yolk plug, brain divisions evident, 42 hours. C. Closure of blastopore, 50 hours. D. 6-7 somites, optic vesicles formed, three blocks of mesodermal tissue formed on both sides of head, 60 hours. E. Lens, brain vesicles, otic capsule formed, Kupfer's vesicle forming, 70 hours. F. Otoliths, olfactory lobes formed, 88 hours. G. Margin of eye pigmented, movement evident in tail, 106 hours. Circulation established, gill slits evident, melanophores on dorsal side of body and adjacent yolk sac, 130 hours. I. Pectoral buds formed, melanophores over entire eye and body, 144 hours. J. Ventricle of forebrain closed, 156 hours. K. Mouth formed, choroid fissure closed, pectoral fins vibratory, 168 hours. L. Hatching stage, hatching occurs head first, 199 hours. (A-L, Swarup, H., 1958: figs. 14-25.)



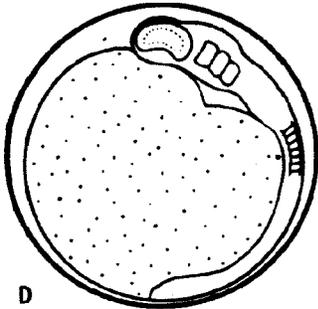
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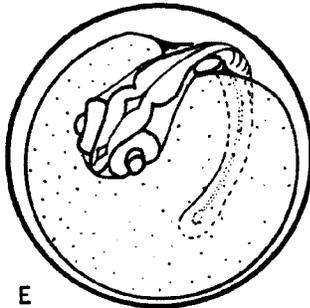
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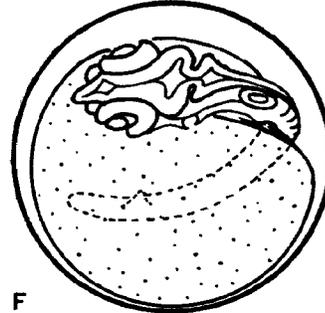
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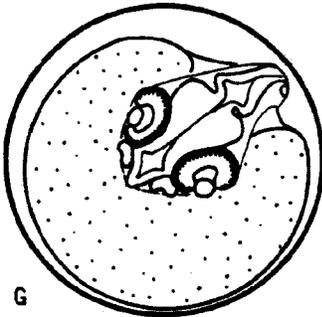
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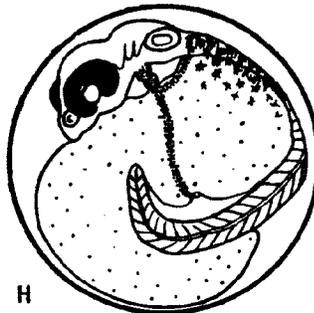
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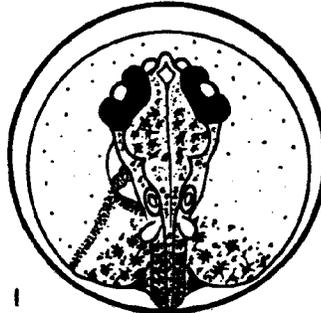
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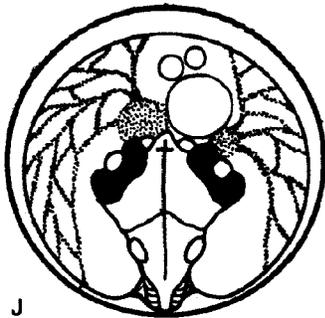
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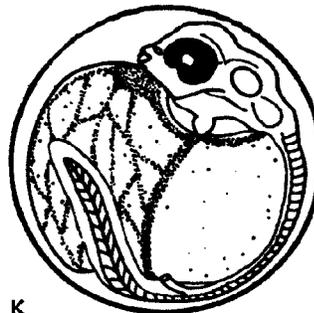
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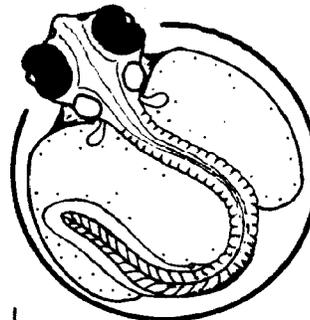
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point of attachment to each other; ^{13,86,99} diameter 1.0 ⁵²⁻1.9 mm; ¹³ published average diameters, "a little less than 1.5 mm," ¹¹¹ 1.67, and 1.71 mm; ⁵⁶ color variable, initially pale yellow to light tan, becoming more transparent as perivitelline space develops, later light yellow-brown, then increasingly opaque and dull white. ^{13,14,16,99,111} Egg membrane tough; ¹⁰ single-layered; ⁹ very thin ^{11,56} to quite thick ^{16,99} (stated thicknesses vary from 0.0035-0.03 mm); smooth, but with netted pattern under magnification. Eggs adhesive to one another, but adhesiveness to other objects apparently variable. ^{13,97} Yolk pale yellow, ⁵⁶ transparent. ¹⁰ Oil globules unequal, ⁹⁹ maximum diameter 0.5 ⁵⁶-0.73 mm, ¹³ capable of coalescing into larger sizes during development. Number of oil globules 5 ⁵⁶⁻25 or more. Larger globules usually arranged in single group on one side of yolk, smaller globules scattered throughout yolk and on yolk surface. ^{13,99}

EGG DEVELOPMENT

Development at 17 C + 0.6 C (the Vrat series): ¹³

Ca. 1 hour, 30 minutes.	Blastodisc formed as lenticular cap.
3 hours.	First cleavage begins, cleavage furrow does not cut completely through yolk.
Ca. 4 hours.	2nd cleavage, meridional and at right angles to first.
Ca. 4 hours, 40 minutes.	3rd cleavage.
Ca. 5 hours, 15 minutes.	4th cleavage.
9 hours, 40 minutes.	Multicellular blastoderm with sharply defined edges.
11 hours, 40 minutes.	Blastocoel well-developed.
13 hours.	Migration of germ ring begins.
Ca. 25 hours, 20 minutes to 26 hours, 20 minutes.	Kupffer's vesicle appears.
30 hours.	Eyes outlined, Kupffer's vesicle at maximum development, 6 somites, heart beating.
35 hours.	Scattered melanophores on dorso-lateral surfaces.
38 hours.	12 somites, embryo around 3/4 yolk, pigmentation on dorsal side accentuated with numerous black and brown melanophores and yellow xanthophores, pigment spreading to cephalic region, eye somewhat pigmented.
57 hours.	Otoliths appear.
59 hours.	Embryo slightly exceeds circumference of yolk; brain lobes visible,

yolk circulations well established, heavy pigment on head and sides of yolk.

83-107 hours.	Finfold, notochord evident; movement established in tail.
140 hours.	Ready to hatch (hatching takes 30 minutes). ¹³

Development at 18-19 C (the Swarup series): ¹⁶

30 minutes.	Blastodisc forms by waves of contraction from vegetal to animal pole.
2 hours, 30 minutes.	2-cell stage.
3 hours.	4-cell stage.
3 hours, 30 minutes.	8-cell stage.
3 hours, 45 minutes.	16-cell stage.
4 hours.	32-cell stage, cells begin to pile up into 2 layers at center of blastoderm.
6 hours.	Early morula, area of blastoderm equal to that of original blastodisc.
10 hours.	Late morula, periblast formation.
15 hours.	Blastocoel formed, incipient embryo evident as thickening on one side of blastoderm.
22 hours.	Invagination begins.
26 hours.	Germ ring formation.
30 hours.	Germ ring extends over yolk, embryonic axis thickened anteriorly.
36 hours.	Blastoderm over 3/4 of yolk; embryo no longer triangular, now elongate.
42 hours.	Embryo narrows transversely, brain divisions evident, blastopore formed.
50 hours.	Blastopore closed, optic lobes evident.
60 hours.	Optic vesicles, 6-7 somites formed.
70 hours.	Optic cups, lenses, otic capsules, pericardium, and Kupffer's vesicle formed.
88 hours.	A deep constriction between mid- and hindbrain, otoliths formed, olfactory lobes developing, heart beat established.
106 hours.	Olfactory lobes cup-shaped, choroid fissure narrow, pigment in margin of eye, movement established in tail.
130 hours.	Auricle, ventricle, sinus venosus developed; gill slits visible; yolk circulation established; melanophores on dorsal side of body and adjacent yolk.
144 hours.	Head noticeably shorter and broad-

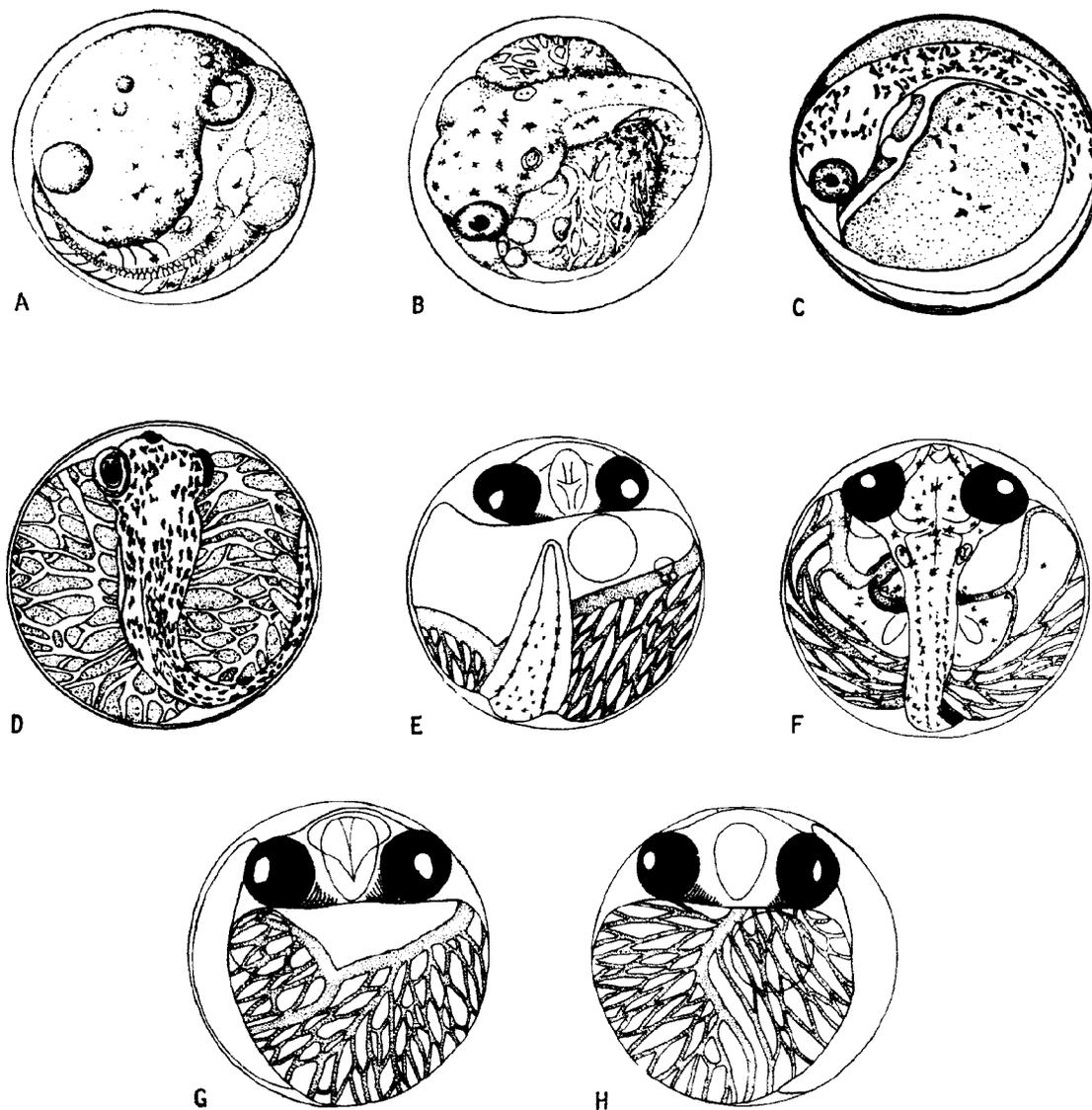


Fig. 211. *Gasterosteus aculeatus*, Threespine stickleback. A. Late embryo of different series, 68 hours after fertilization, otoliths visible. B. Embryo of same series, 4 days after fertilization. C. Embryo ca. 70 hours old, showing early development of vitelline circulation. D. Embryo 4 days old with well established vitelline circulation. E. Embryo 4 days old, ventral view. F. Advanced embryo, pectoral buds established. G. Same as F, ventral view. H. Embryo at the moment of hatching, ventral view. (A, B, Kuntz, A., and L. Radcliffe, 1918: figs. 117-8. C, D, Vrat, V., 1949: figs. 11, 12. E-H, Anthony, R., 1918: figs. 20-23.)

	er; pectoral buds developed; melanophores over entire eye, body, and much of yolk.	Development at unspecified temperature (Moenkhaus series): ¹¹²
156 hours.	Heart bent upon self.	3 hours, 2-cell stage.
168 hours.	Mouth formed, choroid fissure closed, tail fin established, movement in pectoral fins.	55 minutes.
		4 hours, 4-cell stage.
		25 minutes to 4 hours,
192 hours.	Ready to hatch. ¹⁶	40 minutes.

4 hours, 50 minutes to 5 hours, 5 minutes.	8-cell stage.
5 hours, 30 minutes.	16-cell stage.
6 hours, 10 minutes.	32-cell stage.
21 hours, 20 minutes.	Late segmentation, disc beginning to spread.
23 hours, 45 minutes.	Germ ring established.
26 hours, 5 minutes.	Embryonic shield formed.
31 hours, 5 minutes.	Blastoderm over 1/2 yolk.
42 hours, 35 minutes.	Blastopore closed.
56 hours, 5 minutes.	Embryo well-developed, eyes and brain established. ¹¹²

Development at unspecified temperature (Kuntz and Radcliffe series):⁹⁹

24 hours.	Embryo well differentiated, blastopore closed.
68 hours.	Embryo nearly equal to circumference of yolk, head relatively broad, body tapering gradually to posterior end, circulation established in extraembryonic blastoderm. Small melanophores on dorsal surface of anterior region of trunk and in adjacent areas of extraembryonic blastoderm.
4 days.	Yolk greatly reduced and with well-developed network of blood vessels over surface, chromatophores larger, more numerous, and over entire surface of embryo, in adjacent extraembryonic blastoderm, and in series along ventrolateral aspects of body posterior to anus. ⁹⁹

Miscellaneous notes on development: Perivitelline space will not develop in unfertilized eggs;^{10,77} perivitelline space complete in 3 minutes; bipolar differentiation apparently variable, complete in some eggs in 15 minutes at 20 C and in others in 30 minutes at 20–21 C; cytoplasmic contractions accompany blastodisc formation each takes ca. 60 seconds; activation of egg complete in ca. 60 minutes.⁴⁰ Undifferentiated germ cells developed in genital ridge in front of cloaca in 3.0 mm embryo.²⁴ Toward end of development yellow pigment, as well as melanophores found on both body and yolk sac.⁵⁶ Hatching normally head first,^{13,16} but may be tail first or head and tail simultaneously.⁵¹

Incubation period: 4 to ca. 40 days, depending on temperature⁵⁹ (and possibly other factors, JDH); at 6–7 C, ca. 40 days;⁵⁹ at average of 8.8 C, average of 15 days, 8 hours;⁵² at 9–16 C, eyed in 9 days, hatch in 14;¹² at 17 + 0.6 C ca. 5 days, 20 hours;¹³ at average of 17.8 C, average 8 days, 15 hours;⁵² at 18–20 C, 6–8 days;^{16,65,83} at 26 C, 4–5 days;⁵⁹ at "laboratory temperature," ca. 6 days.⁹⁹ Effects of environment on incubation: mutually exclusive adaptive peaks with regard to effects of temperature and salinity can be demonstrated for eggs of salt and freshwater forms.^{29,74} Eggs from southern Europe develop more rapidly at higher temperatures (12–25 C) than eggs from northern Europe, more slowly at lower temperatures (8 C).⁶⁸ Optimal (normal) temperature range, 15–19 C.¹¹ Although hatching may not occur naturally in seawater,^{13,70} eggs have developed "fairly well" in experimental tanks at salinity of 44 ppt.⁶⁸

YOLK-SAC LARVAE

Hatching length 3.0 mm¹⁶ or possibly smaller (some specimens of this size are 6 days old)⁵² to ca. 7.0 mm.⁶⁶ Size at end of stage 12 mm.³⁹ Duration of stage 3^{97,98} to 7 days,⁹⁹ depending on temperature, ca. 4 days at 18–19.¹⁶

Body relatively deep, head either closely attached to yolk or free at hatching; mesencephalic flexure conspicuous; yolk mass deeply oval at hatching^{13,16} (in a specimen 36 hours old, deeper than long⁷¹) or elongate,⁵⁹ half absorbed in 24 hours (ca. 4.0 mm);¹⁶ yolk with single large oil globule;⁵⁶ mouth open¹⁶ or not open and evident only as slight depression at hatching;¹³ choroid fissure still evident at 24 hours (ca. 4.0 mm);¹⁶ auditory vesicles visible for at least 86 hours;⁷¹ anus slightly more than half length of body from anterior end at hatching; gas bladder evident in about 1 week, concurrent with absorption of yolk.^{56,99} Urostyle oblique, extending nearly to edge of caudal fin at 8.0 mm;⁷³ origin of dorsal finfold about over middle of yolk;³⁹ caudal fin initially rounded, more or less heterocercal by end of stage, incipient ventral lobe evident at hatching, with incipient rays by end of stage.^{13,73}

Pigmentation: At hatching body and finfold transparent;^{16,39,51,106} trunk thickly covered with black melanophores, yellow xanthophores, and guanophores; adjacent parts of yolk with yellow¹³ or black⁹⁹ pigment; body pigment may form continuous row of clusters in caudal region;⁵⁶ melanophores may be arranged in discrete cross bands on back;⁵⁹ melanophores especially prominent on dorsal half of body, also along course of intestine and ventral contour of body (particularly near base of ventral finfold), over region of air bladder, and, sometimes, on upper, anterior, and lower surfaces of yolk sac.^{56,99} At 1 day body no longer transparent except for lower jaw.⁵¹ At 3 days (6.2–6.5 mm) generally yellowish, chromatophores more numerous,⁹⁹ dark brown spots developed on

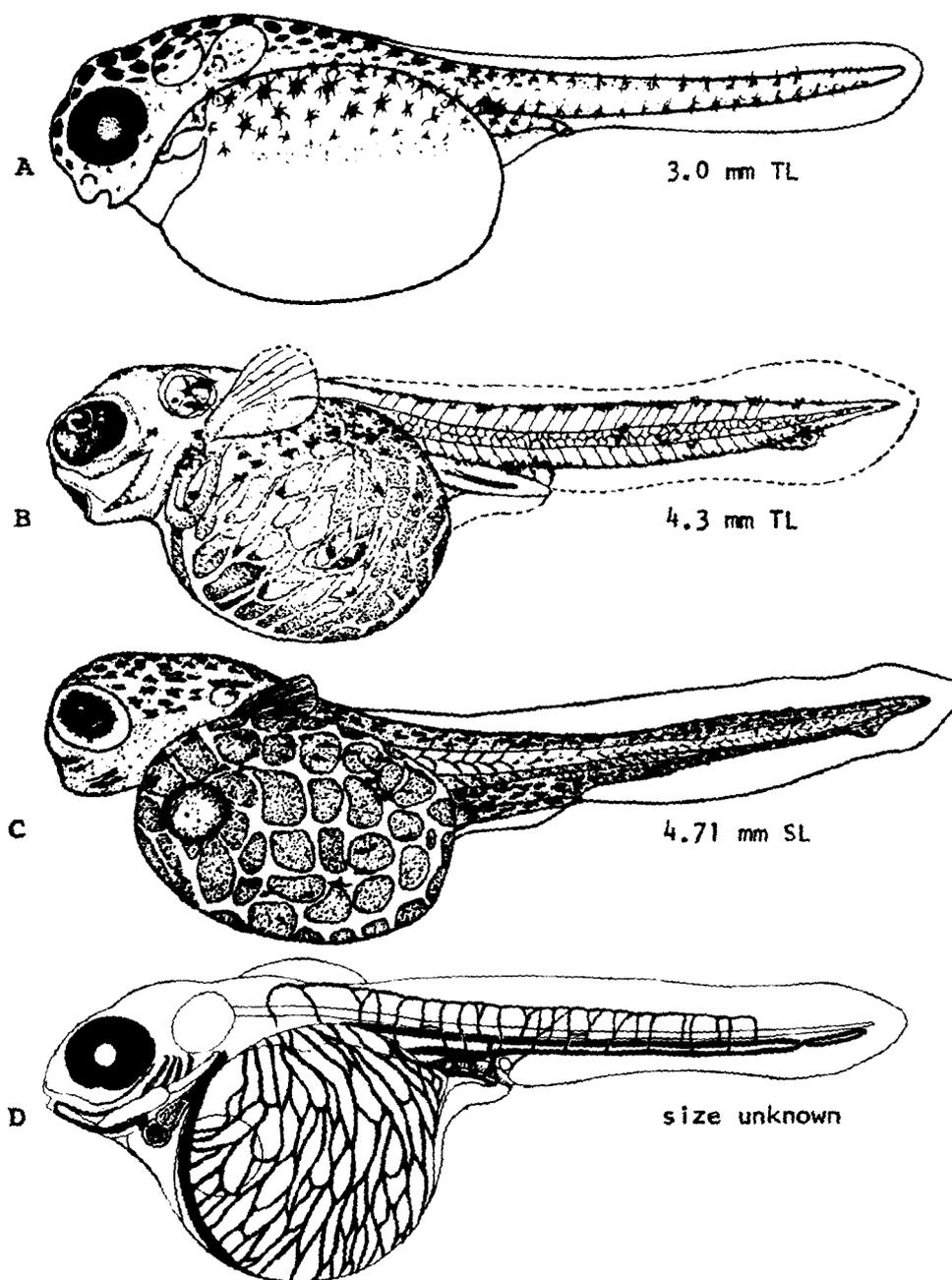


Fig. 212. *Gasterosteus aculeatus*, Threespine stickleback. A. Yolk-sac larva, just hatched, 3.0 mm TL. B. Yolk-sac larva, just hatched, 4.3 mm TL, showing advanced development of pectoral fin. C. Yolk-sac larva, just hatched, 4.71 mm SL. D. Yolk-sac larva, size unknown, showing circulatory pattern, 36 hours old. (A, Swarup, H., 1958: fig. 26. B, Kuntz, A., and L. Radcliffe, 1918: fig. 119. C, Vrat, V., 1949: fig. 13. D, Anthony, R., 1918: fig. 28.)

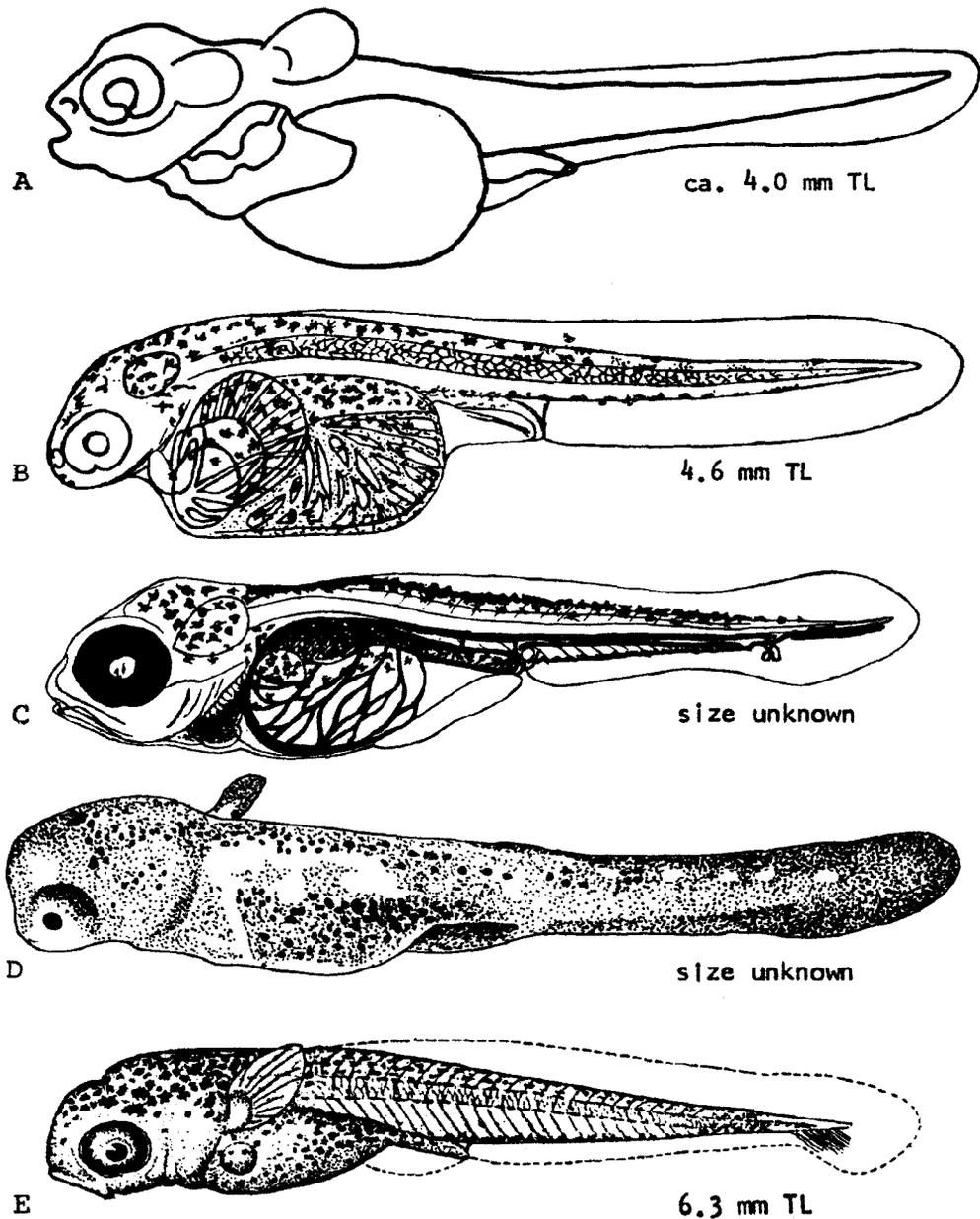


Fig. 213. *Gasterosteus aculeatus*, Threespine stickleback. A. Yolk-sac larva, ca. 4.0 mm TL, yolk greatly reduced. B. Yolk-sac larva, 4.6 mm TL. C. Yolk-sac larva, size unknown, 86 hours. D. Yolk-sac larva, size unknown. E. Yolk-sac larva, 6.3 mm TL. (A, Swarup, H., 1958: fig. 27. B, Ehrenbaum, E., 1905-1909: fig. 115. C, Anthony, R., 1918: fig. 29. D, Leiner, M., 1960: fig. 3, Joan Ellis, delineator. E, Kuntz, A., and L. Radcliffe, 1918: fig. 120.)

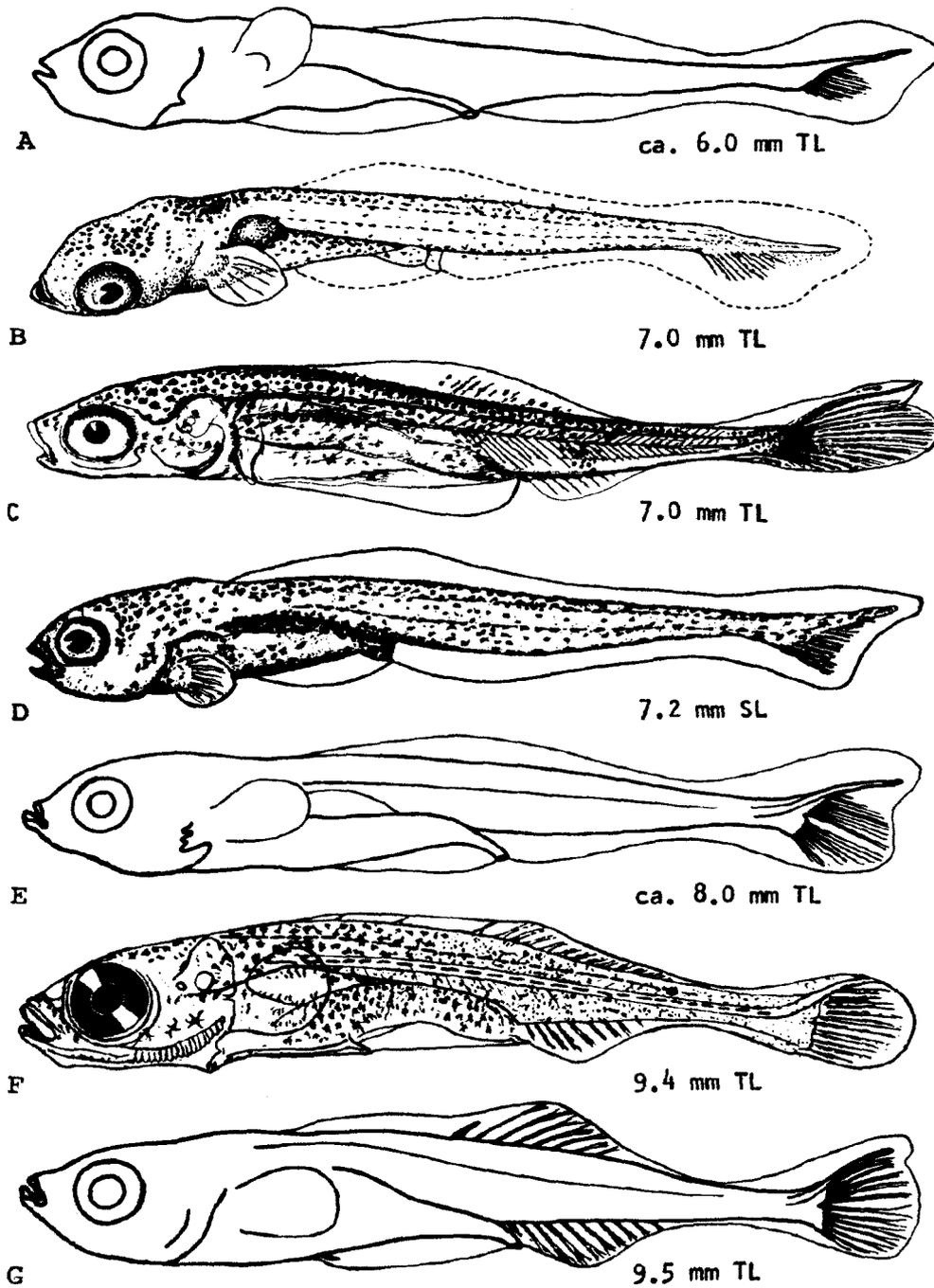


Fig. 214. *Gasterosteus aculeatus*, Threespine stickleback. A. Larva, ca. 6.0 mm TL, 4 days old. B. Larva, 7.0 mm TL. C. Larva, 7.0 mm TL. D. Larva, 7.2 mm SL, 6 days. E. Larva, ca. 8.0 mm, 9 days. F. Larva, 9.4 mm TL. G. Larva, 9.5 mm, 16 days. (A, E, G, Swarup, H., 1958: figs. 28-30. B, Kuntz, A., 1882: pl. 9. D, Vrat, V., 1949: fig. 14. F, Ehrenbaum, E., 1905-1909: fig. 115.)

head. At 4-6 days entire body cinnamon brown; melanophores darker, concentrated. At 7 days incipient anal rays brown, lower jaw still transparent.⁵¹

LARVAE

Size range, 5.0 (based on age of 10-12 days and presumed lack of yolk, JDH) to ca. 15.0 mm.³⁹

Body slender, head sharply defined. Gill covers developed, mouth functional at ca. 6.0 mm; snout elongate at ca. 8.0 mm; lateral line evident at ca. 8.0 mm; gas bladder developed as enlargement on dorsal side of gut in some specimens as small as ca. 6 mm;¹⁶ ovaries differentiated at ca. 9.0 mm, testes at ca. 14 mm.²⁴ Incipient dorsal rays first evident at 7.0³⁶-9.5 mm;¹⁶ 3rd dorsal spine developed at ca. 9.5 mm, rudiment of 1st dorsal spine evident at ca. 12.0 mm. Incipient anal

evident at ca. 8-ca. 9.5 mm, first anal spine at ca. 9.5 mm. At 9.5 mm dorsal and anal separated from caudal, triangular in shape.¹⁶ Caudal either homocercal¹¹⁶ or heterocercal at ca. 8.0 mm; incipient rays at ca. 6.0 mm; definitive rays visible before those of dorsal and anal, complete at least by 15.0 mm;²⁹ pectorals rayed at 9-10 mm;^{16,56} formation of pelvics apparently variable; may not appear until ca. 15.0 mm³⁹ or may have spine developed at 8.0 mm.^{16,118} Dorsal scutes first evident at 13.0 mm⁶⁷ or at age of 2 months;¹³ 3-5 scutes developed in shoulder region at 15.0 mm, and increasing in number anteriorly and posteriorly^{19,20} (in some cases, however, scutes may not appear at all during larval stage⁵). Finfold obliterated, in some specimens, at 12.0 mm;³⁹ urostyle still oblique at 8.0 mm.^{16,73}

Pigmentation: At 8 days from hatching (7.0 mm) black melanophores more abundant but closely aggregated

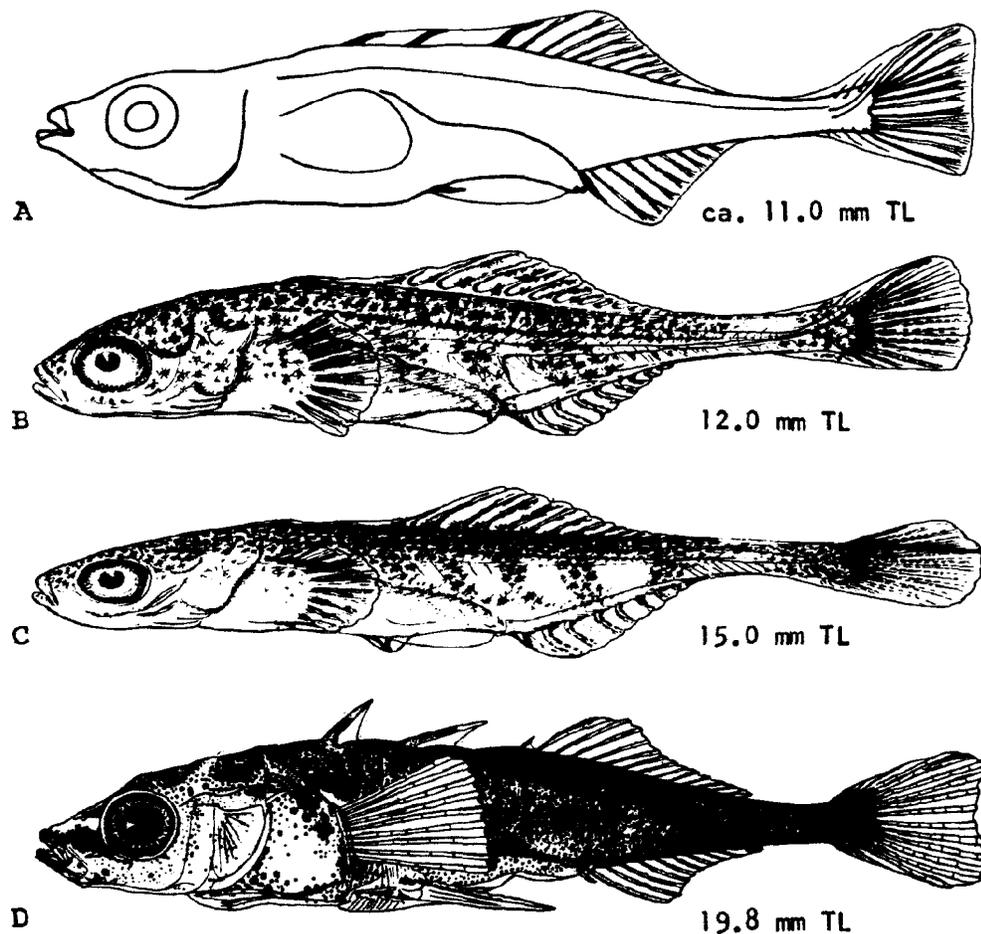


Fig. 215. *Gasterosteus aculeatus*, Threespine stickleback. A. Larva, ca. 11.0 mm TL. B. Larva, 12.0 mm TL. C. Larva, 15.0 mm TL. D. Juvenile, 19.8 mm TL. (A, Swarup, H., 1958: fig. 31. B, C, Agassiz, A., 1882: pl. 9. D, Syojima, Y., 1958: pl. 44.)

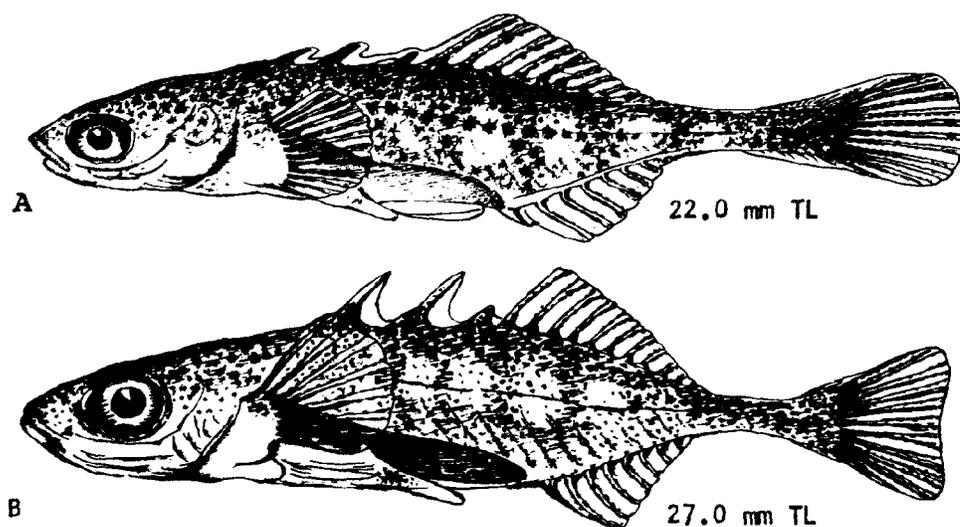


Fig. 216. *Gasterosteus aculeatus*, Threespine stickleback. A. Juvenile, 22.0 mm TL. B. Juvenile, 27.0 mm TL. (A, B, Agassiz, A., 1882: pl. 9.)

only on dorsal and dorsolateral surfaces, yellow pigment reduced.⁹⁹ During stage chromatophores form dendritic spots,³⁹ and banded pattern appears along with development of brown pigment behind head.¹³

JUVENILES

Minimum size described, ca. 11.0 mm.¹⁶ Body fusiform; peduncle short, slender, distinctly keeled at 16.5 mm.⁵ Spinous processes of opercles formed after 27.0 mm.³⁹ At 14.0 mm hypophysis adult-like.¹¹⁶ At 15.0 mm ovaries with short oviducts, at 20.0 mm few melanophores on outer wall of ovary, at 29.0 mm yolk formation begins. At 20.0 mm males with melanophores on outer wall of testes, at 25.0 mm testes completely covered with melanophores.²⁴ First evidence of dermal scutes varies from 13.0^{67,118}–16.5 mm.⁵ In some populations of the nominal subspecies *aculeatus* scutes developed as discrete group on caudal peduncle as well as in shoulder region at ca. 20.0 mm, 21–24 scutes in anterior (shoulder) series, 7–10 in caudal series; at 40.0 mm groups merge into single series.¹⁹ In nominal subspecies *microcephalus*, scutes first evident in shoulder region on lateral line at 13.5 mm, complete at 20.0 mm (posterior scutes never develop).²⁰ At 14–16 mm preanal finfold still evident in some specimens.⁵⁶ At 10.6 mm–15.6 mm pectorals shifted somewhat backward in relative position.³⁷ Serrations of pelvic spines formed after 27.0 mm.³⁹

Pigmentation: At 15.0 mm marine specimens develop silvery iridescence on flanks typical of adults.⁸⁶ At 16.5 mm body greenish, chromatophores arranged thickly

over top of head and in ca. 10 short patches along dorsal ridge, 5 pigment patches on lateral line which connect more or less with the dorsal patches by oblique bars; pigment patches in caudal region extend completely to ventral margin of body; chromatophores also developed around 2 dorsal spines and near base of caudal fin.⁵ At 22.0 mm chromatophores begin to form vertical bands on sides.³⁹ “Young” and “juveniles” green⁸⁶ to dark greenish blue³⁸ and with 6 conspicuous brown stripes or bands along flanks;^{52,54,85,109} frequently paler than adults ventrally.⁹⁰

AGE AND SIZE AT MATURITY

End of first summer⁴⁸ to 2nd spring.^{86,128} (The *trachurus* and *semiaratus* types apparently attain maturity about 4 weeks earlier than the *leirus* type.¹¹⁴) Mature at ca. 20.0 mm in nominal subspecies *microcephalus*,²⁰ 39.0 mm in form *trachurus*,¹¹ ca. 50 mm in nominal subspecies *aculeatus*.⁹⁷

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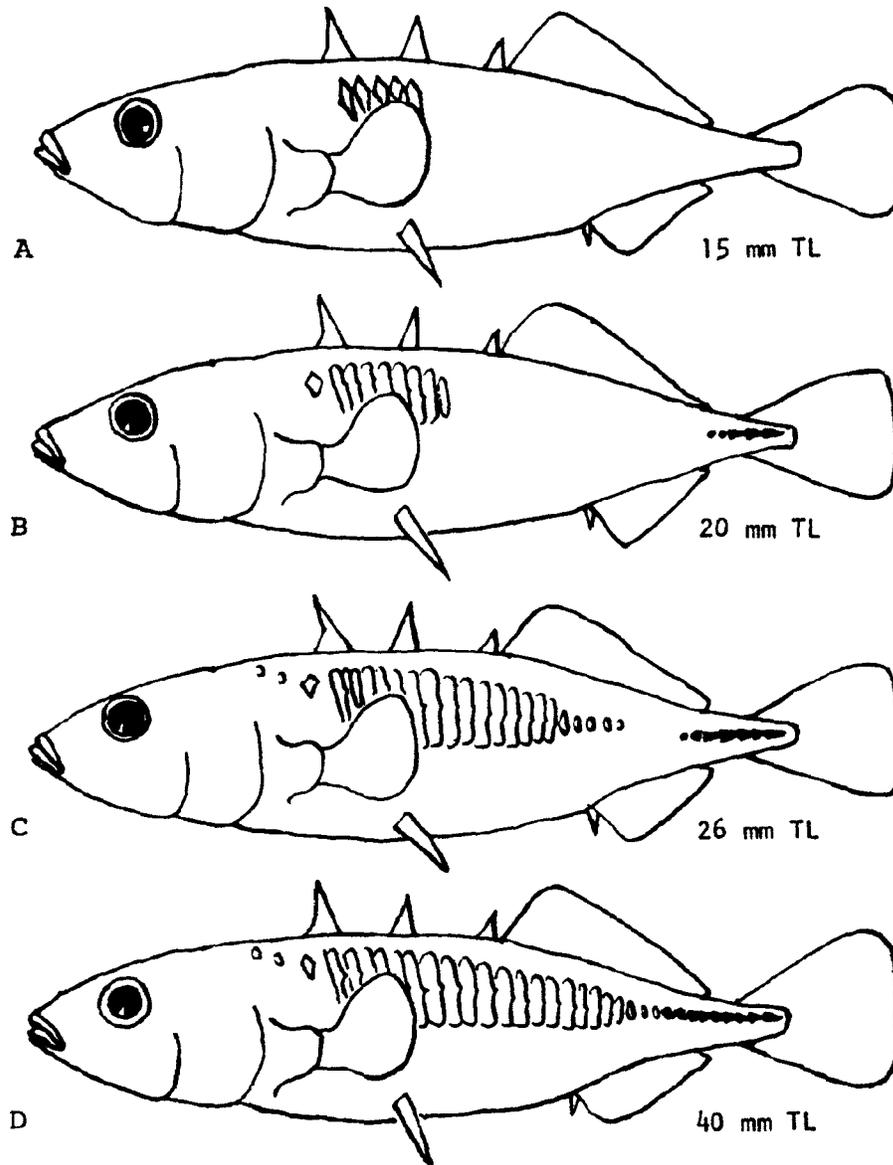


Fig. 217. *Gasterosteus aculeatus*, Threespine stickleback. Development of scutes in landlocked stickleback (*Gasterosteus aculeatus aculeatus*). A. 15 mm TL, scutes evident only in region above pectoral fin. B. 20 mm TL, scutes forming on caudal peduncle. C. 26 mm TL. D. 40 mm TL, scute formation complete. (A-D, Igarashi, K., 1964: fig. 1.)

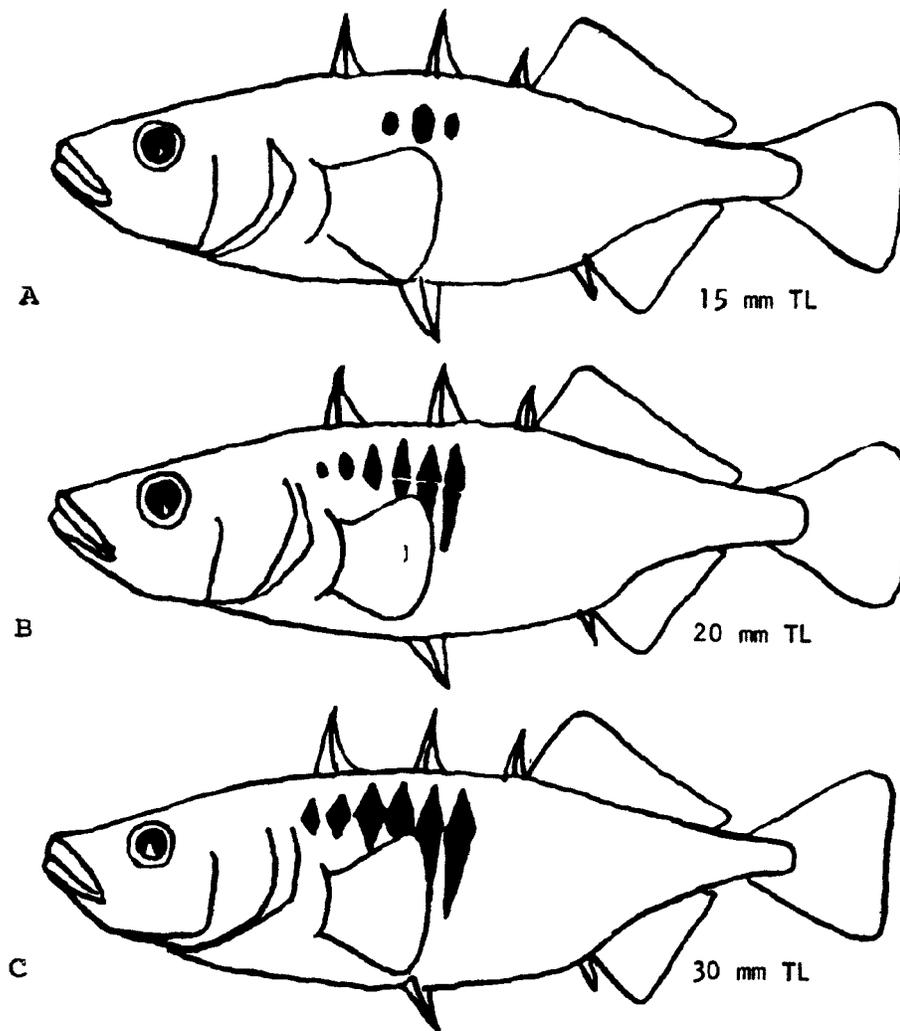


Fig. 218. *Gasterosteus aculeatus*, Threespine stickleback. Development of lateral scutes in landlocked stickleback (*Gasterosteus aculeatus microcephalus*). Note lack of scutes on caudal peduncle. A. 15 mm TL. B. 20 mm TL. C. 30 mm TL. (A-C, Igarashi, K., 1965: fig. 1.)

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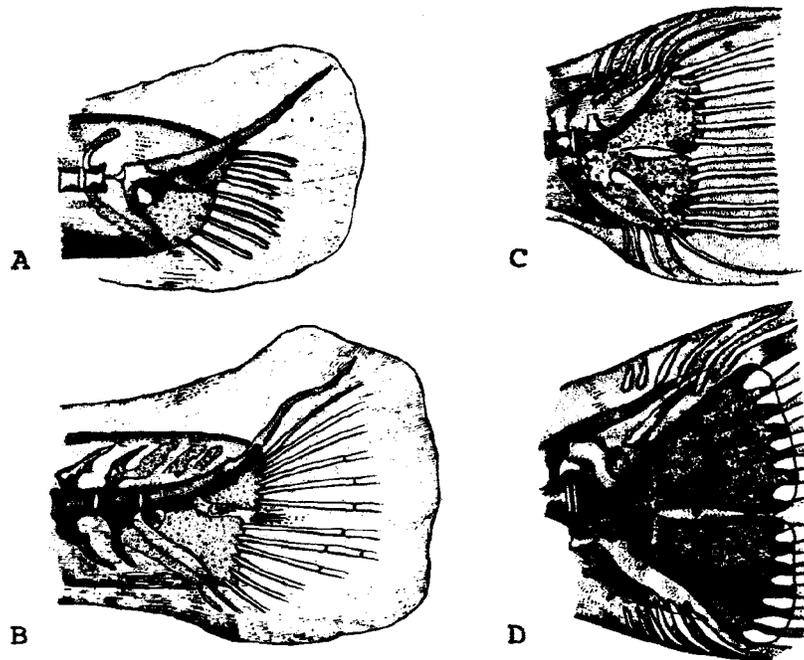


Fig. 219. *Gasterosteus aculeatus*, Threespine stickleback. Development of caudal skeleton. A. 7.60 mm TL, urostyle well-developed, oblique. B. 10.64 mm TL, primary caudal rays developed. C. Half-grown specimen, size unknown, procurent rays developing. D. Adult specimen, caudal skeleton complete. (A-D, Huxley, T. H., 1859: pl. 3.)

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Fistularia petimba
Fistularia tabacaria

cornetfishes
Fistulariidae

FAMILY FISTULARIIDAE

Cornetfishes occur in tropical and subtropical waters throughout the world. One species, *Fistularia tabacaria*, has been reported as far north as Nova Scotia. The family contains four species, two of which (*F. commersonii* and *F. tabacaria*) occur inshore on reefs and grass beds and two of which (*F. petimba* and *F. corneta*) are found in deeper waters along continental margins.

In these fishes, the body is elongate and depressed; the snout is greatly produced and ends in a small, terminal mouth. The two mid-caudal rays extend as a long caudal filament; the lateral line arches strongly anteriorly, almost reaching the middle of the back. The dorsal and anal fins are short and opposite. The first four vertebrae are fused. Scales are lacking. There are posterior lateral line ossifications, sometimes with sharp retrorse spines. A row of elongate bony plates may exist in the skin on the midline of the body just anterior to the dorsal and/or anal fin.

Cornetfishes produce relatively large pelagic eggs (up to 2.1 mm) having clear yolk, no oil globules, and a narrow perivitelline space. Eggs of various species have been observed in December and February.

Newly hatched larvae are characterized by a high preanal myomere count (50-53); an elongate, narrow yolk mass; and a relatively broad finfold. The anus is positioned at a point slightly more than two-thirds the distance to the tip of the tail.

Juvenile cornetfishes go through what has been termed the "villosa form" in which a number of conspicuous rows of small hooked spinules appear on the body.

Fistularia petimba Lacépède, Red cornetfish**ADULTS**

D. 13⁶-17,⁸ \bar{x} 15.5; ⁵ A. 13⁶-16,⁸ \bar{x} 14.5; P. 15-17, \bar{x} 15.9; V. 6; vertebrae 50+26 (4 anteriormost preanals fused).⁵

Preorbital distance 3 times in HL.¹

Body greatly elongate, much depressed; ⁸ upper ridges of snout parallel; upper, lateral, and lower ridges of snout, preorbital and postorbital ridges serrate. Spinules in skin well-developed; a single median row of elongate bony plates along back from level of pelvics to base of dorsal and from rear of dorsal toward tail; a similar row of plates along ventral midline.⁵ Lateral line with dermal ossifications,¹ the posteriormost with large retrorse spines.⁵

Pigmentation: Red to orange-brown above; ⁵ sides pearly or iridescent, with mauve reflections; belly white ⁸ or silvery; pelvic fins with orange cast; ⁵ other fins, tail filament, and eyes red or pink.

Maximum length: 1880 mm.⁷

DISTRIBUTION AND ECOLOGY

Range: Throughout tropical Atlantic, Indo-West Pacific, and Hawaii.^{3,5,6,7,8}

Area distribution: Coastal waters of Virginia (JAM).

Habitat and movements: Adults—soft-bottomed coastal areas usually at depths over 10 meters.⁵

Larvae—no information.

Juveniles—"small" specimens sometimes inshore.⁷

SPAWNING

Season: February in Japan.⁸

EGGS

Location: Pelagic.²

Fertilized egg: Diameter 1.50-2.10 mm, perivitelline space exceptionally narrow, no oil globules.²

EGG DEVELOPMENT

Development at 17-22 C:²

24 hours after Gastrula.
morula stage.

55 hours after 9 myomeres evident.
morula stage.

79 hours after 30 myomeres, eyes forming.
morula stage.

115 hours after Tail elongate, lens formed.
morula stage.

141 hours after Pigment on body, otoliths formed.
morula stage. (Pigment in advanced embryos apparently includes both melanophores and xanthophores.)

152 hours after Hatching.²
morula stage.

YOLK-SAC LARVAE

Hatching length, 7.08 mm TL.

Preanal myomeres 53, postanal myomeres 33; but variation in total myomeres 82-86.²

Anus at point slightly more than 2/3 distance from snout to tip of tail. Pectoral fin rounded at hatching, and lacking rays.²

Pigmentation: At hatching pigment along dorsal and ventral ridge, on yolk, along ventral wall of gut near anus, and extended into ventral finfold on posterior half of tail.²

JUVENILES

Minimum size described, 130 mm.

In "young," body cylindrical (becoming depressed with growth), head relatively larger than in adult, eye smaller, spinules and serrations on head and body stronger (RAF). Keeled scales of dorsal and ventral ridge not developed at 130-170 mm.¹ As development proceeds serrations and spinules become obsolete (RAF).

Pigmentation: A specimen 178 mm long with indistinct crossbars on back.⁴

AGE AND SIZE AT MATURITY

No information.

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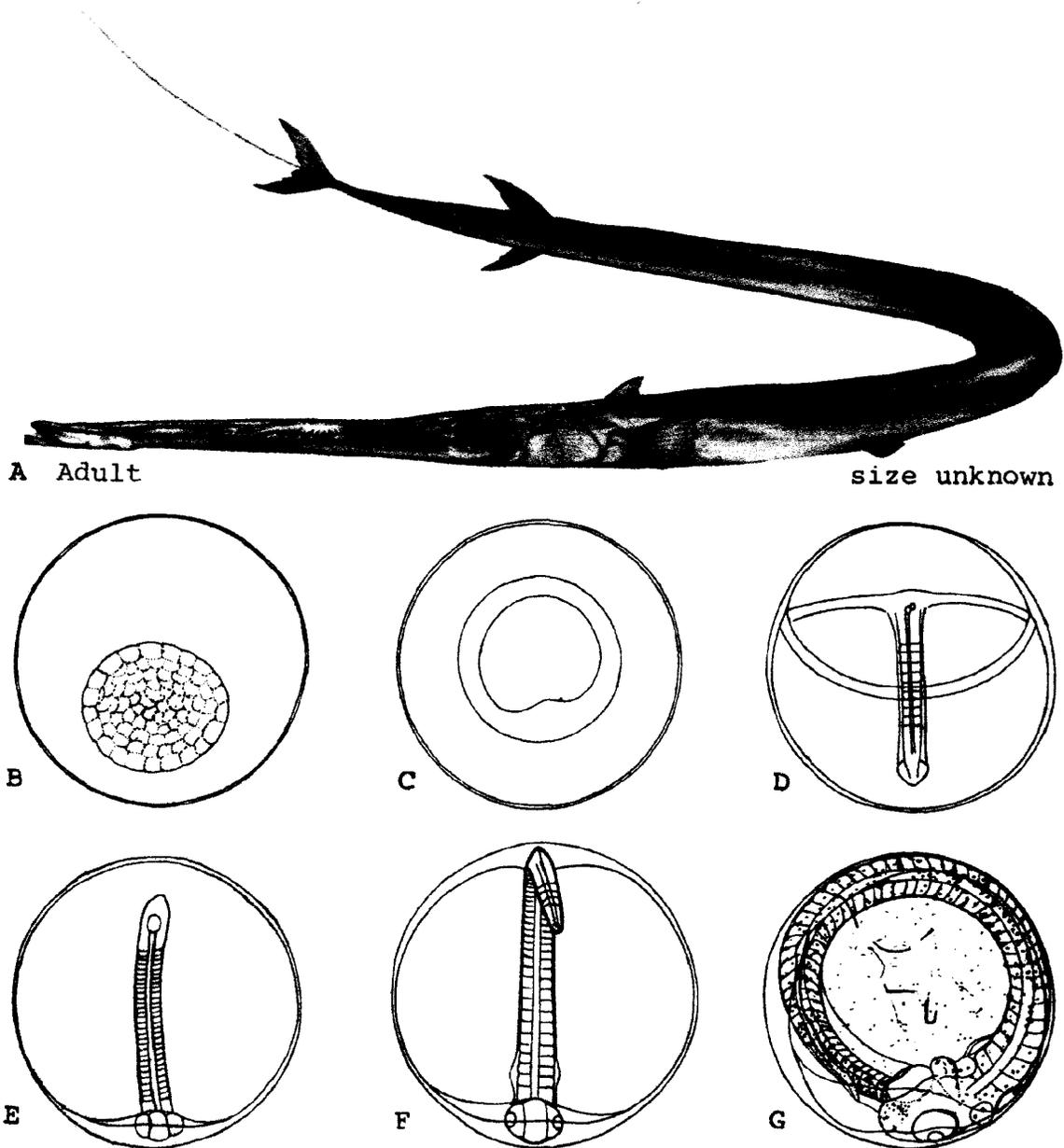


Fig. 220. *Fistularia petimba*, Red cornetfish. A. Adult, size unknown. B. Egg 5 hours after collecting, morula. C. 29 hours after collecting, gastrula. D. 60 hours after collecting, 9 myomeres. E. 84 hours after collecting, 30 myomeres. F. 120 hours after collecting, lens formed, tail apparently free. G. 141 hours after collecting (11 hours before hatching), pigment, otoliths developed. (A, Grant, E. M., 1965: 79. B-G, Mito, S., 1961: pl. 34, figs. 5-10.)

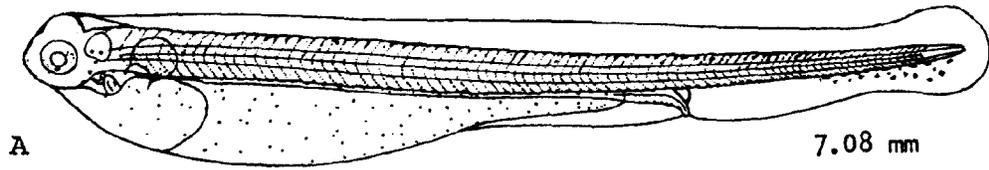


Fig. 221. *Fistularia petimba*, Red cornetfish. A. Yolk-sac larva, 7.08 mm TL. (A, Mito, S., 1961: pl. 34, fig. 11.)

Fistularia tabacaria Linnaeus, Bluespotted cornetfish**ADULTS**

D. 13¹⁶ or 14^{3,14,33-18,22} \bar{x} 14.9; ³³ A. 13^{3,6,9} (a minimum of 11²⁶ is questioned, JDH)—7,²² \bar{x} 14.8; C. 14 (7+7); P. 15^{33-17,5} \bar{x} 15.6; ³³ V. 6; ^{4,5} lateral line pores 100; ²² branchiostegals 5; vertebrae variously counted, 4+49+34 (the first 4 fused),³³ 4+52+31, 4+49+33, 56+33.³⁵

Proportions as times in TL (all data presumably not including caudal filament, JDH): Head 2.6^{9-3.0,36} depth 28–37.¹⁸ As times in HL: Depth 9.8–15.0,⁹ eye 14.0.³⁴ Mandible ca. 4 times in snout.^{21,24} Distance from opercle to pelvic fin origin more than twice pelvic fin to anal fin distance.³³

Body elongate, slender, depressed,^{1,9,26} oval in cross section; ⁵ head depressed; ¹ quadrate in vicinity of eyes, slightly broader than deep; ¹⁸ snout very long, ⁷ tubular; ³⁴ mouth slightly oblique, lower jaw projecting in front of and overlapping upper.^{1,26} Teeth minute, crowded together in rows.^{26,34} Ridges of snout entirely smooth; upper snout ridges parallel; postorbital ridge with some indications of serrations; preorbital and post-temporal ridges smooth; interorbital narrow, with smooth depression.³³ Opercles with fine radiating striae; gill openings extending forward to middle of eye.¹ Eye oval; ³² orbits with angular processes or spines.⁴ Scales lacking; ¹⁰ spinules in skin not visible.³³ Lateral line distinct.^{18,34} Dorsal and anal fins subtriangular, with pointed tips, height equal to that of caudal lobes; ³⁶ dorsal fin inserted at point about one fourth distance between middle of eye and base of caudal, its middle ray the longest; anal fin opposite and equal. Pelvics proportionately small.^{1,19} Caudal forked,⁹ and with elongate median filament.¹⁰

Pigmentation: Brownish,^{4,33} greenish brown,^{9,19,34} or olive³⁸ above (reports of dark red,²⁶ reddish,³⁴ or reddish brown dorsal pigment²¹ are questioned, RAF) with a series of unequal, oblong, pale blue spots extending to dorsal fin.^{1,24,33} Sides semidiaphanous,⁴ and with series of large, oblong blue spots.^{26,34,38} Two lateral rows of spots on snout.^{5,35} Sides and back with ca. 10 cross bars; a little darker than background.^{9,19} Caudal filament blue,³⁴ venter pale,²⁶ white,⁴ or silvery,^{11,19}

Maximum length: Reported to reach 1829 mm,^{1,2,3,34} but maximum confirmed length, 1333 mm.³⁶

DISTRIBUTION AND ECOLOGY

Range: Both sides of the Atlantic; ²⁸ apparently restricted to coast of Africa in the east; ^{30,31,33} in the west Nova Scotia and Newfoundland ^{25,34} south to Rio de Janeiro ²⁸ including Bermuda,^{6,17} the West Indies,^{21,24} and the Gulf of Mexico.¹²

Area distribution: Cape Charles and Hampton Roads, Virginia;¹⁸ Maryland and Virginia seaside bays;³² Indian River Bay, Delaware;¹³ New Jersey.^{1,7}

Habitat and movements: Adults—typically an inshore species,^{14,23,28,29,39} although recorded from water 32–36 m deep.¹² Taken over sandy, stony bottom among shells and sea fans at depths of ca. 20–25 m³¹ (a depth record of 128 m¹⁹ is questioned, RAF); also over “seagrass beds.”³⁹

Apparently a seasonal visitor in temperate waters: Recorded in North Carolina in September and November;¹⁵ in Chesapeake Bay in “summer and early fall”;¹⁸ in New York and Woods Hole from September to November;⁸ and in Canadian waters in September.²⁷

Larvae—a 16.0 mm larva recorded in surface water approximately 400 km off the coast of Africa at a salinity of 34.96 ppt and a temperature of 25 C.³⁷

Juveniles (including specimens up to ca. 200 mm)—recorded inshore²⁰ and at surface floating above sparse growths of turtle grass.²²

SPAWNING

Season: The smallest larva thus far collected was taken in tropical waters in February.³⁷

EGGS

No information.

EGG DEVELOPMENT

No information.

LARVA

Specimen described, 16.0 mm.

At 16.0 mm head blunt; caudal filament, and pelvic fins developing.³⁷

JUVENILES

Minimum size described, 43.0 mm (excluding caudal filament which was ca. 52 mm long).

Lateral ridge on snout with minute serrations in “juveniles.”³³ At 43.0 mm (excluding caudal filament) body covered with proportionately large, hooked spinules, except in a longitudinal stripe along each side of body;

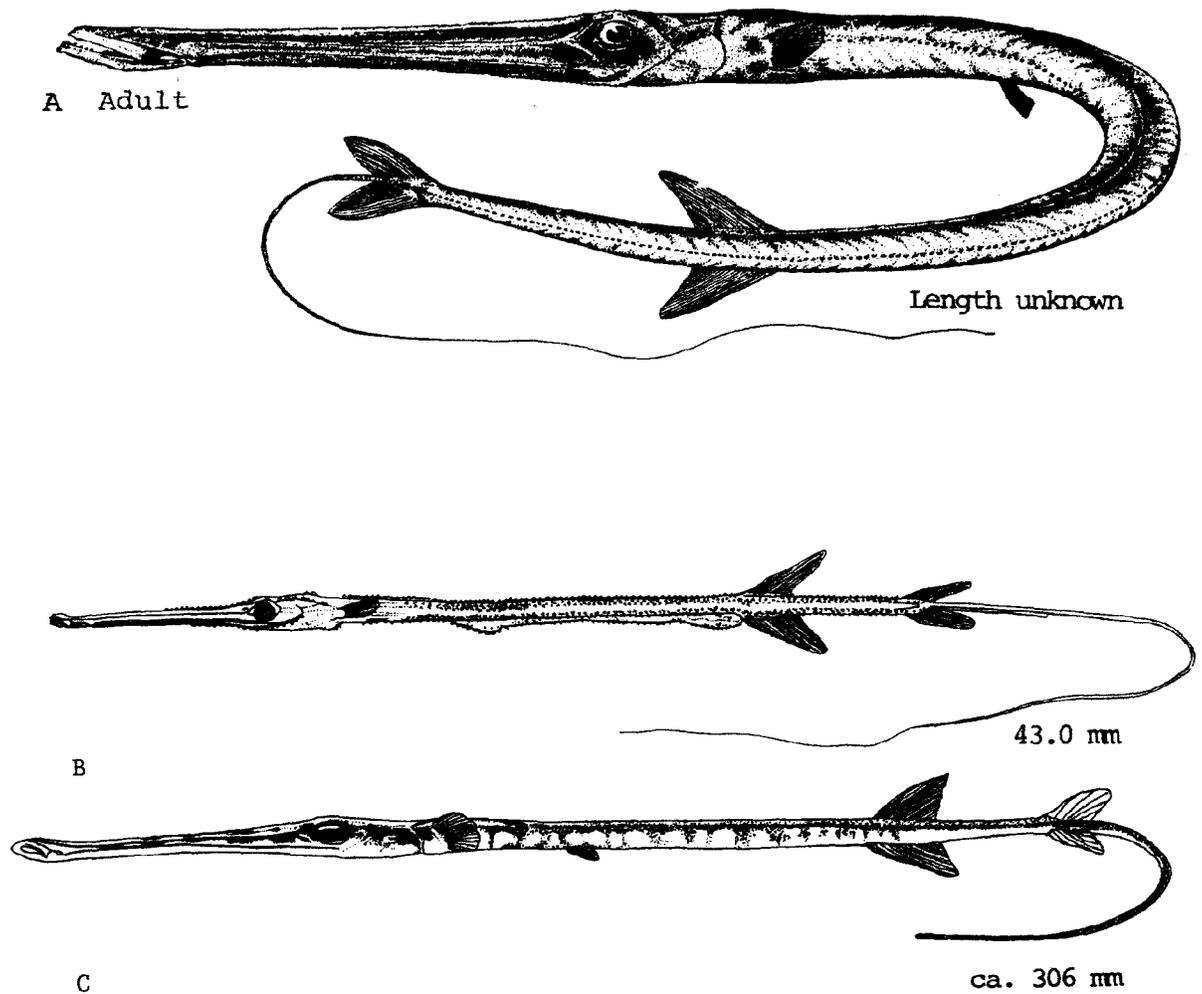


Fig. 222. *Fistularia tabacaria*, Bluespotted cornetfish. A. Adult, length unknown. B. Juvenile, 43.0 mm (excluding caudal filament of ca. 42.0 mm). C. Juvenile, ca. 306 mm. (A, Leim, A. H., and W. B. Scott, 1966: fig. 175. B, Jungersen, H. F. E., 1910: pl. 7, fig. 1. C, Böhlke, J. E., and C. C. G. Chaplin, 1968: 175.)

head and adjoining part of body naked. In a 280 mm specimen spinules still over entire body, most densely developed on tail.³⁵ In another 280 mm specimen spinules restricted to posterior part of body and tail.³⁰ Disappearance of spinules variable. In a specimen of ca. 350 mm limited to area below lateral line on tail; in another specimen ca. 400 mm long sides and venter with spinelets still well-developed.³⁵ At 415 mm spinules still evident on tail.³⁶ A series of "short spindle-shaped ossicles" on forward part of body and to end of tail below and parallel to lateral line (lateral line ossifications? JDH) first evident at ca. 280 mm.³⁵ Pectoral and pelvic fins relatively closer to one another in "younger" fish.³⁶

Pigmentation: A specimen 200 mm long, greenish, crossed by a number of light lines.³⁵

AGE AND SIZE AT MATURITY

Unknown, but Jungersen regards specimens lacking spinules (thus longer than 415 mm) as adults.³⁵

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Macrorhamphosus scolopax

snipefishes
Macrorhamphosidae

FAMILY MACRORHAMPHOSIDAE

Members of this family occur in tropical, subtropical, and temperate waters of the Atlantic, Pacific, and Indian oceans. They are relatively small pelagic fishes (up to about 250 mm) and are found in both mid-ocean and coastal areas. At least one species, *Centriscops obliquus*, swims backward as well as forward and normally assumes a striking head-down position.

In the snipefishes, of which there are three or four genera and about 11 species, the body is compressed and deep, the snout is elongate, the second dorsal spine is greatly projected, and there are usually distinct bony plates on each side of the back which form an imperfect exoskeleton.

The family is represented in the Mid-Atlantic Bight by a single species, *Macrorhamphosus scolopax*. This species is wide-ranging and includes the formerly recognized species *M. sagifue*, *M. japonicus*, and *M. gracilis*.

Ripe ovarian eggs of the regional species (*M. scolopax*) are held together by a common gelatinous mass. After deposition, which is so far known only to occur in March, the eggs float singly. They are relatively small (1.0 mm) and have a rose or violet yolk and a single, large, amber-rose oil globule.

In recently hatched young the yolk is elongate, somewhat tubular, and relatively small. The larvae are characterized by a low preanal myomere count (10), and a broad finfold which is often pigmented and often extends on to the head. The anus varies in position from slightly more than one-half to slightly less than two-thirds the body length. In advanced larvae spines develop on the preopercle and on various parts of the head and trunk.

Early juveniles (prejuveniles in the present account) are characterized by blue dorsal and silvery lateral and ventral pigment. Juveniles 35 mm long or longer have a ground color of reddish brown to brick red.

Macrorhamphosus scolopax (Linnaeus), Longspine snipefish**ADULTS**

D. IV to VIII,¹⁵ 10³-13; ¹⁵ A. 17³-19; ⁵ C. 6-7+9+6-7,²⁵ also to total of 25; ¹⁷ P. 14-17; ^{5,31} V. 4²⁵-6; ⁵ vertebrae 8+16²⁰=23-24.²⁷

Proportions expressed as times in TL: Depth at front of eye 3.7, greatest depth (occurring at anus) 4.9,¹ head 2.5.¹⁹ Ratio of body height to TL 3.8-5.4 depending on age.⁶

Body strongly compressed and covered with small striated scales, each stria terminating in a rather strong spine, and with bony plates arranged in definite longitudinal rows. Teeth lacking. Origin of first dorsal beyond midpoint of body; ¹⁶ 2nd dorsal spine strongly serrated on posterior margin.^{19,24}

Pigmentation: Pinkish, rose, red, or reddish olive above; silvery on sides and belly; sometimes golden above.^{15,16,18,19}

Maximum length: Ca. 200¹⁵ to possibly 300 mm TL.²³

DISTRIBUTION AND ECOLOGY

Range: Worldwide in tropical and temperate waters.²² In western Atlantic from the Gulf of Maine² to Brazil or Argentina;²² in the eastern Atlantic from Norway^{20,21} and southern coast of England^{5,9} to Morocco,¹⁶ including the Mediterranean.²

Area distribution: Coastal waters of New Jersey in 128 m; ^{12,15} Delaware Bay at Deadman Shoal,¹⁰ and off Delaware coast at average depth of 25 m; ¹⁴ in Virginia coastal waters over continental shelf near mouth of Chesapeake Bay.^{13,27}

Habitat and movements: Adults—pelagic,^{8,22} found both in mid-ocean and coastal waters²⁶ at depths of ca. 5¹⁰ to 310 m; ⁹ reported in shallow water over “gritty”¹ and muddy bottoms; sometimes associated with *Capros asper*.²⁸ Temperature range 17-21 C. In some areas concentrate at surface during daytime and move to somewhat deeper water at night.³²

Larvae—pelagic,³⁰ and in surface currents,^{4,28} particularly at night.³³

Juveniles—at surface² particularly during daylight hours; ³³ sometimes associated with jellyfish.⁷

SPAWNING

Location: Ripe females from shallow, muddy water in Italy.²⁸

Season: In the Mediterranean ripe ovaries in January,^{4,28} eggs in March,¹⁷ larvae 6.0-20.0 mm long in March and April.²⁸

Fecundity: Unknown.

EGGS

Location: Apparently float at surface.²⁸

Ripe ovarian eggs: Transparent and with a single large oil globule; held together in ovary by a common gelatinous mass.²⁸

Fertilized eggs: Spherical, diameter 1.0 mm,¹⁷ transparent; ^{4,28} vitelline membrane light amber with grainy reflections; yolk with rose or violet halo depending on

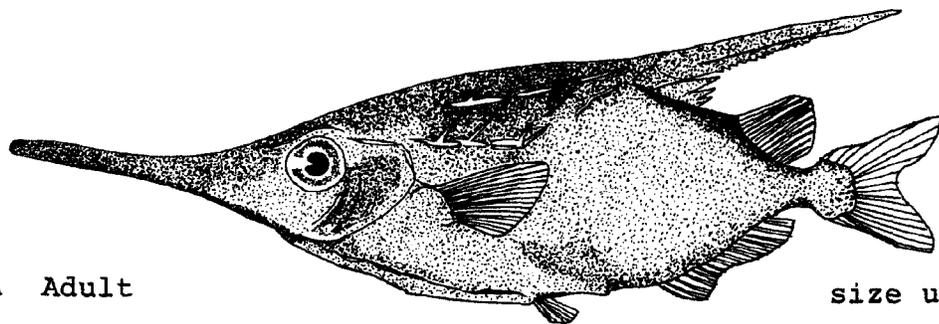


Fig. 223. *Macrorhamphosus scolopax*, Longspine snipefish. A. Adult, size unknown. (A, Kamohara, T., 1967: pl. 17, Joan Ellis, delineator.)

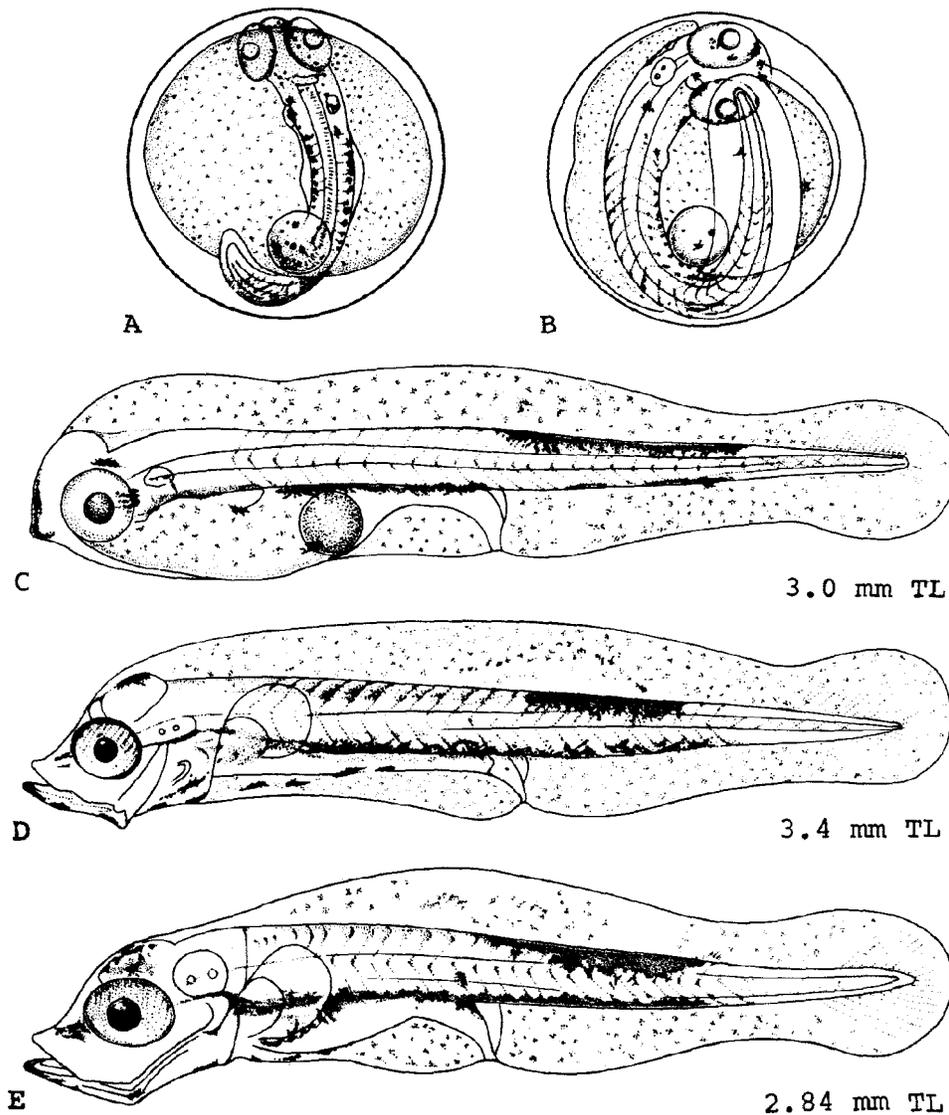


Fig. 224. *Macrorhamphosus scolopax*, Longspine snipefish. A. Embryo, otocysts, pigment developed. B. Advanced embryo, pectoral buds evident. C. Yolk-sac larva, 3.0 mm TL, just hatched, oil globule in posterior part of yolk. D. Larva, 3.4 mm TL. E. Larva, 2.84 mm TL. The length decrease attributed to lack of food and unnatural rearing conditions. (A-E, Sparta, A., 1936: figs. 1-5, Elizabeth Ray Peters, delineator.)

viewing light; oil globule single,^{4,28} amber-rose, 0.2 mm in diameter.¹⁷

EGG DEVELOPMENT

Development at unspecified temperature: Earliest eggs described had optic vesicles and otoliths formed and many black melanophores on sides. One day later the tail had reached the cephalic region, and one day later hatching occurred.¹⁷

YOLK-SAC LARVAE

Hatching length, 3.0 mm TL.

Total myomeres 24-25, preanal myomeres 10.¹⁷

Body compressed; head moderately curved over yolk; yolk mass relatively reduced; oil globule positioned posteriorly in yolk sac; mouth poorly developed; eye oval. Finfold large, originating in front of eye and reaching greatest height a little before anus. At time of

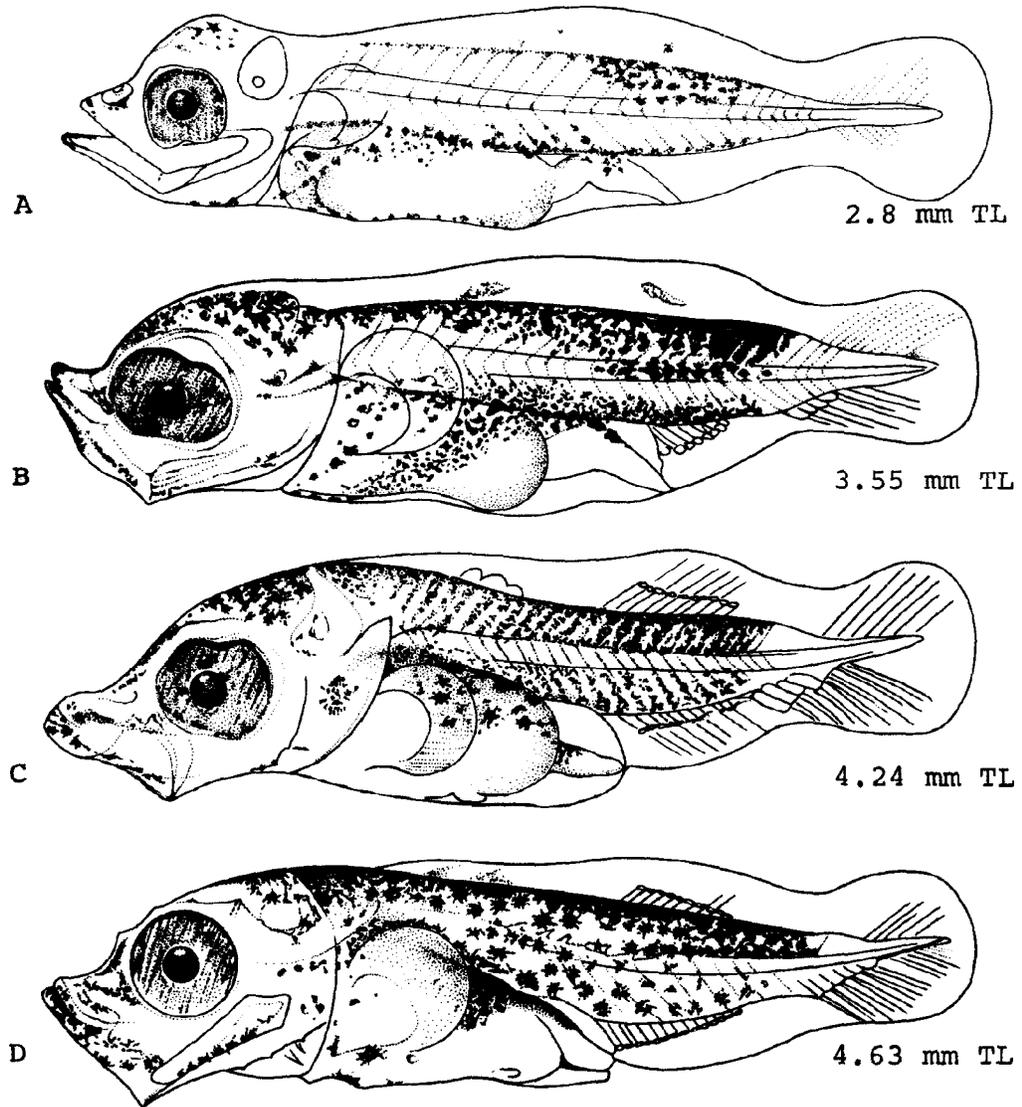


Fig. 225. *Macrorhamphosus scolopax*, Longspine snipefish. A. Larva, 2.8 mm TL, pigment in finfold greatly decreased, anus shifted conspicuously backward. B. Larva, 3.55 mm TL, body depth noticeably increased, incipient rays in caudal and anal. C. Larva, 4.24 mm TL, snout becoming elongate. D. Larva, 4.63 mm TL, head spinations developing. (A-D, Sparta, A., 1936: figs. 6-9, Elizabeth Ray Peters, delineator.)

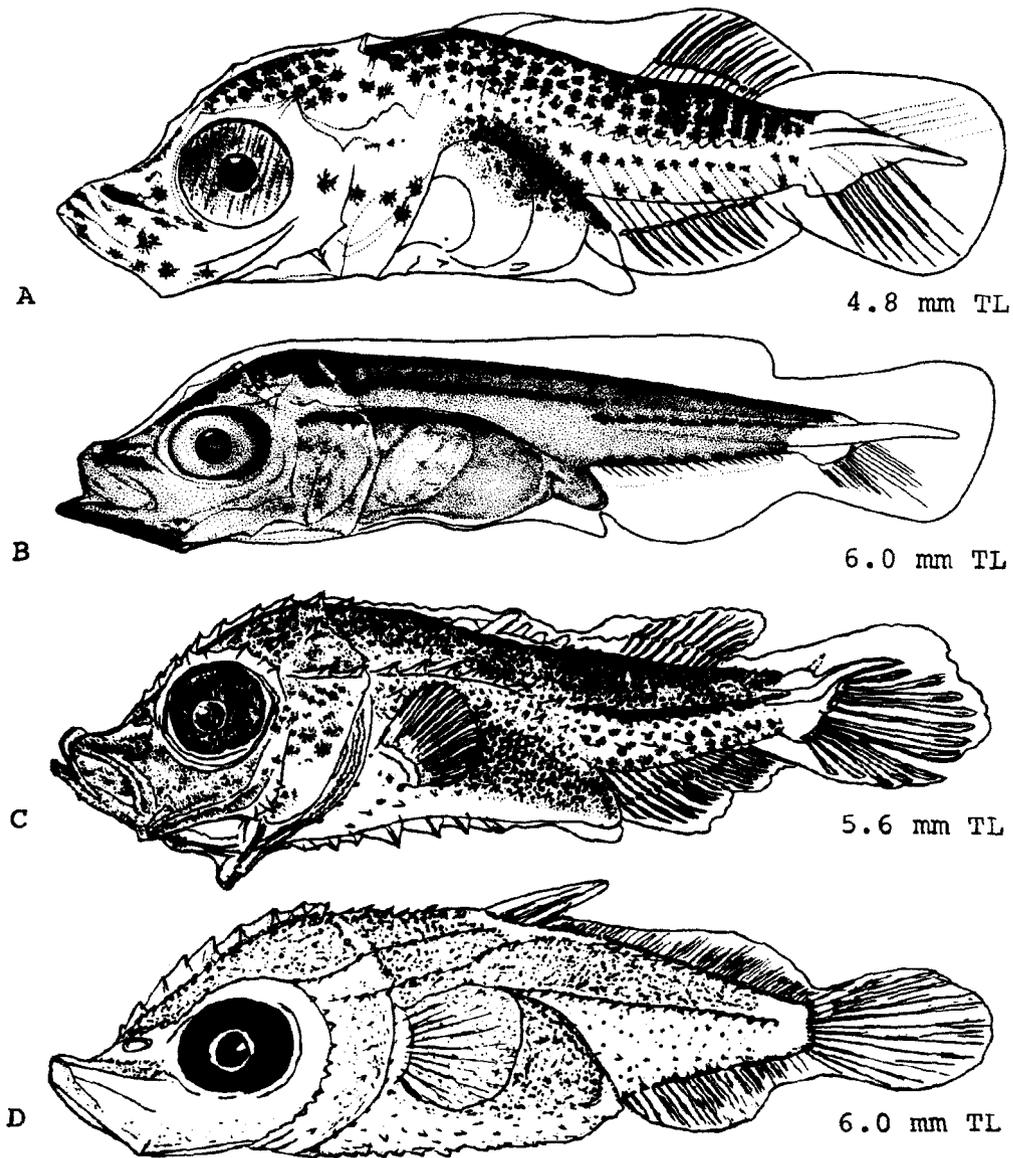


Fig. 226. *Macrorhamphosus scolopax*, Longspine snipefish. A. Larva, 4.8 mm TL. B. Larva, 6.0 mm TL. C. Larva, 5.6 mm TL (but more advanced than previous specimen). D. Larva, 6.0 mm TL. (A, Sparta, A., 1936: fig. 10, Elizabeth Ray Peters, delineator. B, D'Ancona, U., 1933: pl. 18, Elizabeth Ray Peters, delineator. C, Uchida, K., 1958: pl. 45. D, Fage, L., 1918: fig. 2.)

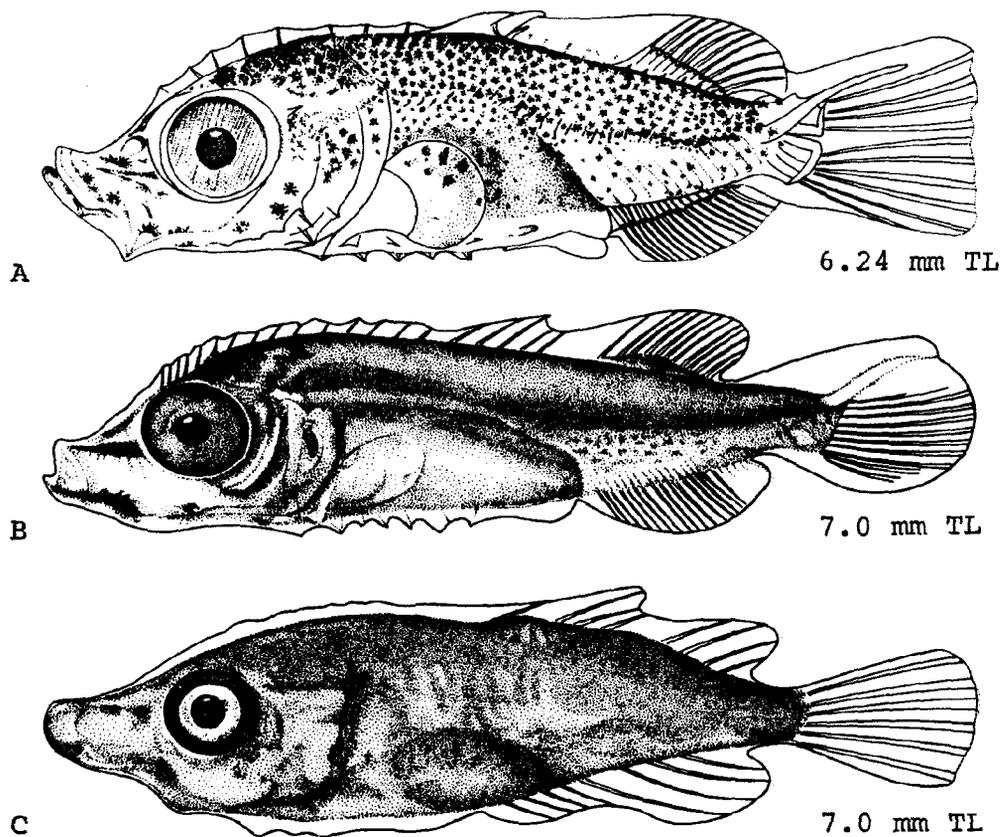


Fig. 227. *Macrothamphosus scolopax*, Longspine snipefish. A. Larva, 6.24 mm TL. B. Larva, 7.0 mm TL. C. Larva, 7.0 mm TL. (A, Sparta, A., 1936: fig. 11, Elizabeth Ray Peters, delineator. B, C, D'Ancona, U., 1933: pl. 18, Elizabeth Ray Peters, delineator.)

hatching incipient rays at dorsal and ventral extremes of caudal fin, pectoral fins just forming. Urinary vesicles prominent and visible.¹⁷

Pigmentation: At hatching (3.0 mm) black melanophores concentrated in posterodorsal region and in an almost continuous line along ventral surface of body from behind eye to caudal region; also a line of melanophores along anterior profile of head, and small groups of melanophores over eye, at pectoral base, and in region of oil globule; eye with some pigment; although reported to be pigment free, finfold appears to be stippled and there is a prominent blotch in the dorsal finfold at approximately mid-body.¹⁷

LARVAE

Size range described, 2.84–16.0 mm TL (reduction in TL as stage progresses from 3.40 mm at 5 days to 2.84 mm at 10 days).

Preanal myomeres, 12 at 2.18–3.40 mm TL.¹⁷

At 7.0 mm snout somewhat elongate, more or less equal to diameter of eye.²⁷ Snout to anus distance into TL 2.0 at 3.0 mm, 1.39 at 6.24 mm.¹⁷

At 6.0 mm body elongate, laterally compressed; greatest depth, measured from occiput, exactly half distance from tip of snout to base of caudal. Abdomen rounded, voluminous. Snout not quite 1/3 length of head and not greater than longitudinal diameter of eye;⁴ at 10 mm snout beginning to elongate.²⁵ At 13 mm occipital crater well formed.⁴ At 3.40 mm (5 days) mouth, branchial cartilage, and Meckel's cartilage developed. Throughout stage depression on dorsal profile of head in front of eye becomes progressively more pronounced.¹⁷ Supraorbital crest barely evident at 4.63–4.80 mm. At 6.0 mm supraorbital crest forms a prominent denticular crater and continues backward to base of first dorsal; also at this size an occipital crest and 2 spiny craters near nasal openings.⁴ Posterior profile of preopercle spined at 4.25 mm¹⁷ and with single prominent spine at 5.0–6.0 mm. Nasal fossa entire at 7.0 mm, divided at 9.0 mm.²⁵ At 3.40 mm otoliths large, located near posterior profile of

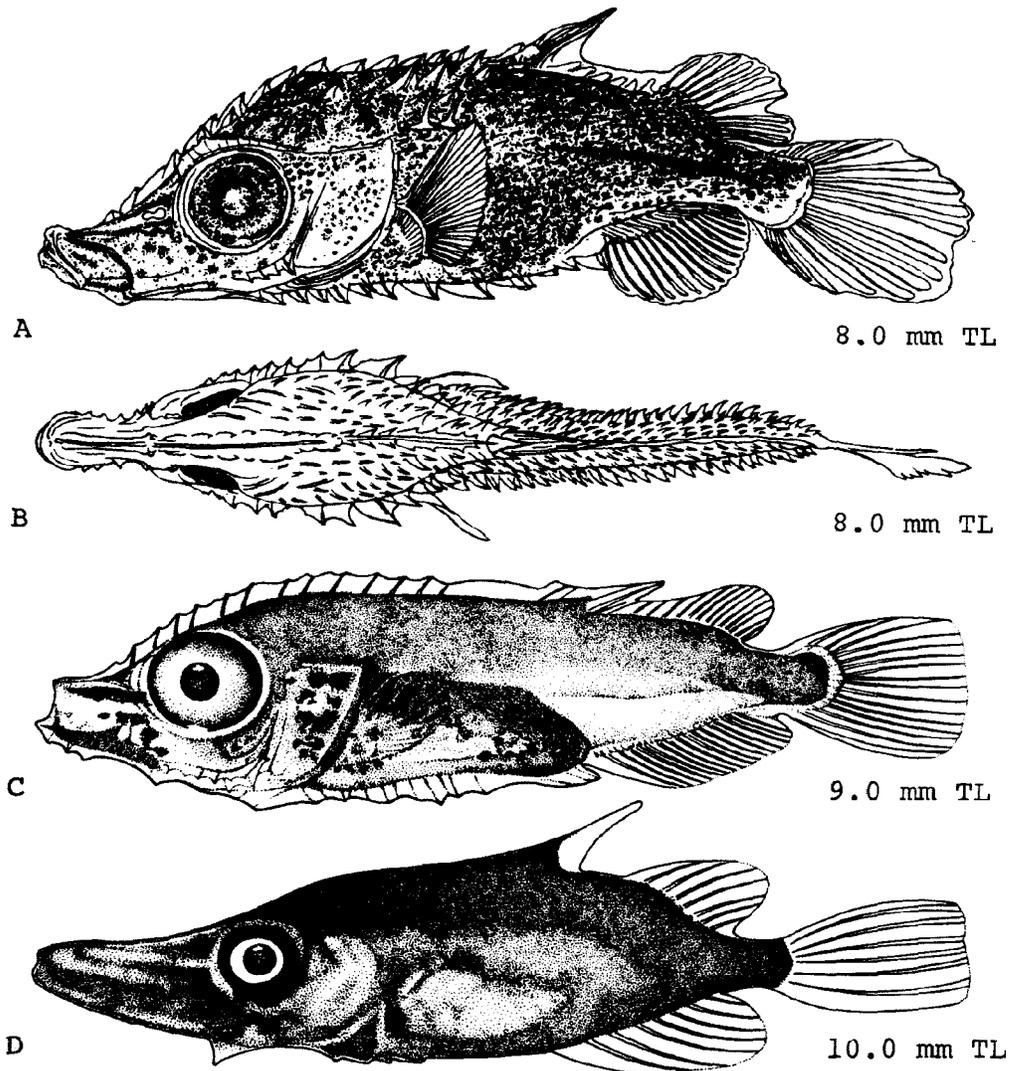


Fig. 228. *Macrorhamphosus scolopax*, Longspine snipefish. A, B. Larva, 8.0 mm TL, lateral and dorsal views. C. Larva, 9.0 mm TL, finfold still evident. D. Larva, 10.0 mm TL. (A, B, Uchida, K., 1953: pl. 45. C, D, D'Ancona, U., 1933: pl. 18, Elizabeth Ray Peters, delineator.)

eye. During stage, shape of eye changes from oval to round.¹⁷

At 4.24 mm 2 ray bases evident in first dorsal,¹⁷ developed as definite spines at 6.0–7.0 mm.^{4,25} In specimens 4.24–6.0 mm long, 6–9 incipient rays in 2nd dorsal.^{4,17} At 10 mm 2nd spine of first dorsal with serrations on posterior margin. At 12 mm 2nd spine of first dorsal longer than diameter of eye.²⁵ At 13 mm 2nd dorsal relatively longer than in adult.⁴ At 16 mm first and second dorsals separated. During larval stages first dorsal displaced posteriorly.²⁵ Incipient anal rays at 3.55–4.68

mm, anal fin with 16 definitive rays at 6.0–6.24 mm. Caudal with 11 well defined rays in 2 distinct groups at 6.0–6.24 mm.^{4,17} Pectorals rounded at 6.0 mm.⁴ Pelvic buds evident at 9.0 mm; pelvics apparently well-formed but without definitive rays at 16 mm.²⁵ Finfold reduced at 4.63–4.80 mm,¹⁷ but still continuous at 6.0 mm. Remnant of finfold still visible at 13 mm.⁴ Urostyle straight in some specimens as large as 6.0 mm; ²⁵ oblique in others at 5.8 mm.²⁹ Spinous scales first evident along lateral line at 4.24 mm, over entire body at 6.24 mm. Anus displaced backward from 10th myomere (in yolk-sac larvae) to 12th myomere in larvae.¹⁷

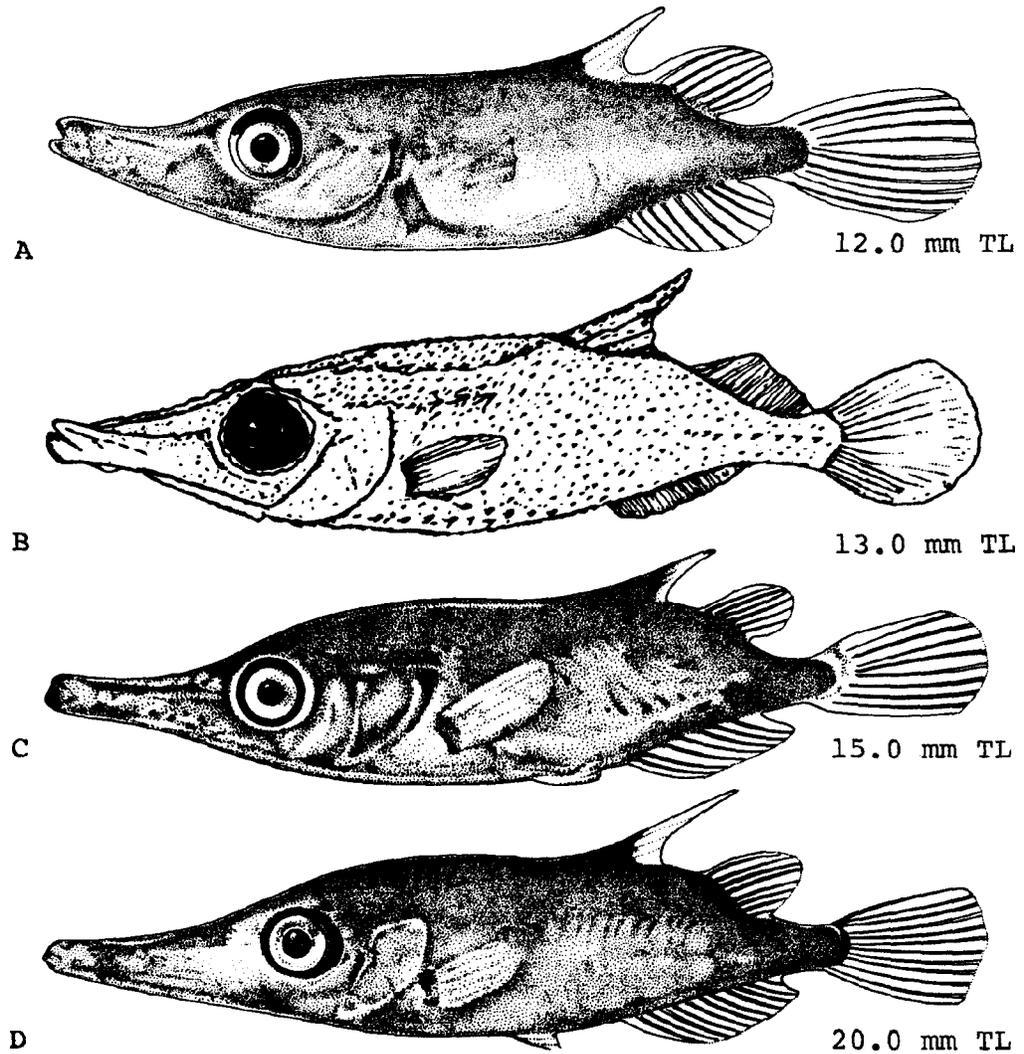


Fig. 229. *Macrorhamphosus scolopax*, Longspine snipefish. A. Larva, 12.0 mm TL. B. Larva, 13.0 mm TL. C. Larva, 15.0 mm TL. D. Prejuvenile, 20.0 mm TL. (A, C, D, D'Ancona, U., 1933: pl. 18. B, Fage, L., 1918: fig. 3.)

Pigmentation: At 3.40 mm eye completely pigmented and with metallic reflections; a series of black melanophores on isthmus extending to about midpoint of intestine; black melanophores concentrated on posterodorsal surface and along ventral line of body; melanophores also in preorbital space, over cranium, and on lower jaw; two large yellow spots on trunk. In a specimen 3.55 mm long pigment noticeably increased, extending into anterodorsal region and developing as a definite line of melanophores in posterolateral region at level of spinal column.¹⁷ At 5.0–6.0 mm ground color of back bluish, sides with silvery reflections, eye silvery.²⁵ In a preserved specimen 6.0 mm long, black melanophores numerous on top of head, stomach, and dorsal half of trunk, scattered on oper-

culum, and lacking on fins and caudal peduncle.⁴ At 6.24 mm pigment generally increased, especially over dorsal wall of abdominal cavity.¹⁷ At 9.0 mm sides and belly more silvery.²⁵ At 13 mm back sky blue, belly silvery.⁴

PREJUVENILE

Size range 19.0²⁵–51.0 mm.² (In this species the prejuvenile stage ends with the disappearance of the blue prejuvenile pattern.)

At 19–20 mm greatest depth ca. 5 times in TL, length of head ca. 2.5 times in TL. At 30–35 mm pectorals ca. 2 times diameter of eye, pelvics almost equal to diameter

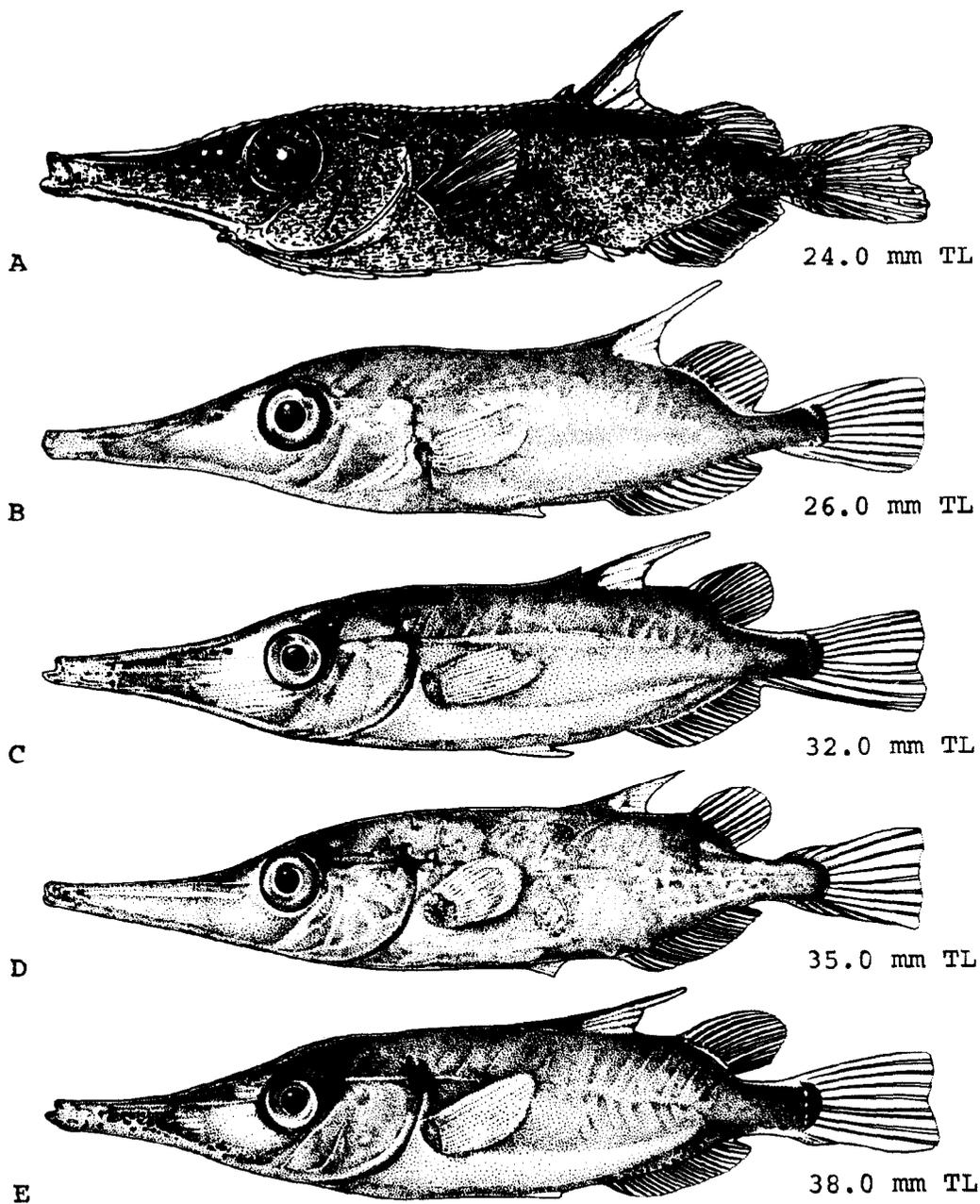


Fig. 230. *Macrorhamphosus scolopax*, Longspine snipefish. A. Prejuvenile, 24.0 mm TL. Prejuvenile, 26.0 mm TL. C. Prejuvenile, 32.0 mm TL. D. Juvenile, 35.0 mm TL. E. Juvenile, 38.0 mm TL. (A, Uchida, K., 1958: pl. 45. B-E, D'Ancona, U., 1933: pl. 18, Elizabeth Ray Peters, delineator.)

of eye. Caudal fin bilobed at 24.0–25.0 mm. Scales adult-like at 25.0 mm.^{4,25}

Pigmentation: Blue above, silvery on sides and below throughout stage. At 30–35 mm black pigment along major spine of first dorsal and at bases of 2nd dorsal and caudal rays. Loss of prejuvenile pigment may take place

in specimens as small as 35.0 mm,²⁵ while in other prejuveniles the blue pigment may be retained to at least 51 mm.²

JUVENILES

Minimum size, 35 mm.²⁵

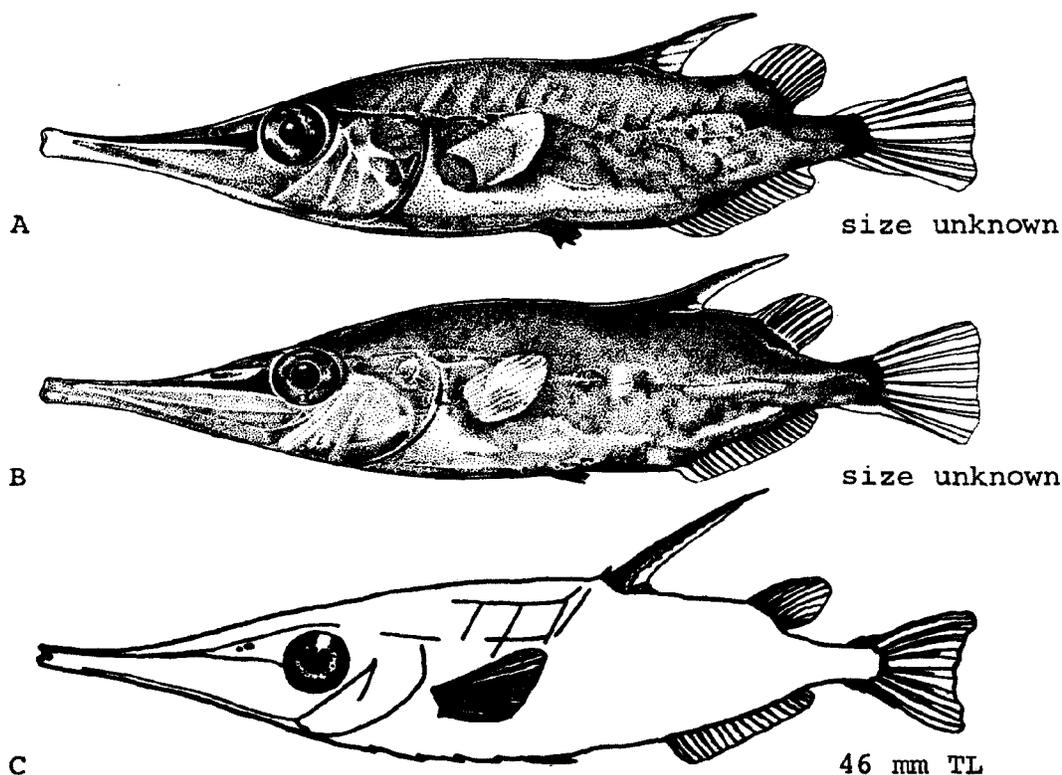


Fig. 231. *Macrorhamphosus scolopax*, Longspine snipefish. A. Juvenile, size unknown. B. Juvenile, size unknown. C. Juvenile, 46 mm TL. (A, B, D'Ancona, U., 1933: pl. 18. C, Miller, D., 1959: fig. 1.)

Pigmentation: At 35 mm reddish brown pigment develops dorsally and, to a lesser extent, ventrally and laterally. In progressively older specimens of unknown size, dorsal surface, down to lateral line, uniform reddish, venter reddish, sides with yellowish red blotches.²⁵ At 75 mm, body brick red.²⁸

AGE AND SIZE AT MATURITY

No information.

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Hippocampus erectus

Hippocampus obtusus

Syngnathus floridae

Syngnathus fuscus

Syngnathus louisianae

Syngnathus pelagicus

pipefishes and seahorses

Syngnathidae

FAMILY SYNGNATHIDAE

Members of the family Syngnathidae occur in tropical and temperate waters throughout the world. There are two subfamilies: the Syngnathinae (pipefishes), which contains 34 genera and approximately 150 species, and the Hippocampinae (seahorses) with two genera and about 25 species. Seahorses are found exclusively in marine and estuarine waters, while some pipefishes occur in freshwater. Syngnathid fishes are primarily inshore, coastal species and are frequently associated with reefs or grass beds. At least one species, *Syngnathus pelagicus*, may occur far offshore among drifting sargasso weed. Certain poorly known species are thought to burrow in the substrate.

These relatively small fishes (adults 25 to about 460 mm) are immediately distinguishable by their elongate bodies which are encased in a series of bony rings. Other characteristics include a tubular snout; a small, toothless mouth; tufted gills; a lack of pelvic fins; a very small anal fin; and a primitive kidney. In the subfamily Syngnathinae the head and body are in the same plane, the caudal fin is not distinct, and the tail is non-prehensile. In the Hippocampinae the tail is prehensile, the head is at a right angle to the body axis, and there is no caudal fin. The prehensile-tailed *Amphelikturus* (currently assigned to Syngnathinae) has a slightly cocked head; and the caudal fin is noticeably reduced. It appears to be intermediate between the two subfamilies.

Spawning, which in some species may occur throughout the year, sometimes involves complex behavioral patterns. In *Syngnathus floridae*, for example, a distinct "liebenspiel" precedes copulation. Both pipefishes and seahorses produce snapping sounds which may or may not be associated with courtship.

Eggs are carried by the male parent. In pipefishes they may be attached to the underside of either the abdomen or the tail; and may be fully exposed to water, or completely covered by the lateral folds of the brood pouch. Four modifications of the pipefish marsupium have been described. The lateral folds may be short and fail to cover the eggs, they may be long and cover the eggs completely by overlapping at the center, they may turn inward and divide the eggs in the pouch into two sections, or one flap may turn back on itself with the other flap overlapping it. In seahorses the marsupium is always under the tail, and is completely sealed for most of its length. During copulation the eggs are transferred directly from the oviduct into the marsupium.

Pipefish eggs are round, ellipsoidal, or irregular in shape. They may be various shades of yellow or orange (depending on the species), and sometimes have numerous brightly colored (red or orange) oil globules. Seahorse eggs are either oval or pear-shaped and are typically red or orange. In the eggs of most species there are, numerous oil globules, but one author has reported that oil globules are absent in *Hippocampus abdominalis*.

Early workers suggested that, in spite of the large amount of yolk present, developing eggs of *Syngnathus dumerili* and *S. typhle* receive additional nourishment directly from the male parent through the brood pouch. More recently Linton and Soloff (1964), working with *Hippocampus erectus*, concluded that the brood pouch epithelium actively transports sodium; that the pouch is, consequently, a highly effective osmoregulatory organ; that calcium is absorbed by the developing embryos from the pouch fluid; that the source of this calcium may be the bony rings of the male parent; and that "the impermeable nature of the pouch makes it almost certain that the exchanges of gases and nitrogenous waste products occur across the pouch epithelium."

The eggs hatch in the marsupium. In at least one seahorse (*Hippocampus*

zosteræ) parturition is accompanied by extreme contortions of the male's body and the young, which are usually born head first, leave the pouch with explosive violence. Young of both subfamilies are well-developed and swim freely immediately after birth. Some young pipefishes (*Entelurus* and *Nerophis*) are born with a larval finfold and may live pelagically for a brief period, while others, such as *S. typhle* and *S. acus*, are born in a very advanced state and may descend immediately to the bottom.

Young stages of the regional syngnathid fishes have not been adequately described and insufficient data exists on which to base a key. A review of meristic and pigmentary characteristics which may be useful in attempting to identify these stages is presented in table 17.

TABLE 17. Meristic and pigmentary characteristics of early stages of syngnathid fishes of the Mid-Atlantic Bight.

	Trunk rings	Caudal rings	Pigmentation
<i>H. erectus</i>	10-11	32-37	At hatching head unpigmented, body with alternating light and dark bands, pigment on gut and along dorsal base.
<i>H. obtusus</i>	10	35	No information.
<i>S. floridæ</i>	16-19 (20)	30-37 (39)	Earliest stages undescribed. At 14 mm a mid-lateral pigment band, chromatophores on belly, top and sides of head, snout, and along dorsal and ventral line.
<i>S. fuscus</i>	17-21	33-42	Slight pigment in eye at hatching, apparently no pigment on body. In later stages a distinct series of dark vertical bands on body.
<i>S. louisianæ</i>	19-21 (23)	34-39	No information.
<i>S. pelagicus</i>	16-18	30-34	(Based on pre-hatched embryos.) Eyes darkly pigmented, a heavy mid-lateral pigment band, pigment on snout and to indeterminate degree along dorsum.

The inclusion of *Hippocampus obtusus* is provisional. Mrs. Myvanwy Dick, of the Museum of Comparative Zoology, is reviewing this species and feels that it may be the juvenile of some other form. The type specimen of *H. obtusus* is presumably an immature male.

Hippocampus erectus Perry, Lined seahorse

ADULTS

D. 17-22;¹⁶ A. 3²⁸⁻⁴; ⁸ P. 15-19;²⁴ V. 4;⁵ trunk segments 10^{1,11-12}; ³² caudal segments 32¹⁻³⁷; ⁴¹ vertebrae 13 + 36-38.⁴³

Proportions as times in length: Head 3.9-4.7; depth 5.0-5.6 in females, 4.25-5.1 in males.⁴⁷ Snout 1.9¹⁵-2.7 times in head. Eye 2.4-2.9 times in snout,⁴⁷ 5.1-6.6 times in head.¹⁵ Head in trunk, measured over back from gill opening to end of dorsal base, 1.6-2.3.³²

Body deep, compressed, robust, 7-angled; tail tapering, quadrangular, prehensile; head deep, compressed, at right angle to body; profile deeply concave posteriorly; mouth vertical.^{8,19,16,32} Dorsal fin over 2.5-4.0 body segments, 1-2 caudal segments.^{16,32}

Pigmentation: Color and pattern highly variable. Ground color blackish, silver-gray,²² ash gray,³³ light brown, dusky, yellow,³¹ or brick red.^{22,36} Nearly uniform⁸ to

variously mottled and blotched,^{33,34} the blotches with contrasting paler or darker edges. Some specimens with hourglass blotch extending down each side of back;³⁸ others with striped pattern composed of a single narrow dark brown or black transverse line on trunk.¹¹ Sometimes sprinkled with white,³⁶ silver,³⁴ or light blue dots,³⁸ particularly on head and posterior part of body. Edge of dorsal fin orange in males, yellow in females.^{11,36} Capable of color changes, as from uniform black by day to lightly barred at night.¹⁷

Maximum length: Ca. 203 mm.¹⁶

DISTRIBUTION AND ECOLOGY

Range: Nova Scotia and Georges Bank to Argentina,^{5,39} Bermuda;¹¹ and at least part of the West Indies.^{6,11,39}

Area distribution: North in Chesapeake Bay at least to vicinity of Calvert County, Maryland;^{28,42} Virginia;³²

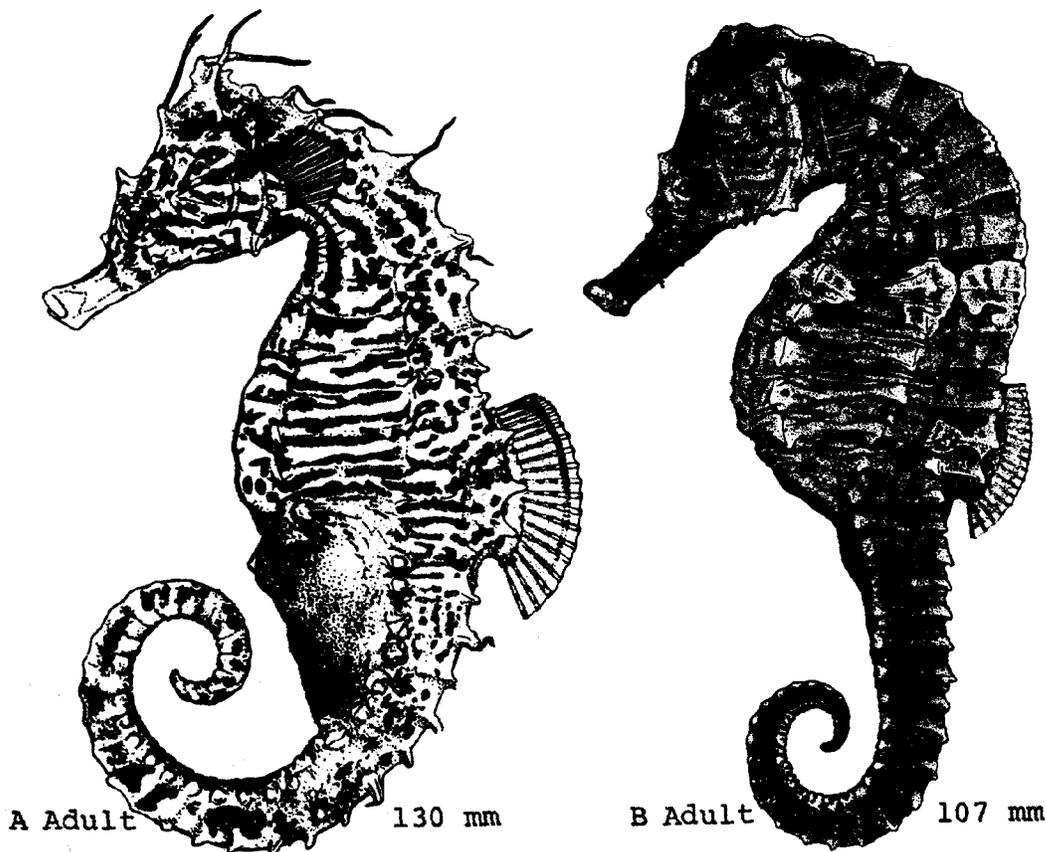


Fig. 232. *Hippocampus erectus*, Lined seahorse. A. Adult male, subspecies *erectus*, from Mississippi, 130 mm TL. B. Adult male, subspecies *punctulatus*, from Cuba, 107 mm TL. (A, B, Ginsburg, I., 1937: figs. 62-3.)

Chincoteague and Sinpuxent Bays; ²⁰ Delaware; ^{9,29} New Jersey.^{8,9}

Habitat and movements: Adults—at surface ¹⁹ and bottom ³⁵ of both shallow water ⁶ and deeper areas of channels ^{14,40} in bays, ²⁷ along beaches, ³⁵ in or near salt marshes, ^{23,35} and over oyster beds ⁹ and weed covered banks. ¹⁵ May enter rivers, ³ and sometimes at surface in water up to 38 m deep. ^{15,19} Usually associated with or clinging to aquatic vegetation such as *Thalassia*, *Agardhiella* ²⁰ eel grass, ^{23,35} and sargasso weed. ^{19,35} Salinity range, 10.0 ⁴⁵–36.6 ppt. ⁴⁸ Temperature range, 5.0–29.9 C. ⁴⁵ Maximum distance from shore, 22 km. ³⁰ Maximum depth, 46 m. ³² Apparently make annual inshore-offshore movements: Inshore from July to September at Woods Hole, Massachusetts; April to November and sometimes February in New York. ³¹ In Florida, however, less abundant inshore during warmer months (June through September). ⁴⁰ In Chesapeake Bay may retire to deeper water during colder months. ³²

Larvae—presumably hatch in brood pouch of male and retained for indefinite period. ^{2,18,22,26} Newborn (possibly juveniles) swim in cluster near surface, possibly phototropic; ²⁶ tail prehension developed at 1 day. ²

Juveniles—"Recently born" recorded from rivers entering the Potomac; ⁵⁰ specimens 6.0–33.0 mm long in masses of floating sea weed in lower Chesapeake Bay. ²⁵ Specimens up to 95.0 mm long pelagic, in comparatively deep offshore waters; ^{10,21,27} recorded from near the 183 m contour. ⁴⁴ A 30 mm specimen recorded from 12.1 ppt salinity. ⁴⁶

SPAWNING

Location: Presumably inshore (JDH); incubating males recorded in Great South Bay, Long Island, New York. ³ Unknown except by inference.

Season: Young 6.0–33.0 mm recorded from Chesapeake Bay June 6 to September 13; ²⁵ in Florida possibly year round, ¹⁴ although males with eggs and young only in late February, ²² December, ¹⁴ and (at Tortugas) August; ³⁶ gravid males at Campeche, Mexico in February, ¹⁸ and in North Carolina and New Jersey in late August; ^{7,26,37} young may be liberated as early as June at Block Island. ¹⁰

Fecundity: Unknown, brood pouch capacity: 75 ¹³–ca. 1000. ^{2,4}

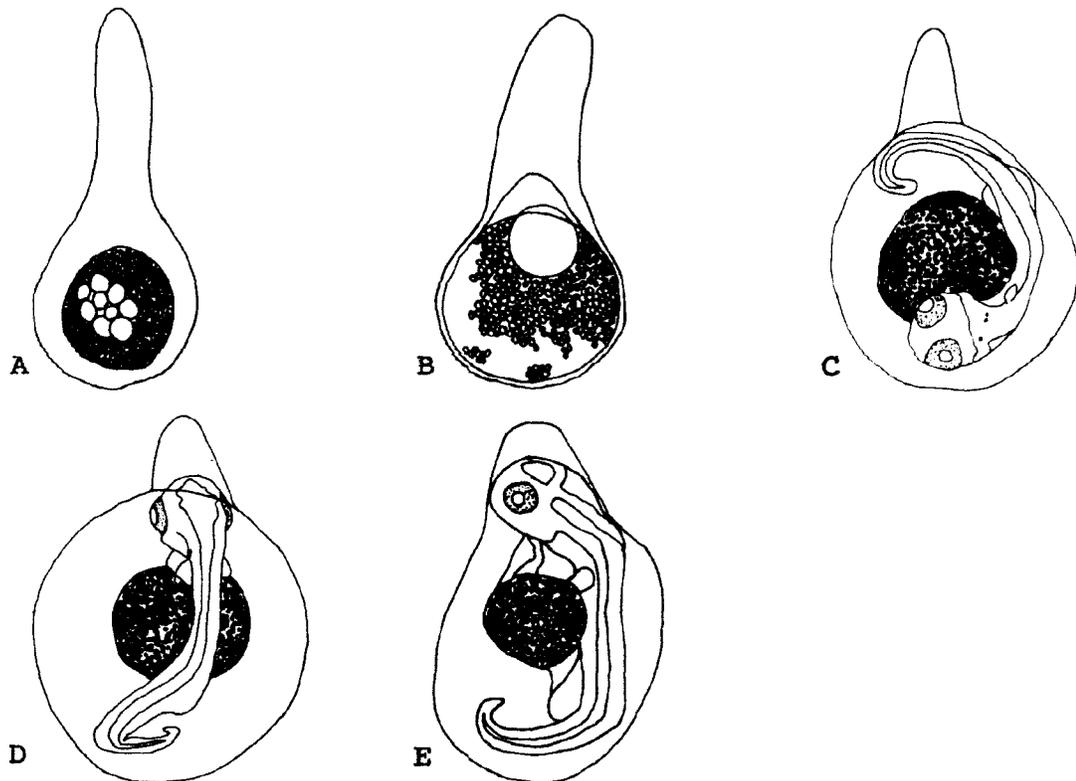


Fig. 233. *Hippocampus erectus*, Lined seahorse. A-E. Various stages in development of the egg. (A-E, Original illustrations, Linda L. Hudson.)

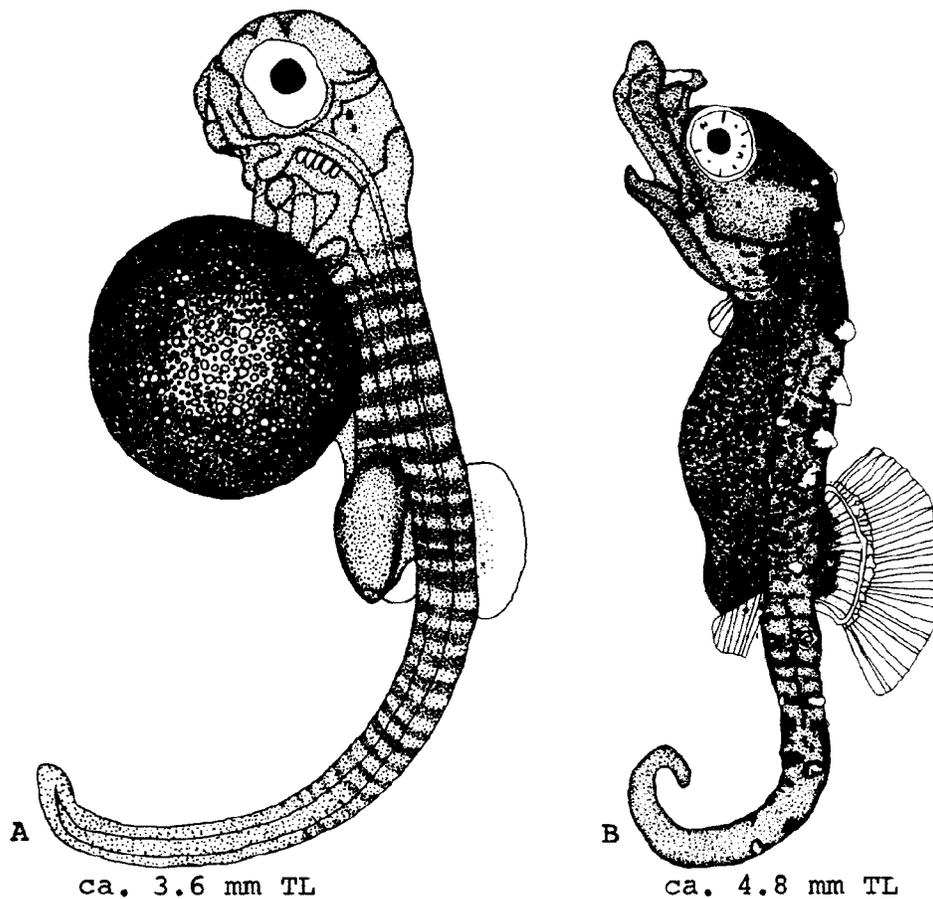


Fig. 234. *Hippocampus erectus*, Lined seahorse. A. Yolk-sac larva, ca. 3.6 mm TL. B. Yolk-sac larva, ca. 4.8 mm TL (measurements estimated from tip of snout to tip of tail). (A, B, Original illustrations, Linda L. Hudson.)

EGGS

Location: Placed in brood pouch of male.¹²

Fertilized eggs: Pear-shaped; length 3.1–3.9 mm; yolk light orange⁴⁹ or orange-yellow;¹² 1 or more large oil globules in early eggs, numerous small deep orange oil globules in advanced eggs.⁴⁹

EGG DEVELOPMENT

A distinct segmentation cavity develops; embryo first evident at edge of blastoderm; finfolds lacking throughout development.¹² In advanced embryos pectoral fins formed, eyes pigmented, head thrust into neck of pear-shaped egg.⁴⁹

Incubation period given as not less than 12–14 days in marsupium.¹²

YOLK-SAC LARVAE

Size range described (estimated measurements) ca. 3.6 to ca. 4.8 mm TL.⁴⁹

In “premature young,” muzzle short, wide;² at ca. 3.6 mm, head blunt, snout not elongate; mouth well-developed at ca. 4.8 mm. Yolk sac spherical and with many small orange and brown oil globules at ca. 3.6 mm, greatly reduced and with bright orange oil globules at ca. 4.8 mm. Otoliths visible early in stage. At ca. 4.8 mm cirri developing on body.⁴⁹ In “premature young” tail round, not quadrangular.² Rays evident in all fins at ca. 4.8 mm.⁴⁹

Pigmentation: At ca. 3.6 mm head unpigmented, body stippled with melanophores which form alternate light and dark bands; scattered melanophores on developing gut and at base of incipient dorsal fin. At ca. 4.8 mm pigment increased on body; top of head darkly pig-

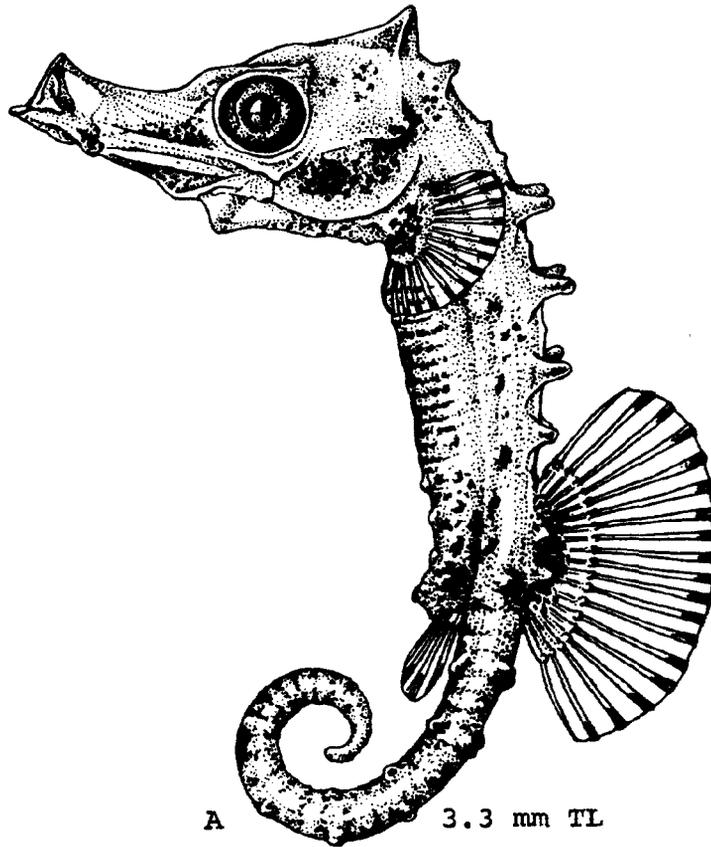


Fig. 235. *Hippocampus erectus*, Lined seahorse. A. Juvenile, 3.3 mm TL (measured from top of head to curve of tail, excluding protuberances). (A, Lippson, A. J., and R. L. Moran, 1974: 159.)

mented; cheeks and lower part of head lightly stippled; several large stellate chromatophores behind eye; eye gold and green with metallic reflections; pupil black.⁴⁹

LARVAE

A larval stage cannot be distinguished in this species (JDH).

JUVENILES

Specimens described, 3.3 mm (measured from top of head to curve of tail)⁵⁰ to 17.0 mm TL.¹¹ Also described, specimens several days¹² to 4 or 5 weeks old.²² Length at parturition, 6.0 mm or smaller (based on free-living specimens)²⁷ to ca. 12.7 mm;^{2,4} average ca. 7.0 mm.¹³

In specimens several days old, anal fin with 4 unsegmented hyaline rays; ventral dermal plates not yet developed; notochord still evident; elements of vertebral column not yet fully segmented; gill chamber roofed

over (opercular opening later evident only as a small spiracle); esophagus sharply bent; alimentary canal widened anteriorly behind esophagus; gas bladder evident as diverticulum from intestine at level of pectoral fin.¹² Cirri developing on body in some specimens at 7.0 mm,¹¹ in others at age of 4–5 weeks;²² spines longer in young than in adults;^{8,11,15} cirri of young females better developed than those of young males. Male brood pouch first evident in some males 3 1/2 months old as small pigmented area ca. 3 segments long on underside of tail.²²

Pigmentation: "Juveniles" with light-colored blotches around base of dermal spines more or less coalescent;¹¹ "half grown" individuals remain in "dark phase" constantly.¹⁷

AGE AND SIZE AT MATURITY

Age at maturity unknown, but more than 3 1/2 months.²² Largest immature males reported as 95.0 mm long and

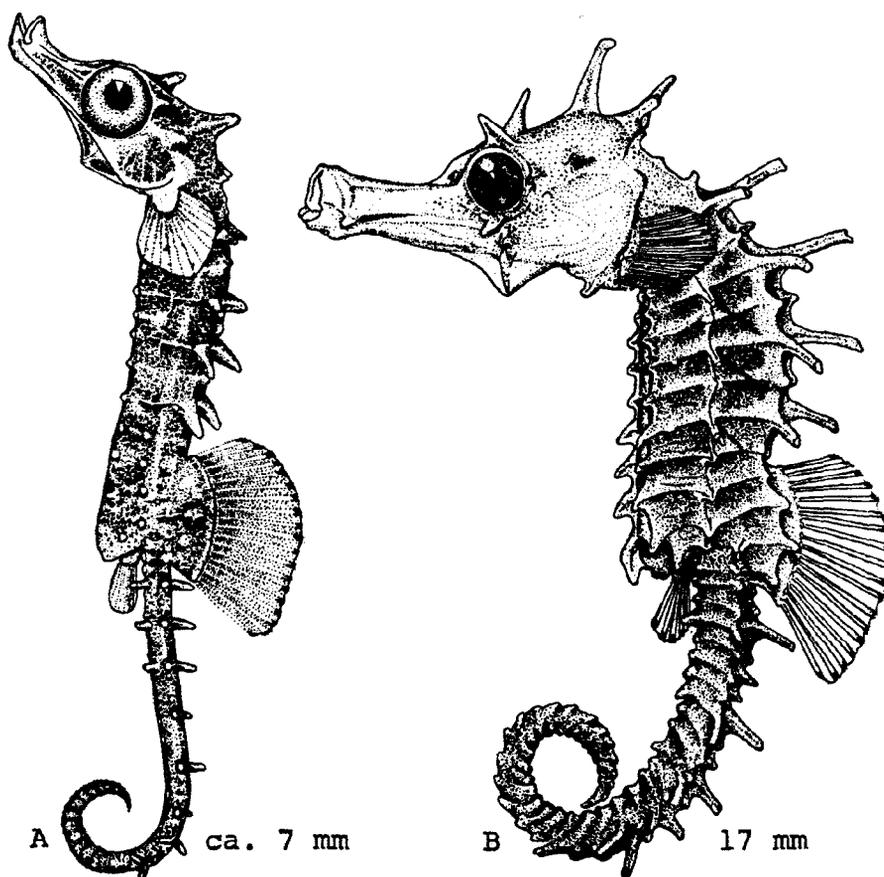


Fig. 236. *Hippocampus erectus*, Lined seahorse. A. Juvenile, ca. 7 mm TL. B. Juvenile, ca. 17 mm TL. (A, B, Ginsburg, I., 1937: figs. 59–60.)

lacking brood pouches.¹¹

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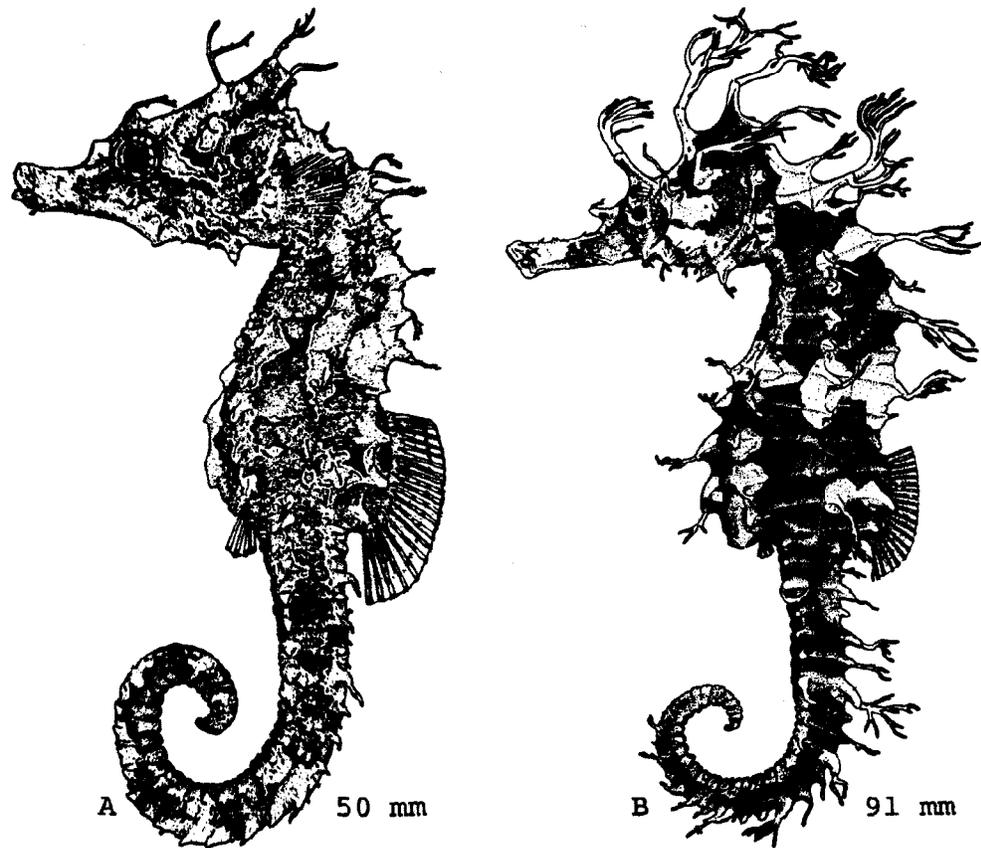


Fig. 237. *Hippocampus erectus*, Lined seahorse. A. Juvenile male, 50 mm TL. B. Juvenile male with rudimentary brood pouch, 91 mm TL. (A, B, Ginsburg, I., 1938: figs. 61, 64.)

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Hippocampus obtusus Ginsburg, Offshore seahorse**ADULTS (OR ADVANCED JUVENILE)**

D. 17; ¹ P. 16 ⁴-17; trunk rings 11; ¹ caudal rings 35.⁴

Proportions as percent length: Depth 18.8, head 24.5, snout 10.7, eye 4.4, postorbital 10.8, trunk 35.2, tail 60.9.⁵

Trunk conspicuously slender, snout rather long. First caudal segment hexangular, last caudal trunk segment octangular. Every third or fourth tubercle on trunk and anterior part of tail very stout, bluntly obtuse.⁴

Pigmentation: No information.

Maximum size: 70 mm.⁴

DISTRIBUTION AND ECOLOGY

Range: Atlantic coast from New Jersey ³ to Florida; ¹ in Gulf of Mexico recorded from Louisiana; ² also St. Lucia in the Caribbean, and Bermuda.¹

Area distribution: Various stations within the 183 m contour between central New Jersey and mouth of Chesapeake Bay.³

Recorded temperature range 22.2 ²-31.0 C.¹

SPAWNING

No information.

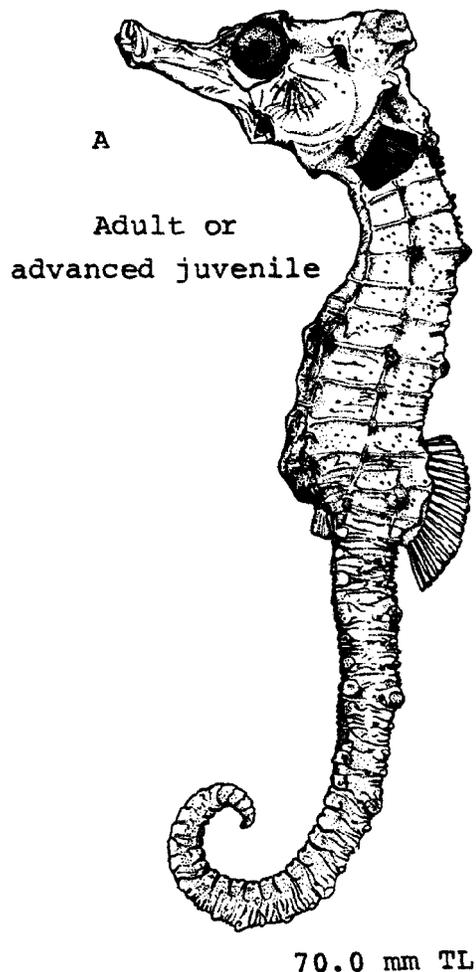


Fig. 238. *Hippocampus obtusus*, Offshore seahorse. A. Adult or advanced juvenile, 70.0 mm, a male with brood pouch just developing. (A, Ginsburg, I., 1937: fig. 67.)

EGGS

No information.

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LARVAE

No information.

JUVENILES

No information.

AGE AND SIZE AT MATURITY

A 70 mm male with brood pouch just developing.⁴

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Syngnathus floridae (Jordan and Gilbert), Dusky pipefish

ADULTS

D. 27⁴–34; ²⁴ A. 3; C. 10; ^{2,4} P. 13–15; ⁹ trunk rings 16–19 ^{2,4} or 20; ²² caudal rings 30–37⁴ or 39; ¹¹ vertebrae 18+33–34.²⁹

Proportions as times in SL: Head 5.2–6.8, usually 5.4–5.9. Proportions as times in TL: head 4.75²⁰–7.8, tail 1.7–1.8.¹¹ Proportions as times in head: dorsal 1.35–1.85, usually 1.45–1.70; snout 1.6–1.88.²

Caudal portion of body quadrangular.³¹ Females slightly V-bellied,^{2,4} and apparently increasing significantly in depth from 165–200 mm.²⁴ Dorsal fin on 1/2–2² or 3¹¹ trunk rings and 4.5–7^{11,22,36} caudal rings. Brood pouch on 17–20 rings⁴ (counts of 13–15²⁴ are probably based on immature or nonegg-bearing males, JDH). Contacting edges of brood pouch covered with small papillae.⁴

Pigmentation: Usually light to dark green,^{1,14} the shade varying with surroundings;²³ also reported as yellow, buff,¹¹ or light gray;²⁴ center of each segment slightly lighter than ground color;¹¹ lateral stripe lacking;^{16,25} sides more or less spotted or streaked with gray, white, or blue^{11,14,24,25} and with 5–10 narrow light bands before dorsal, 5–7 behind; underside of belly and tail sprinkled with light on dark background in males; area below lateral keel light lemon yellow in large females;²⁴ tail marked with faint broken bars, broader than interspaces,

and pale oblong spots; snout mottled, especially on sides; lower part of opercle nearly plain; dorsal fin translucent, yellow at base; anal fin plain; caudal fin yellow, dusky at base.^{6,14,16,25}

Maximum reported length: Ca. 229 mm.¹⁴

DISTRIBUTION AND ECOLOGY

Range: Chesapeake Bay to Panama,^{2,27} also the West Indies,²¹ Bermuda^{2,9,19} and vicinity of the Azores;³⁰ absent between Seabrook Beach, South Carolina, and Miami, Florida.²

Area distribution: North in Chesapeake Bay to Plum Point, Calvert County, Maryland;^{2,5} Virginia;^{4,8,20} Chincoteague Bay.¹³

Habitat and movements: Adults—over sand⁸ or mud^{1,10} bottoms of shores,^{3,8,25} flats,¹⁰ bays,⁷ harbors,^{1,18} tide basins,¹² and mouths of creeks;²⁰ usually associated with aquatic vegetation such as *Zostera*,^{1,14} *Ulva*, *Agardhiella*,²⁷ and turtle grass;^{15,24} also sometimes associated with sargassum.³⁰ Salinity range, 12.3⁷–38.8 ppt³⁴ but most abundant at 17.0–22.0 ppt.²⁷ Maximum recorded temperature, 31.0 C.³⁴ In vicinity of Chesapeake Bay move out into deeper water during winter months,⁴ return inshore in early June (when water temperatures average 22.5 C),

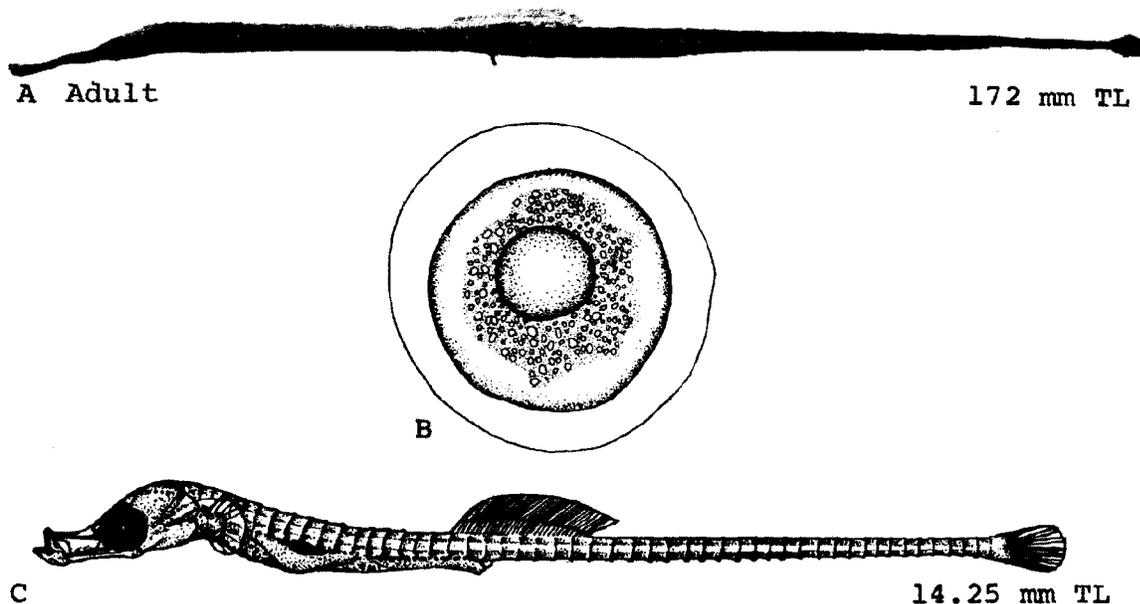


Fig. 239. *Syngnathus floridae*, Dusky pipefish. A. Adult, 172 mm TL. B. Egg, diameter ca. 1.0 mm, blastodisk formed. C. Larva, 14.25 mm TL. (A, Böhlke, J. E., and C. C. G. Chaplin, 1968: 191. B, Gudger, E. W., 1906: fig. 1. C, Original drawings, A. J. Lippson.)

reaching peak inshore abundance in late July and early August, remain inshore until October.²⁷ In more southern latitudes, movements apparently reversed, most abundant inshore in Florida Bay from October through February.¹⁷

Larvae—carried in brood pouch of male until about 11.5 mm long.²⁸

Juveniles—"small specimens" in harbors and bays;³³ specimens 41.6–79.0 mm long inshore in June at Tampa, Florida.¹⁷ Salinity range, 19.0–27.0 ppt. Temperature range 25.1–29.8 C.³⁶

SPAWNING

Location: Not definitely stated, but presumably inshore (JDH).

Season: In Tortugas, males with eggs in June and July; June to August at Beaufort, North Carolina;¹⁴ males with eggs from May to October in Chesapeake Bay,²⁰ although spawning possibly as early as April in lower Chesapeake Bay, peak activity in late July and August;²⁷ during all months but January in Florida.^{2,10,17,24,30}

Time: Occurs at night or early morning.^{1,14}

Fecundity: Mature ova 140–ca. 1100, average 519. Brood pouch capacity: 130–447, average 263.9.¹⁰

EGGS

Location: Deposited in brood pouch of male. Initially loosely arranged, later in 2–4 rows and 1–2 layers in each side of pouch^{2,4,15} and firmly attached to pouch within 36–48 hours (eggs in 3 different stages of development may be found in brood pouch).

Unfertilized egg: Diameter ca. 1.0 mm, yolk straw-colored and with many oil globules in periphery.¹

Fertilized egg: Diameter, from average of 0.9 mm² to extreme of 1.2 mm.⁴

EGG DEVELOPMENT

Development at unspecified temperature:¹

Blastodisc stage—blastodisc button-shaped, highly arched, clearly marked off by circumferential furrow; disc rests on orange-red layer of oil globules covering about 1/4 of yolk; during this stage yolk clears; disc may form without fertilization.

2-cell stage (probable age 4–6 hours)—just prior to cleavage, blastodisc somewhat elongated; blastomeres may be of unequal size; cleavage furrow not reaching yolk.

4-cell stage—second cleavage crosses first at right

angles; segmentation cavity evident.

8-cell stage—blastoderm considerably elongated, blastomeres may be irregular in size and shape and develop in layers rather than flat.

32-cell stage—cells piled up and irregular (a 16-cell stage was described in which 90% of the eggs examined were atypical of normal teleostean development).

Advanced morula—surface cells flattened, periblast free from yolk.

Just prior to invagination—blastoderm spreading over yolk; cells crowded into high arched band; subgerminal cavity large.

At ca. 4 days—tail free.¹

Incubation period: Ca. 10 days.¹⁴

YOLK-SAC LARVAE

Specimen described, 11.5 mm TL.

At 11.5 mm TL, yolk visible only in cross-section¹ (although other specimens of this size apparently lack yolk).²⁸

LARVAE

Size range described, 14.25–18.5 mm TL.

At 14.25 mm TL, body segments 19 + 31; dorsal, caudal, and pectoral fins fully developed (AJL). Remnant of continuous finfold evident, especially ventrally, in specimens less than 18.5 mm long.¹

Pigmentation: At 14.25 mm TL, a clear band mid-laterally on body; chromatophores developed over belly, on top and sides of head, on snout, and dorsally and ventrally along body (AJL).

JUVENILES

Minimum size unknown.

Body more slender in "young" than in adults.²⁰ Incipient male brood pouch at 46 mm.⁹

AGE AND SIZE AT MATURITY

Minimum age at maturity unknown. Minimum size at maturity, for males 104 mm,⁹ females 75 mm.⁴

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Syngnathus fuscus Storer, Northern pipefish**ADULTS**

D. 35–43; A. 3; C. 10; P. 12–16; trunk rings 17²⁹–21; ²³ tail rings 33³–42; ³⁰ vertebrae 19–21 + 36–39.⁵⁰

Proportions expressed as times in TL: Head 6.5²⁹–9.0; ^{10,39} depth 35 in males, 30 in females; ³¹ dorsal 38.¹ Snout in head 1.7⁶–2.36.³ Tail in trunk 1 2/3.¹⁰ Pectoral base in pectoral length 1.6–2.1.⁶

Body elongate, slender,¹ distinctly ridged,⁶ hexagonal in cross-section in front of anus, four-sided behind dorsal; ³¹ males and immature females always flat-bellied, adult females from localities north of South Carolina decidedly V-bellied.^{3,6} Head slender, tapering; ¹ occiput, nuchal plates, opercles carinate; ²⁴ snout tube-like, blunt ended; ³¹ mouth oblique, toothless; mandible protuberant, eye slightly ellipsoid.¹ Origin of dorsal fin a little behind first third of body; ¹ dorsal on 4^{6,29}–6¹ trunk segments (a count of 3 is questionable²⁹) and 4³–6⁶ caudal segments; caudal fin rounded.³¹ Brood pouch over 12.5³–18⁶ caudal segments.

Pigmentation: Dark green²³ to olive brown¹ or brown²³ above, rarely brick red; ⁴ sides lighter, ¹ grading imperceptibly to pale or golden yellow below.³¹ Trunk usually with 4 dark cross bands composed of diamond-shaped reticulations, irregular streaks, or solidly pigmented areas; tail with 8–9 similar bands. Some Chesapeake Bay specimens with indistinct vertical silver bars below lateral ridge on each trunk segment.⁶ Lower parts of opercle silvery.^{22,23} Iris pale brassy and with conspicuous dark streak.¹ Dorsal fin uniform pale^{31,32} or with 8–9 oblique bands; ⁶ anal fin plain; caudal fin brown.²⁷

Maximum length: Ca. 305 mm.¹¹

DISTRIBUTION AND ECOLOGY

Range: Prince Edward Island, Gulf of St. Lawrence,^{6,31} to Jupiter Inlet, Florida;⁵² also a relict population in vicinity of Corpus Christi, Texas.^{3,39}

Area distribution: North in Chesapeake Bay and associated rivers to Baltimore, Maryland;^{10,29} Chincoteague Bay; ²⁰ Virginia; ³⁶ Delaware; ²⁵ New Jersey.²⁶

Habitat and movements: Adults—shallow bays,⁶ harbors, rivers, creeks, salt marshes,^{31,40,51} ponds,^{17,33} sloughs,⁶ and tide pools; ⁴ also over bars,¹² near shores,² and in surf; ¹ rare in open ocean; ²⁷ frequently associated with eelgrass,^{11,12,33,42,46} sea lettuce,^{22,46} and floating rockweed; ^{6,36} reported over bottoms of mud, sand, and gravel.⁵¹ Maximum distance from shore 16 km.²⁸ Maximum depth 49 m.²⁹ Salinity range 0.0 ppt^{15,29,30}–31.3⁵⁵ ppt, but prefer salinity range 13.0–20.0 ppt.⁴⁶ Reported temperature

range 6.2¹³–27.0 C.⁵¹ In Chesapeake Bay, move inshore in late March or early April, return to deeper water (up to 49 m) in late October and November; ^{6,29,35} in vicinity of Long Island during winter (at temperature of 10.6 C) observed in torpid state lying motionless on bottom, also partially buried in sand, or curled around sand dollars; ⁴⁷ inshore March to October in Delaware,²¹ mid-April (at temperature of ca. 6.0 C) to end of October (temperature ca. 13.0 C) in southern New England.¹³

Larvae—retained in brood pouch of male to lengths of 8.0³¹ to 12.0 mm.^{33,37} Apparently pelagic for first few weeks after parturition; a 13.0 mm SL specimen recorded at surface outside Sandy Hook, New Jersey; ¹³ also recorded from upper Mystic River, Connecticut.⁴¹ Salinity range 2.0–22.0 ppt.⁴⁹

Juveniles (may include some larvae)—pelagic⁵ or semi-pelagic⁸ and found considerable distances offshore^{3,7} (up to ca. 176 km¹⁴), although also recorded from tidal creeks; ⁵¹ sometimes associated with floating algae or detritus; ⁵ also reported along shore over sand and gravel bottom.¹⁰ In surface collections at Woods Hole mid-May to early November, but with great variation in seasonal appearance in different years; ⁹ juveniles inshore in York River, Virginia, in June.⁴⁶ “Young” subject to transport by tidal currents; ⁵ if carried offshore, return to sublittoral zone at lengths of 30⁴³–70 mm.⁸ Salinity range 2.0–22.0 ppt.⁴⁹

SPAWNING

Location: Breeding specimens seined from eelgrass in Rhode Island; ³³ also in “slightly brackish” water in Hudson River.⁴⁵

Season: In lower Chesapeake Bay breeding probably begins in early March and continues until late August, peak in May and early June; ⁴⁸ spawning also reported as late as October in Chesapeake Bay; ²⁹ mid-May^{11,13,49} or possibly March^{31,32} to July⁴¹ or August from various localities between New Jersey and New England; ^{22,34,38} larvae reported in September in Maine; ³³ males with eggs and larvae in August in Cobequid, Canada.²⁷

Fecundity: Reported maximum of 860. Brood pouch capacity 104–570.²⁹

EGGS

Location: Deposited in brood pouch of male. In males 82–100 mm long, in single row on each side of pouch; in larger males in 2–4 rows and 2–3 layers on each side.

Fertilized eggs: Diameter 0.75¹⁸–1.0 mm; ⁶ yolk lemon- or

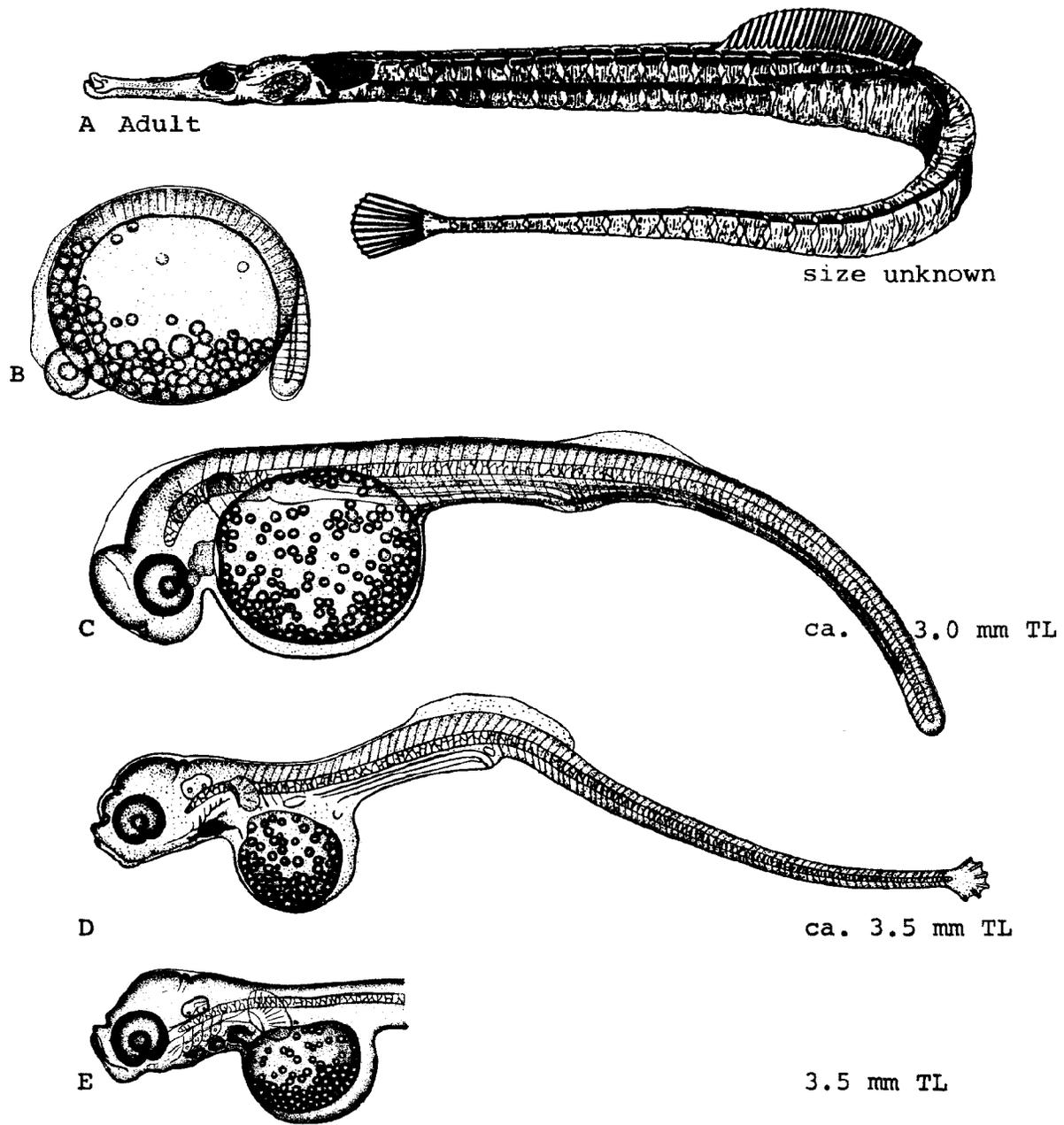


Fig. 240. *Syngnathus fuscus*, Northern pipefish. A. Adult, size unknown. B. Embryo, tail free. C. Embryo, ca. 3.0 mm TL. D. Embryo, ca. 3.5 mm TL. E. Detail of anterior end of a second embryo 3.5 mm TL. (A, Bigelow, H. B., and W. C. Schroeder, 1953: fig. 172. B-E, Ryder, J. A., 1887: figs. 19-22.)

orange-yellow, and with deeper-colored oil globules.^{18,19}

EGG DEVELOPMENT

Incubation period: Ca. 10 days.³¹

YOLK-SAC LARVAE

Minimum hatching length, ca. 3.0 mm.¹⁸ Maximum length described 6.0–7.0 mm.²

Head deflected downward at 3.0 mm, straight at 3.5 mm.¹⁸ Snout beginning to elongate at 6.0–7.0 mm.² Yolk mass nearly spherical at 3.0–3.5 mm,¹⁸ oval at 4.0–7.0 mm.² Mouth apparently not formed at 3.0 mm, well-developed and vertically oriented at 3.5 mm. Choroid fissure retained to at least 3.5 mm.¹⁸ Auditory capsules, otoliths first visible at 3.0–4.0 mm.² Branchial arches formed at 3.5 mm,¹⁸ branchial cavity completely enclosed

in cartilage throughout stage.³⁴ Nares developed, visible from above, at 6.0–7.0 mm.² Finfold poorly developed,¹⁹ or absent.¹⁸ Origin of incipient dorsal fin over anus at ca. 3.0 mm; anus under center of developing dorsal fin at 3.5 mm. Anal fin may be absent at hatching,¹⁸ although evident, at least in some specimens, at 3.0–4.0 mm.² End of tail rounded and lacking fin at 3.0 mm; incipient caudal rays at 3.5 mm. Pectoral buds evident at 3.0 mm, pectoral fins partly rotated on bases at 3.5 mm.¹⁸ Urostyle oblique at 3.0–4.0 mm. Gut straight, intestinal valve developing at ca. 7.0 mm.²

Pigmentation: Undescribed, but illustrations suggest that eye is partially pigmented at hatching (JDH).

LARVAE

Size range described, 7.75 (AJL)–20.0 mm.⁶

At 12.0 mm, 5 branchial arches formed, olfactory nerves

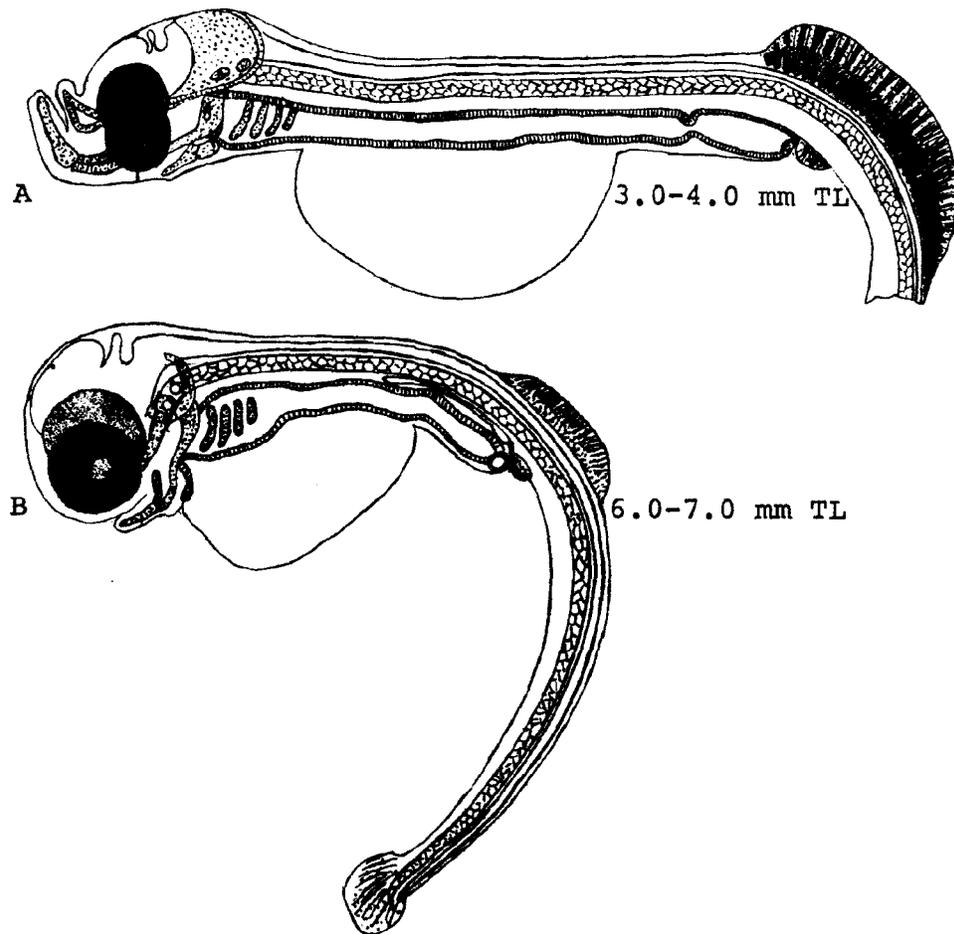


Fig. 241. *Syngnathus fuscus*, Northern pipefish. A. Yolk-sac larva, 3.0–4.0 mm TL. B. Yolk-sac larva, 6.0–7.0 mm TL. (A, B, McMurrick, J. P., 1883: figs. 1–2.)

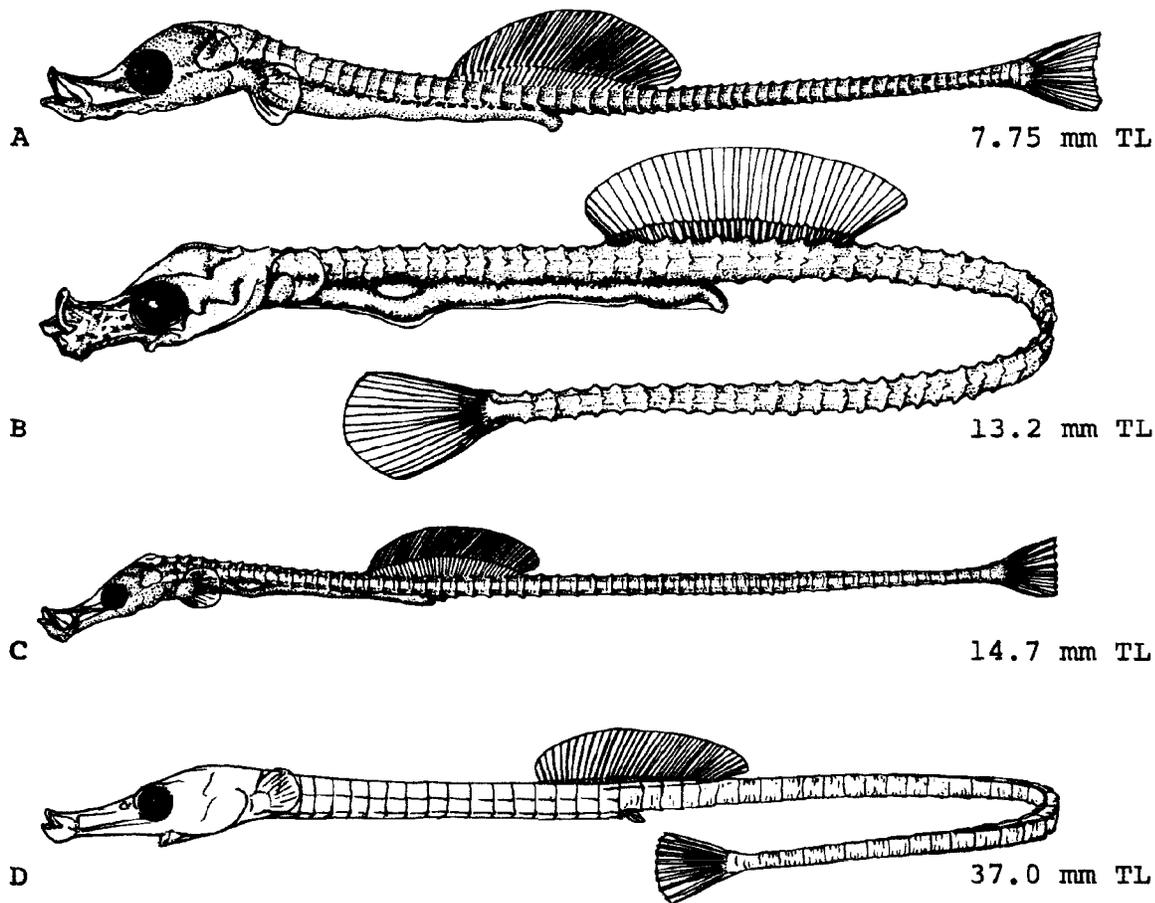


Fig. 242. *Syngnathus fuscus*, Northern pipefish. A. Larva, 7.75 mm TL. B. Larva, 13.2 mm TL. C. Larva, 14.7 mm TL. D. Juvenile, 37.0 mm TL. (A, C, D, Original drawings, A. J. Lippson. B, Lippson, A. J., and R. L. Moran, 1974: 161.)

not yet separated by cartilage.^{37,44} Remnant of ventral finfold evident at 8.5 mm, notochord hyaline at this size (NSS). Ossification of dorsal scales simultaneous with that of neural and transverse processes of vertebrae.⁵⁴ At 20.0 mm minute serrations along ridges of trunk and tail.⁶ Gas bladder well-developed at 13.2 mm.⁴⁹

Pigmentation: At 8.5 mm, about 5 dark bands behind dorsal fin, 2 in front of dorsal fin; at 8.7 mm postdorsal bands increased to around 9 (NSS).⁵⁴ At 13.2 mm a series of chromatophores along dorsal and ventral edge of gut, pigment over developing gas bladder, large chromatophores on snout in front of eye.⁴⁹

JUVENILES

Specimens illustrated, 37.0 mm (AJL).

Pigmentation: Body transparent and lacking pigment

early in stage; star-shaped melanophores over entire body surface by end of stage.⁴⁹

AGE AND SIZE AT MATURITY

Mature at about 1 year.^{13,33} Males, 83.0 mm; ⁶ females, unknown.

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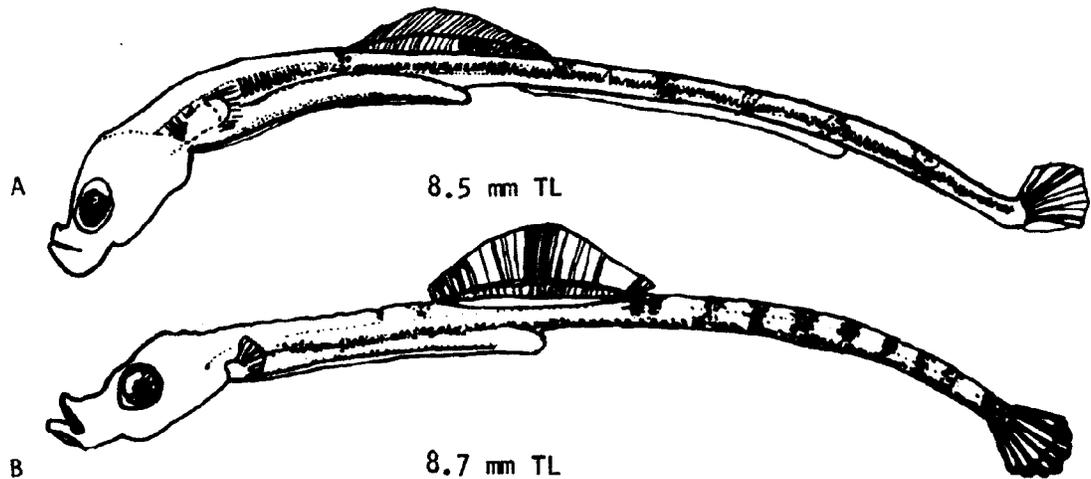


Fig. 243. *Syngnathus fuscus*, Northern pipefish. A. Larva, 8.5 mm TL. B. Larva, 8.7 mm TL. (A, B, Scotton, L. N., et al., 1973: 160.)

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Syngnathus louisianae Günther, Chain pipefish

ADULTS

D. 30–40; A. 2–3; ^{22,31,33} C. 10; P. 13–16; trunk rings 19–21 ¹ (but also reported to 23 ⁴), usually 20; ^{24,25} tail rings 34–39; ¹ vertebrae 19–20 + 32. ²⁷

Proportions expressed as times in TL: Depth 27–32, ¹⁸ head 6.5 ³¹–8.5, ¹⁸ tail 1.78. ² Snout in head 1.58–1.88. ³³

Trunk broader below, ² flat ²⁹ or slightly concave and with median ridge; ^{2,19} occiput, nuchal plates, and opercle somewhat keeled. ¹¹ Dorsal fin over 1.5 ³³–4 ⁴ + 4–6 rings, ¹ average dorsal coverage, 7.5 rings. ³¹ Brood pouch on 17–19 ¹⁸ or possibly 20 ²⁵ rings.

Pigmentation: Usually light brown with or without darker diamond-shaped reticulations; lower parts of trunk and abdomen lighter; with or without a well-marked lateral brown band extending through eye to end of snout; dorsal sometimes with 7 vertically diagonally dark brown stripes; caudal usually blackish brown; other fins plain. ^{1,4,9,17}

Maximum length: 326 mm. ²⁴

DISTRIBUTION AND ECOLOGY

Range: In continental North America from Chesapeake Bay, Maryland, to Aransas Bay, Texas; ^{1,22} also reported from Campeche, Mexico, ³³ Bermuda, ⁴ Jamaica, ³² and throughout Gulf of Mexico. ²⁰

Area distribution: Cape Charles City, Virginia; ^{15,16} north in Chesapeake Bay to St. Mary's County, Maryland. ¹¹

Habitat and movements: Adult—sometimes pelagic; ³² recorded in water 0.6 m ¹⁴ to 128 m ²⁴ deep in lagoons, bays, ^{1,23} rivers, ²¹ tide basins, ⁵ grassy flats, ^{7,12} and harbor mouths; ¹³ possibly more abundant offshore. ¹² Typically associated with aquatic vegetation ^{8,10,26} such as eelgrass, ⁹ *Halodule*, *Thalassia*, ⁷ and floating clumps of *Sargassum*. ^{1,18} Maximum distance from shore, 48 km. ²⁴ Salinity range

0.00 ²¹–45.0 ppt. ⁸ Maximum recorded temperature 34.9 C. ²⁹

Larvae—held within male brood pouch (JDH).

Juveniles—apparently more inshore than adults; ¹² taken from “boiling surf” in Texas. ¹ Salinity range 13.1–36.5 ppt. Temperature range 12.4–30.8 C. ³³

SPAWNING

Location: Unknown; males with advanced eggs on grassy shoals at Beaufort, North Carolina, ⁹ also in offshore waters of Gulf of Mexico. ^{6,7}

Season: May and June in Texas, ⁸ with brooding males reported in Texas in July; ⁷ brooding males reported in early June at Beaufort, North Carolina, ⁹ mid-February at Campeche, Mexico, ⁶ July in Gulf of Mexico, ⁷ and September in Florida. ¹³

EGGS

Deposited in 1 or 2 layers and 4–6 rows on each side of male brood pouch; diameter, 0.7–0.8 mm. ¹

YOLK-SAC LARVAE

No information.

LARVAE

No information.

JUVENILES

Minimum size described, “less than 50 mm.”

In “juveniles” an anterior orbital projection usually present. Specimens of less than 50 mm sometimes with pro-

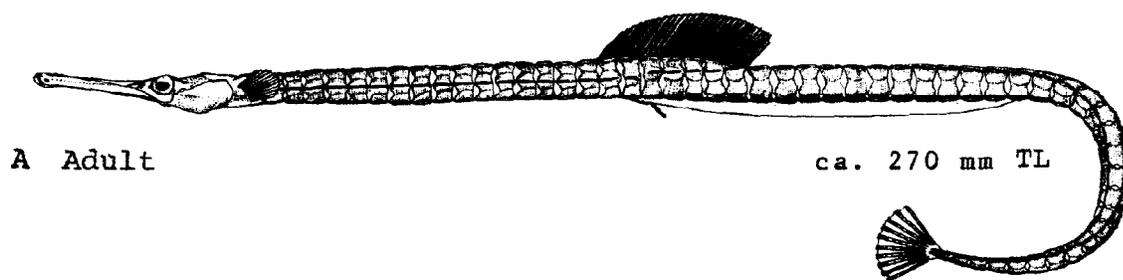


Fig. 244. *Syngnathus louisianae*, Chain pipefish. A. Adult, ca. 270 mm TL. (A, Herald, E. S., 1943.)

nounced spines or ridges. Brood pouch beginning to form at ca. 180 mm.¹

Pigmentation: In "juveniles" often ca. 5 trunk and 8-9 caudal rings of dark brown,¹ "young" also described as with reticulated chain-like pattern.³³

AGE AND SIZE AT MATURITY

Smallest confirmed mature male 200 mm,¹ but possibly as small as ca. 185 mm.¹³

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Syngnathus pelagicus Linnaeus, Sargassum pipefish

ADULTS

D. 28–31; ⁶ A. typically 3 (CED); C. 10; P. 13–14; ⁴ trunk rings 16–18; ⁶ tail rings 30–34; dorsal fin on 0.75–2.25 trunk rings, 4.25–7.00 tail rings; ⁶ brood pouch under 12–15 tail rings.⁶

Head 6.6 times in TL, about twice in trunk; eye ca. 6 times in HL; ⁴ pectoral fin 5.2–6.3 times in HL.⁶

Body rather slender, trunk heptagonal, tail tetragonal,⁴ females distinctly V-bellied.⁶ Body rings transversely striated, their edges pronounced but smooth.⁴

Pigmentation: Ground color brown,⁴ lower half of each trunk segment usually with a narrow black-margined vertical white line or spot; upper half of trunk and all of tail not distinctly marked, but with some light areas on each segment; ⁶ also described as having a faint silvery transverse bar on trunk rings and a light transverse bar on every third caudal ring; ⁴ dorsal fin with a dark stripe down middle and several basal clumps of dark pigment.⁶

Maximum length: 165 mm SL (CED).

DISTRIBUTION AND ECOLOGY

Range: Atlantic, Indian, and western Pacific oceans, and the Mediterranean Sea; in the western Atlantic, Gulf of Maine to Argentina,¹ (but southern limit questioned, CED) including Bermuda,¹ the Sargasso Sea,³ the West Indies,⁴ and the Gulf of Mexico. Also recorded from the coast of West Africa.⁵

Area distribution: Inshore along coast of northern New Jersey.⁷

Habitat and movements: Adults—associated with sargasso weed.^{2,9}

Larvae—recorded over depths of 73–3220 m;¹⁰ a specimen 9.5 mm long collected ca. 1370 km off the coast of Africa.⁵ Recorded salinity range 23.3⁸–35.9.⁵

Juveniles—no information.

SPAWNING

No information.

EGGS

Early eggs round, advanced eggs elongate, tubular. Advanced embryos with a heavy mid-lateral pigment band, pigment on snout and to indeterminate degree along dorsum; eyes darkly pigmented (JDH).

EGG DEVELOPMENT

No information.

YOLK-SAC LARVAE

No information.

LARVAE

No information.

JUVENILES

No information.

AGE AND SIZE AT MATURITY

Males with eggs in brood pouch as small as 71 mm SL (CEL).

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Fig. 245. *Syngnathus pelagicus*, Sargassum pipefish. A. Adult, 100 mm TL. (A, Böhlke, J. E., and C. C. G. Chaplin, 1968: 190.)

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INDEX TO COMMON AND SCIENTIFIC NAMES

<i>Ablennes hians</i>	87	<i>Euleptorhamphus velox</i>	128	lined seahorse	391
<i>aculeatus, Gasterosteus</i>	347	Exocoetidae	111	longfin hake	290
<i>acus, Tylosurus</i>	96	<i>Fistularia</i>	368	longspine snipefish	378
<i>aeglefinus, Melanogrammus</i>	260	<i>petimba</i>	368	<i>louisianae, Syngnathus</i>	407
<i>affinis, Gambusia</i>	206	<i>tabacaria</i>	371	<i>Lucania parva</i>	196
agujon	96	Fistulariidae	367	<i>luciae, Fundulus</i>	181
<i>Ahlia egmontis</i>	49	flat needlefish	87	Macrorhamphosidae	377
<i>albidus, Merluccius</i>	328	<i>floridae, Syngnathus</i>	399	<i>Macrorhamphosus scolopax</i>	378
American eel	18	flying halfbeak	128	<i>majalis, Fundulus</i>	186
<i>Anguilla rostrata</i>	18	flyingfish, Atlantic	113	<i>marina, Strongylura</i>	90
Anguillidae	17	fourbeard rockling	226	marsh killifish	152
<i>Apeltes quadracus</i>	342	fourspine stickleback	342	<i>Melanogrammus aeglefinus</i>	260
Atlantic cod	236	<i>Fundulus</i>		Merlucciidae	327
Atlantic flyingfish	113	<i>confluentus</i>	152	<i>Merluccius albidus</i>	328
Atlantic needlefish	90	<i>diaphanus</i>	156	<i>Merluccius bilinearis</i>	330
Atlantic saury	72	<i>heteroclitus</i>	162	<i>Microgadus tomcod</i>	278
Atlantic tomcod	278	<i>luciae</i>	181	minnow, sheepshead	145
		<i>majalis</i>	186	moray, green	34
ballyhoo	129	<i>funebis, Gymnothorax</i>	34	<i>morhua, Gadus</i>	236
banded killifish	156	<i>fuscus, Syngnathus</i>	402	mosquitofish	206
Belonidae	85	Gadidae	219	mummichog	162
<i>bilinearis, Merluccius</i>	330	<i>Gadus morhua</i>	236	Muraenidae	33
bluespotted cornetfish	371	<i>Gambusia affinis</i>	206	<i>Myrophis punctatus</i>	52
<i>brasiliensis, Hemiramphus</i>	129	Gasterosteidae	341		
		<i>Gasterosteus aculeatus</i>	347	needlefish	
Carolina hake	314	<i>gomesi, Ophichthus</i>	58	Atlantic	90
chain pipefish	407	green moray	34	flat	87
<i>Cheilopogen heterurus</i>	113	<i>Gymnothorax funebis</i>	34	northern pipefish	402
<i>chesteri, Phycis</i>	290	haddock	260		
chuss, <i>Urophycis</i>	305	hake		<i>obtusus, Hippocampus</i>	397
<i>cimbrius, Enchelyopus</i>	226	Carolina	314	<i>oceanicus, Conger</i>	40
cod, Atlantic	236	longfin	290	<i>ocellatus, Ophichthus</i>	61
<i>confluentus, Fundulus</i>	152	offshore	328	offshore hake	328
conger eel	40	red	305	offshore seahorse	397
<i>Conger oceanicus</i>	40	silver	330	Ophichthidae	45
Congridae	39	spotted	316	<i>Ophichthus</i>	
cornetfish		white	321	<i>gomesi</i>	58
bluespotted	371	halfbeak	133	<i>ocellatus</i>	61
red	368	halfbeak, flying	128	palespotted eel	61
<i>crocodilus, Tylosurus</i>	102	Hemiramphidae	127	<i>parva, Lucania</i>	196
<i>cruentifer, Pisodonophis</i>	64	<i>Hemiramphus brasiliensis</i>	129	<i>pelagicus, Syngnathus</i>	409
<i>Cyprinodon variegatus</i>	145	<i>heteroclitus, Fundulus</i>	162	<i>petimba, Fistularia</i>	368
Cyprinodontidae	141	<i>heterurus, Cheilopogon</i>	113	<i>Phycis chesteri</i>	290
		<i>hians, Ablennes</i>	87	pipefish	
<i>diaphanus, Fundulus</i>	156	<i>Hippocampus</i>		chain	407
dusky pipefish	399	<i>erectus</i>	391	dusky	399
		<i>obtusus</i>	397	northern	402
<i>earli, Urophycis</i>	314	houndfish	102	sargassum	409
eel		<i>Hyporhamphus unifasciatus</i>	133	<i>Pisodonophis cruentifer</i>	64
American	18	key worm eel	49	Poeciliidae	205
conger	40	killifish		<i>Pollachius virens</i>	292
key worm	49	banded	156	pollock	292
palespotted	61	marsh	152	<i>punctatus, Myrophis</i>	52
shrimp	58	rainwater	196		
snake	64	spotfin	181	<i>quadracus, Apeltes</i>	342
speckled worm	52	striped	186		
<i>egmontis, Ahlia</i>	49			rainwater killifish	196
<i>Enchelyopus cimbrius</i>	226			red cornetfish	368
<i>erectus, Hippocampus</i>	391				

red hake	305	snipefish, longspine	378	tomcod, Atlantic	278
<i>regius</i> , <i>Urophycis</i>	316	speckled worm eel	52	<i>tomcod</i> , <i>Microgadus</i>	278
rockling, fourbeard	226	spotfin killifish	181	threespine stickleback	347
<i>rostrata</i> , <i>Anguilla</i>	18	spotted hake	316	<i>Tylosurus</i>	
sargassum pipefish	409	stickleback		<i>acus</i>	96
<i>saurus</i> , <i>Scomberesox</i>	72	fourspine	342	<i>crocodilus</i>	102
saury, Atlantic	72	threespine	347	<i>unifasciatus</i> , <i>Hyporhamphus</i>	133
<i>scolopax</i> , <i>Macrorhamphosus</i>	378	<i>Strongylura marina</i>	90	<i>Urophycis</i>	
Scomberesocidae	71	striped killifish	186	<i>chuss</i>	305
<i>Scomberesox saurus</i>	72	Syngnathidae	389	<i>earlli</i>	314
seahorse		<i>Syngnathus</i>		<i>regius</i>	316
lined	391	<i>floridae</i>	399	<i>tenuis</i>	321
offshore	397	<i>fuscus</i>	402	<i>variegatus</i> , <i>Cyprinodon</i>	145
sheepshead minnow	145	<i>louisianae</i>	407	<i>velox</i> , <i>Euleptorhamphus</i>	128
shrimp eel	58	<i>pelagicus</i>	409	<i>virens</i> , <i>Pollachius</i>	292
silver hake	330	<i>tabacaria</i> , <i>Fistularia</i>	371	white hake	321
snake eel	64	<i>tenuis</i> , <i>Urophycis</i>	321		