*Journal of the Marine Biological Association of the United Kingdom*

**cambridge.org/mbi**

# Filling a gap: predators becoming prey. A revision of teuthivorous Mediterranean predators

Amanda Luna[1], Pilar Sánchez[2] and Giambattista Bello[3]

[1]Departamento de Ecología y Biología Animal, Centro de Investigación Mariña, Universidade de Vigo, Vigo, Spain; [2]Marine Resources, Institut de Ciencies del Mar-CSIC, Barcelona, Spain and [3]Via Valadier 1, Casamassima, Italy

**Review**

**Cite this article:** Luna A, Sánchez P and Bello G (2025) Filling a gap: predators becoming prey. A revision of teuthivorous Mediterranean predators. *Journal of the Marine Biological Association of the United Kingdom* **105**, **e139**, 1–13. https://doi.org/10.1017/S0025315425100775

Received: 1 April 2025
Revised: 1 October 2025
Accepted: 4 October 2025

**Keywords:**
cephalopoda, diet, feeding, Mediterranean sea, predators, teuthofagous, trophic ecology

**Corresponding author:** Amanda Luna; Email: amluna@uvigo.gal

**Abstract**

A review was carried out of studies on the diet of various Mediterranean teuthivorous predators (marine mammals, chondrichthyans, osteichthyans, seabirds, turtles, crustaceans, and cephalopods) and their cephalopod prey. Data extracted from the literature were analysed using multivariate statistical techniques. Three distinct groups of predators were identified according to the cephalopod species consumed. The most common prey of the predators are the 'unidentified Cephalopoda', followed by the sepiolid *Heteroteuthis dispar* and the ommastrephid squid *Illex coindetii*. The most important cephalopod predators are the striped dolphin, *Stenella coeruleoalba*, the chondrichthyans *Scyliorhinus canicula* and *Galeus melastomus*, the swordfish *Xiphias gladius*, and the ommastrephid squid *Todarodes sagittatus*. The dietary preferences of the different teutophages, their geographical distribution and some ecological implications are discussed.

## Introduction

Cephalopod prey play a crucial role in many trophic webs and is consumed in tonnes (Clarke, 1996) despite the fact that cephalopods are much less diverse than finfish and crustaceans. It should be noted that there are about 70 species of cephalopods in the Mediterranean (of which 57 are autochthonous and 13 are suspected to be non-indigenous; Bello *et al.,* 2020) compared with 650 species of finfish and 2251 of crustaceans (Coll *et al.,* 2010). This may indicate the abundance and high biodiversity of cephalopod communities, as in other North-eastern Atlantic places (Bay of Biscay, North Sea, or Irish Sea; Lordan *et al.,* 1996; Oesterwind *et al.,* 2010; Velasco *et al.,* 2001). Furthermore, some large predators became specialised in a strictly or predominantly teuthivorous or teuthofagous diet, such as the cosmopolitan Risso's dolphin, *Grampus griseus* (G. Cuvier, 1812) (Hartman, 2018; Luna *et al.,* 2022). Both oceanic and demersal cephalopods are widely preyed upon in all oceans, although the former appear to attain a biomass-wise predominant role in marine food webs with respect to the latter (Clarke, 1996). From this standpoint, oceanic ones can be considered ubiquitous prey items (Boyle and Rodhouse, 2005).

Cephalopods play a key role in the world's marine ecosystems (Boyle and Rodhouse, 2005). Large cephalopods (*Taningia danae* Joubin, 1931, *Nototeuthis dimegacotyle* Nesis & Nikitina, 1986 – Navarro *et al.*, 2013 – and *Gonatus* J. E. Gray, 1849 in Arctic waters – Golikov *et al.,* 2022, 2018) have isotopic values that are similar to those of sperm whales or some dolphins in the same oceanic area (Das *et al.,* 2003, 2000), acting as top predators in some systems, preying on large fishes and other cephalopods. They are important consumers (Clarke, 1996), and oceanic squids in particular are valuable prey items for many top marine predators such as large bony fishes, sharks, marine mammals, and seabirds (Clarke, 1996; Croxall, Prince and Clarke, 1996; Klages and Clarke, 1996; Smale and Clarke, 1996). Octopuses, however, are voracious mesopredators that play a key role in coastal marine food webs, thanks to their ability to adapt well to a dynamic, constantly changing environment with an abundance of prey types (Lankow, 2022). In addition, cephalopods are fast-growing animals that optimise their food intake energy-wise and, in turn, act as efficient energy transmitters in food webs from bottom feeders to large predators (Amaratunga, 1983).

The examination of cephalopods ingested by predators provides information not only about the predators themselves (e.g., biology, biomass, population composition, size-frequency), but also about their feeding habits (Villanueva *et al.,* 2017), habitats and ecological niches (Roscian *et al.,* 2022), and their phylogenetic and ecological drivers (Sánchez-Márquez *et al.,* 2022). Currently, dietary studies, combined with stable isotope techniques, allow the trophic position of specimens to be inferred, opening up a wide range of new possibilities in ecological, biogeographical, fisheries and environmental studies (Xavier *et al.,* 2022).

The purpose of this paper is to review the available information on the dietary preferences and feeding behaviour of teuthivorous predators in the Mediterranean Sea. We present this

© The Author(s), 2026. Published by Cambridge University Press on behalf of Marine Biological Association of the United Kingdom. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/S0025315425100775

article at a regional rather than a global level for one main reason: historically, in the Mediterranean important studies on the diet of different predators have been carried out. Besides, a global approach would obviously be extremely difficult to accomplish. This work opens a window on a very important aspect, not only in terms of knowledge of the relationships in the ecological web between predators and prey cephalopods, but also in filling a gap that fisheries data cannot provide, data that can be used in the management of marine resources. They also provide information on the feeding strategies and behaviour of many species, highlighting where possible the presence of alien species. We focus on the Mediterranean as a case study, approached from a selection of Mediterranean teuthivorous predators, because the world literature on cephalopods as predators and prey is quite extensive.

## Materials and methods

The literature relating to the diet of marine predators in the entire Mediterranean Sea was reviewed. We have tried to include as many studies as possible on the diets of these Mediterranean teutophagous species. The specific criterion used for the bibliographic searches is to find out which teuthivorous predators are present in the Mediterranean and what prey species they eat. The keywords used were 'diet', 'feeding', 'teutophagous predators', 'teuthivorous predators', 'teuthivores predators', 'cephalopods diet', 'cephalopods feeding', 'Mediterranean', and the names (scientific and common) of the different predators (Supplementary Table S1). The following search engines, bibliographic repositories, and platforms were used to search specific databases: PROA (ICM-CSIC), University of Vigo's Interlibrary Loan Service, Google Academic and Web of Science. The search was conducted in 2024, in several languages (English, Italian, Spanish and French). Due to the paucity of data in the articles on this topic, none were excluded from the results. There is therefore a significant collection of articles here, many of which are not indexed in electronic bibliographic search engines. We want to provide an outlet for these articles so that the information they contain, which is very valuable for dietary studies, is captured. Many of the papers reviewed do not have standardised data because they are old or grey literature, and some of them do not follow standards in data collection. Older publications do not have all the information needed for this type of work. For example, some of them lack biomass, so in some cases they only have frequency data (Bello, 1985; Bingel and Avsar, 1988; Würtz and Palumbo, 1985). So, to make this information available at a glance, we have focused on the most important predators in terms of abundance in the area, number of studies focusing on them and type of feeding habits, giving priority to predators that are considered to be mainly teuthivorous. All available data were extracted from them to carry out the analyses. Of these papers, 120 were found to relate to cephalopod predators (Supplementary material).

Statistical techniques were used to investigate trends in the diet of these predators. A matrix of the presence and absence of cephalopod predators and their prey was constructed. Neither the percentage of occurrence nor the biomass (in terms of number and/or weight of prey) of ingested cephalopods was reported, as such data are only partially available and, in many cases, difficult to compare. We used PRIMER statistical software to perform multivariate analyses on prey species data (Clarke and Warwick, 1994). Cluster analysis was performed on the presence/absence data using the normalised Euclidean distance index, and dendrograms were constructed using the group-average clustering method. The resulting similarity matrices were then used to perform non-metric multidimensional scaling (nMDS). To make the results clearer, only predators with more than 12 different cephalopod prey items in their stomachs were included in this latter analysis.

To confirm the literature findings, the distribution of prey and predators was compared to see if the identified cephalopods had the same distribution as the identified teuthivorous predators (see Table 1 and Supplementary Table S1). Only species distributions are shown, as there may be different distribution patterns within the same family or genus, which would add uncertainty to the discussion of these results. Species distributions have been extracted from WoRMS Editorial Board (2025), except in certain specified cases as for the distribution of bony fishes, where the work of Hureau and Monod (1979) has been followed, or for cephalopods, where FAO volumes have generally been followed (Jereb and Roper, 2005, 2010; Jereb *et al.*, 2016 (see Table 1). Information on the feeding behaviour of selected predators throughout the Mediterranean, inferred from their prey cephalopods, is also reported in the discussion (e.g., Bello, 1994; Bello and Biagi, 1995; among others).

## Results

In the Mediterranean Sea, eight marine mammals, two turtles, 23 chondrichthyans, two birds, 26 bony fishes, nine cephalopods and three crustaceans have been reported as consumers of cephalopods (Figure 1). This does not mean that there are no other cephalopod predators, just that they are not yet known or studied. The results show the most important teuthivorous only in terms of prey variety (i.e., not in terms of quantity). For the same reason, it is not possible to determine which is the most abundant prey in terms of quantity, but only in terms of frequency of occurrence. According to the literature consulted, at least 46 different cephalopod species have been identified among the remains recovered from the digestive tracts of predators. Other remains could only be assigned to taxa above the species level, i.e., seven to the genus level, seven to the family level and two to the order level; some others could only be assigned to the class Cephalopoda (Table 1).

The results of the cluster analysis and the nMDS (Figure 2) do not show the occurrence of defined groups of predator species, except for the separation of *Stenella coeruleoalba* (Meyen, 1833), *G. griseus* and *Xiphias gladius* Linnaeus, 1758 with respect to the other species. In the case of nMDS, in addition to the three species mentioned above, a group of species slightly separated from the main cluster is observed. The nMDS (Figure 3) allows three groups of large cephalopod predators to be distinguished. One is clearly formed by the largest cephalopod consumers, in terms of diversity of consumed prey: *S. coeruleoalba, G. griseus* and *X. gladius*. Of the 65 prey items identified, *S. coeruleoalba* consumed 68.9% of the total number of possible prey items, and *G. griseus* and *X. gladius* 62.3%. The next group is made up of *Scyliorhinus canicula* (Linnaeus, 1758) (which consumed 44.3% of the possible prey items), *Galeus melastomus* Rafinesque, 1810 (37.7%) and *Thunnus alalunga* (Bonnaterre, 1788) (32.8%). The third group is formed by *Thunnus thynnus* (Linnaeus, 1758) and *Tursiops truncatus* (Montagu, 1821) (both consumed 26.2%), *Coryphaena hippurus* Linnaeus, 1758 (24.6%), *Etmopterus spinax* (Linnaeus, 1758) and *Todarodes sagittatus* (Lamarck, 1798) (both with 23.0%), followed by *Squalus blainville* (Risso, 1827), *Lophius budegassa* Spinola, 1807 and *Conger conger* (Linnaeus, 1758), which consumed 19.7% of the total documented prey species.

When analysing prey cephalopods, Table 1 shows that *Heteroteuthis dispar* (Rüppell, 1844) and *Illex coindetii* (Vérany,

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

**Table 1.** Cephalopods identified in the predators' stomachs in the literature (see Supplementary Table S1)

| Prey species | Distribution | Predator species |
|---|---|---|
| ***Abralia veranyi*** | Atl, Med | *Grampus griseus, Stenella coeruleoalba, Galeus melastomus, Etmopterus spinax, Scyliorhinus canicula, Squalus blainville, Conger conger, Lepidopus caudatus, Xiphias gladius* |
| ***Abraliopsis morisii*** | Atl, Med | *G. griseus, S. coeruleoalba, X. gladius* |
| ***Alloteuthis media*** | N Atl, Med | *S. coeruleoalba, S. canicula, Mustelus mustelus, Raja clavata, Merluccius merluccius, Phycis blennoides, Lophius budegassa, Trisopterus capelanus, Pagellus erythrinus, Todarodes sagittatus, Eledone cirrhosa* |
| ***Alloteuthis subulata*** | NE Atl, Med | *S. coeruleoalba, Thunnus alalunga, L. budegassa* |
| ***Ancistrocheirus alessandrinii*** | Atl, Med | *G. griseus, S. coeruleoalba, Physeter macrocephalus, Ziphius cavirostris, X. gladius, Thunnus thynnus, T. alalunga, Tetrapturus belone* |
| ***Ancistroteuthis lichtensteinii*** | Atl, Med | *G. griseus, S. coeruleoalba, Tursiops truncatus, P. macrocephalus, Z. cavirostris, G. melastomus, X. gladius, T. thynnus, T. alalunga, Coryphaena hippurus, Micromesistius poutassou, L. caudatus, Lophius piscatorius, T. sagittatus* |
| ***Argonauta argo*** | Atl, Med, Ind, Pac | *G. griseus, S. coeruleoalba, S. canicula, G. melastomus, X. gladius, T. thynnus, T. alalunga, T. belone, C. hippurus* |
| ***Bathypolypus sponsalis*** | N Atl, Med | *G. griseus, Monachus monachus, S. canicula, E. spinax, L. piscatorius, T. sagittatus* |
| ***Brachioteuthis riisei*** | Atl, Med | *G. griseus, S. coeruleoalba, G. melastomus, X. gladius* |
| ***Pinnoctopus macropus*** | Atl, Med | *G. griseus, Careta caretta, Muraena helena* |
| **Cephalopoda spp.** | | *S. coeruleoalba, T. truncatus, Delphinus delphis, S. canicula, G. melastomus, E. spinax, Centroscymnus coelolepis, Mustelus punctulatus, S. blainville, R. clavata, Raja polystigma, Dasyatis pastinaca, C. conger, C. hippurus, M. merluccius, L. budegassa, P. erythrinus, Pagrus pagrus, Lepidion lepidion, Alepocephalus rostratus, Trachinus draco, Lagocephalus scelarus, Alloteuthis media, Loligo vulgaris, Loligo forbesii, T. sagittatus, Illex coindetii, Octopus vulgaris, Octopus salutii, E. cirrhosa, Eledone moschata, Bathypolypus sponsalis, Aristaeomorpha foliacea* |
| **Chiroteuthidae spp.**[a] | | *G. melastomus, Dalatias licha* |
| ***Chiroteuthis veranii*** | Atl, Med | *G. griseus, S. coeruleoalba, P. macrocephalus, Z. cavirostris, X. gladius, T. thynnus, L. caudatus* |
| ***Chtenopteryx sicula*** | Atl, Med | *S. coeruleoalba, E. spinax* |
| **Cranchiidae spp.** | | *S. coeruleoalba, X. gladius* |
| ***Cranchia scabra*** | Circumglobal | *X. gladius* |
| ***Eledone cirrhosa*** | N Atl, Med | *G. griseus, S. coeruleoalba, T. truncatus, M. monachus, C. caretta, R. clavata, Scyliorhinus stellaris, X. gladius, T. alalunga, C. conger, E. cirrhosa* |
| ***Eledone moschata*** | N Atl, Med | *G. griseus, S. coeruleoalba, T. truncatus, M. monachus, C. caretta, S. canicula, M. punctulatus, Lamna nasus, C. hippurus, O. vulgaris, E. moschata* |
| **Enoploteuthidae spp.** | | *S. coeruleoalba* |
| ***Galiteuthis armata*** | Atl, Med | *G. griseus, S. coeruleoalba, P. macrocephalus, Z. cavirostris, G. melastomus, X. gladius* |
| ***Heteroteuthis dispar*** | N Atl, Med | *G. griseus, S. coeruleoalba, Z. cavirostris, Prionace glauca, S. canicula, G. melastomus, E. spinax, C. coelolepis, S. blainville, R. clavata, Raja asterias, Raja montagui, Leucoraja circularis, Chimaera monstrosa, X. gladius, T. thynnus, T. alalunga, C. conger, Mora moro, Helicolenus dactylopterus, P. erythrinus, T. sagittatus, Geryon longipes* |
| ***Histioteuthis bonnellii*** | Atl, Med, Ind, Pac | *G. griseus, S. coeruleoalba, P. macrocephalus, Dermochelys coriacea, C. caretta, S. canicula, P. glauca, G. melastomus, E. spinax, X. gladius, T. thynnus, T. alalunga, T. belone, C. conger, C. hippurus, T. sagittatus* |
| ***Histioteuthis reversa*** | Atl, Med, | *G. griseus, S. coeruleoalba, P. macrocephalus, Z. cavirostris, P. glauca, G. melastomus, E. spinax, X. gladius, T. thynnus, T. alalunga, T. belone, C. hippurus, T. sagittatus, A. foliacea* |
| ***Histioteuthis* spp.** | | *G. griseus, Globicephala melas, D. delphis, G. melastomus, C. coelolepis, T. alalunga, C. hippurus, L. caudatus* |
| ***Illex coindetii*** | Atl, Med | *G. griseus, S. coeruleoalba, T. truncatus, P. glauca, S. canicula, S. stellaris, G. melastomus, M. punctulatus, S. blainville, R. clavata, D. pastinaca, X. gladius, T. thynnus, T. alalunga, T. belone, C. hippurus, P. blennoides, M. poutassou, L. budegassa, T. sagittatus, I. coindetii* |
| ***Loligo forbesii*** | NE Atl, Med | *G. griseus, S. coeruleoalba, S. canicula, T. sagittatus, I. coindetii* |
| ***Loligo* spp.** | | *S. coeruleoalba, D. delphis, M. monachus, S. stellaris, T. alalunga, C. hippurus, Saurida undosquamis, Lagocephalus scelarus, L. vulgaris* |

(*Continued*)

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

**Table 1.** (*Continued.*)

| Prey species | Distribution | Predator species |
|---|---|---|
| ***Loligo vulgaris*** | E Atl, Med | *G. griseus, S. coeruleoalba, T. truncatus, C. caretta, S. canicula, M. punctulatus, M. mustelus, Carcharhinus plumbeus, L. nasus, Pteroplatytrygon violacea, M. merluccius, M. poutassou, L. budegassa, P. erythrinus, Lagocephalus scelarus, L. vulgaris, O. vulgaris* |
| ***Mastigoteuthis* spp. ?** | | *G. griseus* |
| ***Megalocranchia* sp.** | | *G. griseus* |
| ***Neorossia caroli*** | Atl, Med | *S. coeruleoalba, S. canicula, G. melastomus, S. blainville, C. conger, I. coindetii* |
| **Octopodidae spp.** | | *S. coeruleoalba, D. delphis, Larus audouinii, C. caretta, T. alalunga, C. conger, Phycis phycis, A. foliacea* |
| ***Octopoteuthis sicula*** | Atl, Med | *G. griseus, S. coeruleoalba, P. macrocephalus, Z. cavirostris, C. caretta, S. stellaris, X. gladius, T. sagittatus* |
| ***Octopus salutii*** | NE Atl, Med | *G. griseus, S. canicula, E. spinax, S. blainville* |
| ***Octopus vulgaris* sensu stricto** | NE Atl, Med[b] | *G. griseus, T. truncatus, M. monachus, S. canicula, S. stellaris, C. plumbeus, C. conger, M. helena, P. pagrus, Lagocephalus scelarus, O. vulgaris* |
| ***Ocythoe tuberculata*** | Atl, Med, Ind, Pac | *G. griseus, S. coeruleoalba, P. glauca, X. gladius, T. alalunga, C. hippurus* |
| **Oegopsida spp.** | | *G. griseus, S. coeruleoalba, T. truncatus, L. audouinii, S. canicula, G. melastomus, E. spinax, C. coelolepis, R. clavata, T. alalunga, P. blennoides, L. vulgaris, L. forbesii, A. foliacea, Aristeus antennatus* |
| ***Ommastrephes caroli*** | N Atl, Med[b] | *G. griseus, S. coeruleoalba, G. melas, D. delphis, C. coelolepis, X. gladius, T. thynnus* |
| **Ommastrephidae spp.** | | *G. melastomus, T. thynnus, C. conger, C. hippurus, M. merluccius, A. foliacea* |
| **Onychoteuthidae spp.** | | *G. melas, D. delphis, S. canicula, T. alalunga, L. caudatus* |
| ***Onychoteuthis banksii*** | Atl, Med[b] | *G. griseus, S. coeruleoalba, P. macrocephalus, P. glauca, G. melastomus, S. blainville, S. stellaris, X. gladius, T. thynnus, T. alalunga, C. hippurus, T. sagittatus* |
| ***Pteroctopus tetracirrhus*** | Atl, Med | *G. griseus, S. stellaris, X. gladius, T. thynnus, T. alalunga, O. salutii* |
| ***Pterygioteuthis giardi*** | Atl | *S. coeruleoalba* |
| ***Pyroteuthis margaritifera*** | Atl, Med, Ind, Pac | *G. griseus, S. coeruleoalba, S. canicula, S. blainville, X. gladius* |
| ***Rhombosepion elegans*** | Atl, Med | *T. truncatus, S. canicula, R. clavata, Raja miraletus, C. hippurus, L. budegassa* |
| ***Rhombosepion orbignyanum*** | Atl, Med | *Larus audouinii, M. merluccius, L. budegassa* |
| ***Rondeletiola minor*** | Atl, Med | *G. griseus, T. truncatus, C. caretta, X. gladius* |
| ***Rossia macrosoma*** | N Atl, Med | *S. canicula, G. melastomus, E. spinax, S. blainville, C. conger, L. budegassa* |
| ***Scaeurgus unicirrhus*** | Atl, Med | *G. griseus, S. coeruleoalba, S. canicula, S. blainville, X. gladius, T. alalunga, L. budegassa* |
| ***Sepia officinalis*** | Atl, Med | *G. griseus, S. coeruleoalba, T. truncatus, M. monachus, S. canicula, M. punctulatus, M. mustelus, L. nasus, P. violacea, Torpedo torpedo, X. gladius, M. helena, L. budegassa, P. erythrinus, Lagocephalus sceleratus, O. vulgaris* |
| **Sepiidae spp.** | | *S. coeruleoalba, L. audouinii, C. caretta, S. canicula, G. melastomus, C. plumbeus, Myliobatis aquila, P. violacea, P. blennoides, S. undosquamis, L. sceleratus, L. vulgaris* |
| ***Sepietta oweniana*** | N Atl, Med | *S. coeruleoalba, S. canicula, M. merluccius, L. budegassa, L. vulgaris, T. sagittatus, E. moschata* |
| ***Sepietta* spp.** | | *S. coeruleoalba, S. canicula, G. melastomus, E. spinax, R. clavata, R. miraletus, X. gladius, C. conger, P. blennoides, Gnathophis mystax* |
| ***Sepiola intermedia*** | Med | *X. gladius* |
| ***Sepiola robusta*** | Med | *X. gladius* |
| ***Sepiola* spp.** | | *G. griseus, S. coeruleoalba, S. canicula, G. melastomus, E. spinax, M. punctulatus, R. clavata, R. miraletus, D. pastinaca, X. gladius, C. conger, M. merluccius, P. blennoides, M. poutassou, L. caudatus, T. capelanus, P. erythrinus, E. cirrhosa* |
| **Sepiolidae spp.** | | *S. coeruleoalba, T. truncatus, S. canicula, S. stellaris, G. melastomus, E. spinax, R. clavata, R. miraletus, D. pastinaca, T. alalunga, M. merluccius, O. vulgaris* |
| ***Sepioteuthis lessoniana*** | Ind-Pac, Med[b] | *Lagocephalus scelarus* |
| ***Taoniinae* spp.** | | *G. griseus, A. foliacea* |

(*Continued*)

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

**Table 1.** (*Continued.*)

| Prey species | Distribution | Predator species |
|---|---|---|
| ***Taonius pavo*** | Atl, Med | *X. gladius* |
| ***Teuthowenia megalops*** | N Atl, Med[b] | *S. coeruleoalba*, *X. gladius* |
| ***Thysanoteuthis rhombus*** | Atl, Med | *X. gladius*, *T. thynnus*, *T. sagittatus* |
| ***Todarodes sagittatus*** | Atl, Med | *G. griseus*, *S. coeruleoalba*, *T. truncatus*, *Z. cavirostris*, *P. glauca*, *S. canicula*, *S. stellaris*, *G. melastomus*, *E. spinax*, *C. coelolepis*, *S. blainville*, *D. pastinaca*, *X. gladius*, *T. thynnus*, *T. alalunga*, *T. belone*, *C. hippurus*, *M. merluccius*, *Ophichthus rufus*, *T. sagittatus*, *I. coindetii* |
| ***Todaropsis eblanae*** | Atl, Med, Ind | *G. griseus*, *S. coeruleoalba*, *T. truncatus*, *S. canicula*, *C. coelolepis*, *S. blainville*, *X. gladius*, *T. thynnus*, *L. budegassa*, *T. sagittatus*, *I. coindetii* |
| ***Tremoctopus violaceus*** | Atl, Med, Ind, Pac | *G. griseus*, *X. gladius*, *T. thynnus*, *T. belone*, *C. hippurus* |

For the prey species distribution, some abbreviations have been used. Atl: Atlantic, Med: Mediterranean, N Atl: North Atlantic, NE Atl: North-east Atlantic, S Afr: South Africa, Ind: Indian, Pac: Pacific.
[a]Since the only chiroteuthid species known to live in the Mediterranean is *Chiroteuthis veranii*, records of Chiroteuthidae spp. most likely refer to this species. Colour code: **osteichthyans** (black), **chondrichthyans** (blue), **marine mammals** (green), **seabirds** (orange), **turtles** (brown), **crustaceans** (red) and **cephalopods** (purple).
[b]Distribution extracted from FAO volumes (Jereb and Roper, 2005, 2010; Jereb *et al.*, 2016). For *Teuthowenia megalops*, from Sánchez, 1985; Santos *et al.*, 2001; Bello *et al.*, 2020; for *Sepioteuthis lessoniana* from Salman (2002); for *Octopus vulgaris* sensu stricto, from Amor *et al.* (2017); for *Loligo forbesii* from Riad (2020); for *Ommastrephes caroli*, from Fernández-Álvarez *et al.* (2020); for *Eledone moschata*, from Luna *et al.* (2021); for *Chtenopteryx sicula* from Fernández-Álvarez *et al.* (2023); for *Thysanoteuthis rhombus* from Deville *et al.* (2024); for *Ancistrocheirus alessandrinii* from Arnold *et al.* (2025).

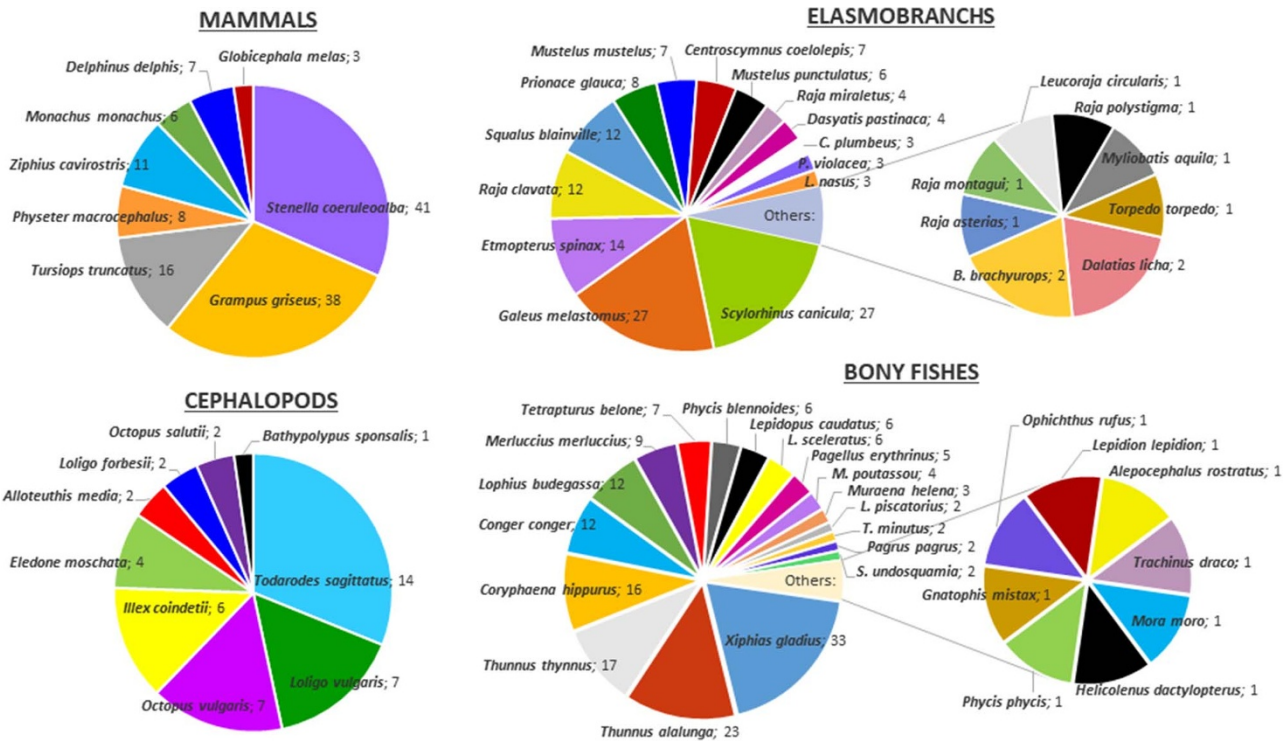


**Figure 1.** Pie diagram of the different groups of cephalopod predators, showing the number of prey species of each of them.

1839) are the most frequent prey of different predators (23 and 21, respectively). *Todarodes sagittatus* is also very frequent (found in 20 predators). The large occurrence of 'unidentified Cephalopoda', the category with the highest frequency of occurrence as prey species for so many different predators (32), is largely due to the fact that in many cases, cephalopod remains from the predators' stomach contents are represented only by fragments of beaks or eye lenses, preventing any identification below the class level. This category is not directly comparable with the individual species listed in Table 1, as it most likely includes several species.

Comparing the distribution of prey and predators reveals that of the 73 predators studied, 39.7% have a global or wide distribution. It is the case of the seven cetaceans *Delphinus delphis* Linnaeus, 1758, *Globicephala melas* (Traill, 1809), *G. griseus, Physeter macrocephalus* Linnaeus, 1758, *T. truncatus, S. coeruleoalba* and *Ziphius cavirostris* Cuvier, 1823 (Boldrocchi *et al.*, 2024; WoRMS Editorial Board, 2025); six chondrichthyans *Lamna nasus* (Bonnaterre, 1788), *Prionace glauca* (Linnaeus, 1758), *Pteroplatytrygon violacea* (Bonaparte, 1832), *Carcharhinus plumbeus* (Nardo, 1827), *Centroscymnus coelolepis* Barbosa du Bocage and de Brito Capello, 1864 and *Dalatias licha* (formerly *Scymnorhinus licha*

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

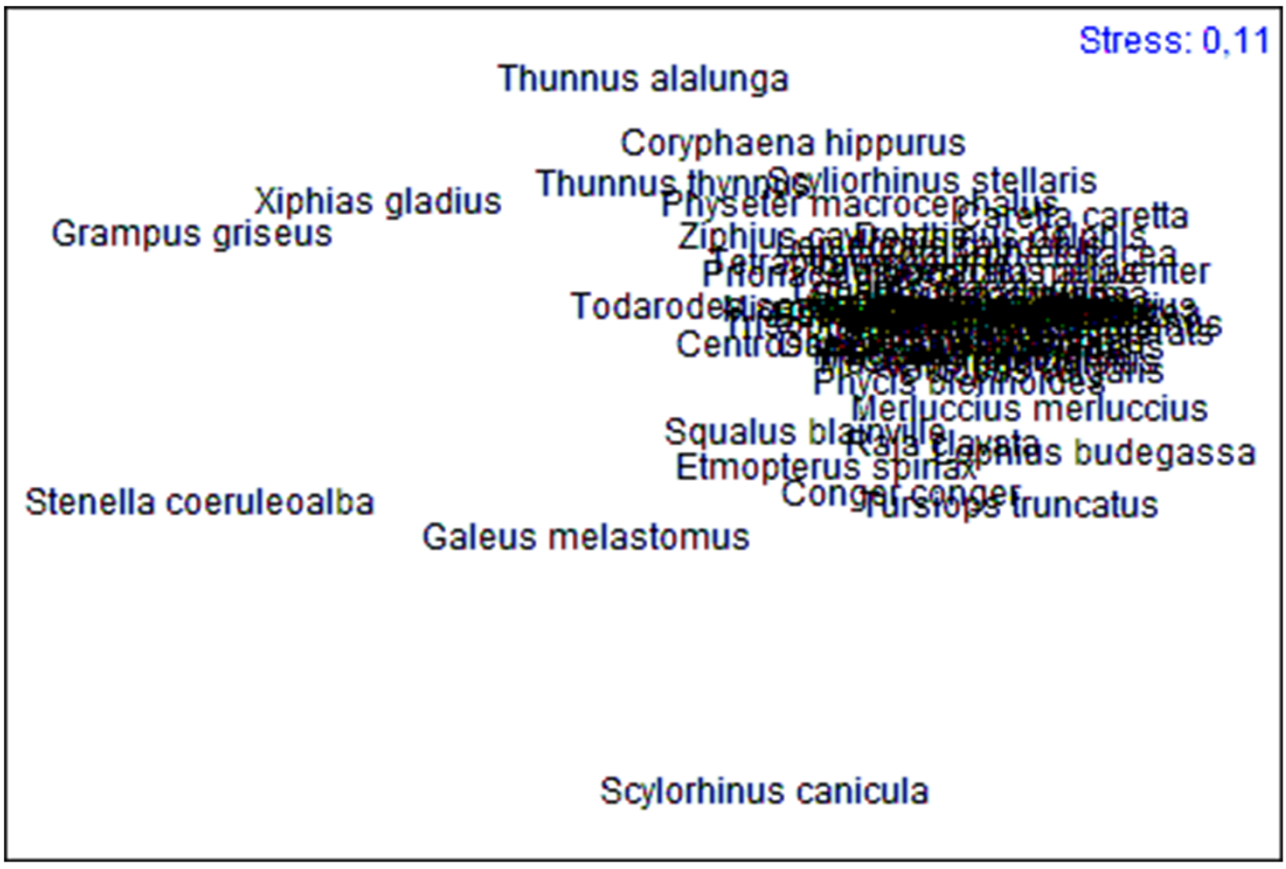


**Figure 2.** Non-metric multidimensional scaling (nMDS) representation of cephalopod predators in the Mediterranean Sea.

[Bonnaterre, 1788]); three osteichthyans, *C. hippurus, T. alalunga, T. thynnus* and *X. gladius*; the giant red shrimp (*Aristaeomorpha foliacea* (Risso, 1827)); and the sea turtles *Dermochelys coriacea* (Vandelli, 1761) and *Caretta caretta* (Linnaeus, 1758).

53,4% of the predators have an Atlantic distribution, including the Mediterranean Sea. This is the case of the crustaceans *Aristeus antennatus* (Risso, 1816) and *Geryon longipes* A. Milne-Edwards, 1882, the chondrichthyans *S. blainville* (although this species appears to be a species complex; Ebert and Stehman, 2013), and *G. melastomus*, or the osteichthyans *Helicolenus dactylopterus* (Delaroche, 1809), *Merluccius merluccius* (Linnaeus, 1758), *Micromesistius poutassou* (Risso, 1827), *Mora moro* (Risso, 1810), the monk seal (*Monachus monachus* [Hermann, 1779]), the common eagle ray (*Myliobatis Aquila* [Linnaeus, 1758]), *Dasyatis pastinaca* (Linnaeus, 1758) and most cephalopod predators (*Alloteuthis media* [Linnaeus, 1758]), *Bathypolypus sponsalis* (Fischer and Fischer, 1892), *I. coindetii, Loligo vulgaris* (Lamarck, 1798), *Octopus salutii* (Vérany, 1839), *Octopus vulgaris* sensu stricto (Cuvier, 1797), and *T. sagittatus*. There are three endemic Mediterranean predators (4.1% of species: *Raja polystigma* [Regan, 1923], *Tetrapturus belone* [Rafinesque, 1810], and *Trisopterus capelanus* [Lacepède, 1800]; WoRMS Editorial Board, 2025). Two are invasive Lessepsian species and one anti-Lessepsian species. The Lessepsian species, one of which is *Lagocephalus sceleratus* (Gmelin, 1789), occurs in the western Pacific and Indian Oceans (from where it entered the Mediterranean through the Suez Canal). Another one is *Saurida undosquamis* (Richardson, 1848), which Inoue and Nakabo (2006) consider to be a group of species. One of these must have been introduced into the Mediterranean from the Red Sea, as it has been found on the coasts of Israel and Turkey (Bilecenoğlu *et al.*, 2014). The anti-Lessepsian species is *Muraena helena* Linnaeus, 1758, expanded from the Mediterranean Sea to the Indian Ocean.

## Discussion

The overall faunal picture provided by cephalopod predators is quite different from that provided by fisheries. Small-sized species such as *H. dispar*, which rarely appear in trawl catches, are abundant in the diet of teuthivorous predators (P.S. pers. obs.). Likewise, deep-sea pelagic species such as *Histioteuthis* spp. appear to be common prey for large predators (Clarke, 1996) (see Table 1).

Currently, researchers conducting studies on the diet of teuthivorous are finding gaps in knowledge that have already been studied and cannot be found on the internet. As researchers in this field, we know how valuable it is to find a paper with the information you need (species present in the diet of a particular predator, or a morphometric equation for a particular species), in addition to the time it can save. The study of predators' diets using a purely morphological approach, i.e., identification of gut contents based on visual assessment, is generally rejected by researchers because it is time-consuming and requires high taxonomic skills. As a result, the number of researchers working in this area, which provides very valuable biological and ecological information, is decreasing. This purpose will be fulfilled by examining the prey cephalopods

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

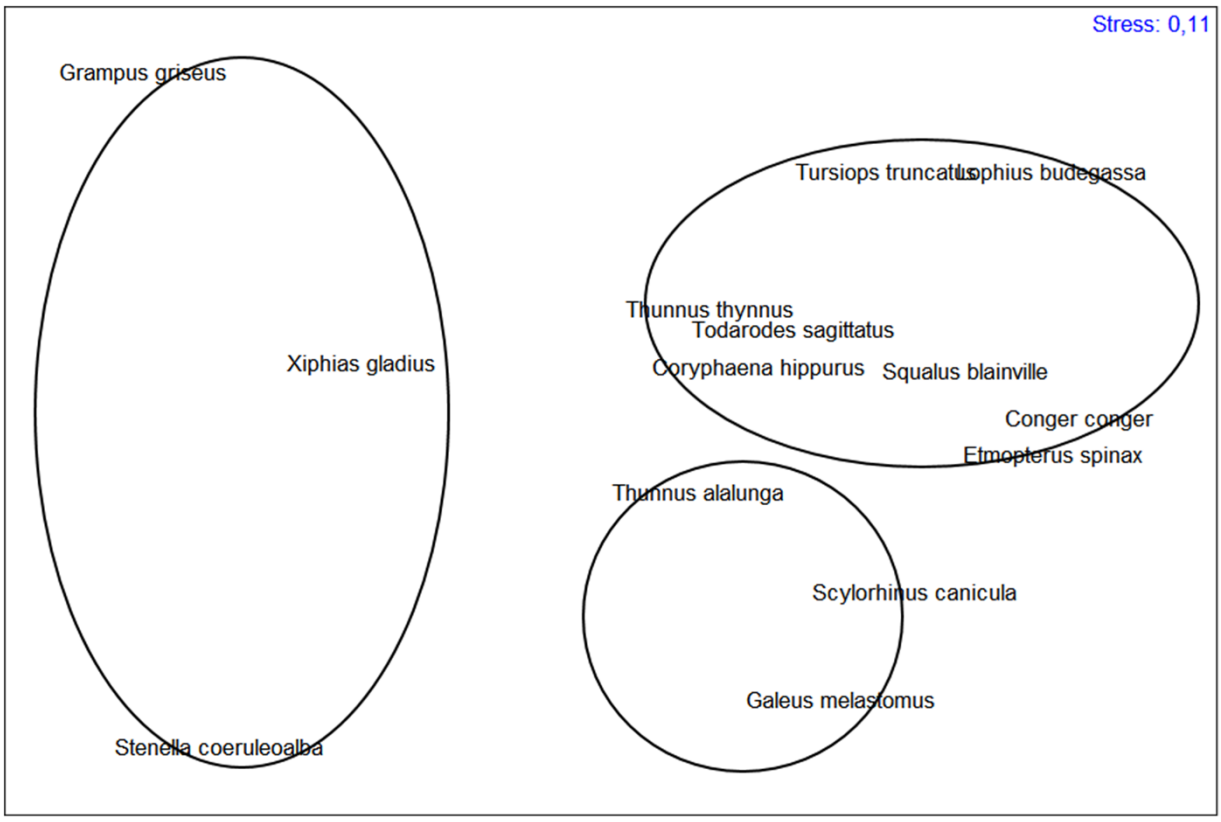


**Figure 3.** nMDS representation of the three assemblages identified among the principal of cephalopod predators.

for seabirds, fish, marine mammals and other predators. This compilation can be very useful for future authors studying trophic relationships, especially due to the difficulty of finding some of the papers reviewed.

Of the 70 cephalopod species reported in the Mediterranean by Bello *et al.* (2020), only 48 have been identified in the digestive tract of predators. For instance, 11 Sepiolida have not been reported in their stomachs, eight of them belonging to the genus *Sepiola* Leach, 1817, two to the genus *Sepietta* Naef, 1912 and the species *Stoloteuthis cthulhui* Fernández-Álvarez *et al.* (2021) (to the establishment of this new species, all previous records of *S. leucoptera* in the Mediterranean would correspond to *S. cthulhui* [Fernández-Álvarez *et al.,* 2021]). Some of them are possibly included in the category 'Sepiolidae'.

Several species considered to be non-indigenous species (NIS) have been recorded in the Mediterranean Sea, some of them coming from the Atlantic Ocean via the Strait of Gibraltar and others from the Red Sea via the Suez Canal (Bello *et al.,* 2020). There are several plausible hypotheses as to why these species are present in the Mediterranean, and these hypotheses are not mutually exclusive. 1) Given the short time that has elapsed since the introduction of most of them, their populations are still rather small, which may explain why only one of them, *Taonius pavo* (Lesueur, 1821), has been reported in very few predators' gastric remains, i.e., *G. griseus* (Luna *et al.,* 2022) and a juvenile *X. gladius* (Fernández-Corredor *et al.,* 2023). Of particular relevance is *Sepioteuthis lessoniana* R. P. Lesson, 1831, which has been reported in the stomach contents of *L. sceleratus*, both species being Lessepsian migrants (Gomes *et al.,* 2025). In this regard, Clarke (1980) cautioned against inferring geographic distributions of prey species based on their occurrence in the stomach contents of predators capable of swimming long distances in short periods of time. This is the case with sperm whales, which can reach places far from their feeding grounds in a matter of days. Their stomachs could therefore contain beaks of squid that do not live in the area where the prey died. This could be the case for predators with a global distribution (such as *D. delphis, P. glauca*, or *T. alalunga*) or with a wide distribution (such as *C. plumbeus, T. thynnus*, or *C. caretta*). This point has already been widely discussed. There is no doubt that species with this type of distribution raise doubts ('Is this species from the Pacific or the Mediterranean?'), but the valuable information provided by the collection of beaks of different predators cannot be ignored. In this sense, the works that relate the erosion of the beaks to the time that the beaks remain in the stomach can be useful in determining the rate of digestion (Van Heezik and Seddon, 1989; Xavier *et al.,* 2007, 2022), as well as the works on the erosion of the tips of the beaks during the feeding process (Perales-Raya *et al.,* 2020). There is a lack of studies in this direction, and they would be very useful in determining the time the beaks spend in the stomach. It would be possible to deduce whether the prey was recently ingested or not. The mobility of the predator is also important, since a species with a limited distribution, such as a shrimp, is not the same as a species with a wide range of movements, such as a cetacean. Relevant here is the work of Whitehead *et al.* (2003), who analysed the differences in niche breadth of some cetaceans, pointing out that some prey species may be less likely to accumulate in the stomach, and that the prey of the prey may be inadvertently included in the diet (Clarke, 1980; Clarke *et al.,* 1988). 2) It is possible that the NIS has been overestimated. These species may have been present in the Mediterranean earlier than reported, but they would not have

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

been found in this area until recently. This could reflect a sampling bias. For example, this could be because a species' sampling area was not sampled, or not sampled at sufficient depth in the case of deep-sea species (Zaragoza *et al.,* 2015, who found a clear difference in the species composition of shallow-water and deeper-water cephalopod paralarvae in the Balearic Mediterranean). There are many other possible causes, such as sudden demographic explosions of rare species considered NIS in the area (finding unexploited or underexploited ecological niches, or the absence of predators). However, this would mean that they would be found in abundance in surveys during the bloom (e.g., blue crab in many Mediterranean locations; Marchessaux *et al.,* 2023). 3) Species rarely caught in Atlantic waters (e.g., *Cranchia scabra* Leach, 1817, *T. pavo, Megalocranchia* spp., *Teuthowenia megalops* (Prosch, 1849), *Cycloteuthis sirventi* Joubin, 1919, *T. danae*) could just be scarce, with the added difficulty of sampling bias (Bello, 2003; Quetglas *et al.*, 2013; Escánez Pérez and Perales-Raya, 2017). Bottom trawling is simply not an effective sampling tool for some species. For example, the oceanic flying squid (*Ommastrephes caroli* (Furtado, 1887)) is difficult to obtain, despite probably reaching enormous biomasses in the Mediterranean Sea, as it is almost absent from most trawls. Fernández-Álvarez *et al.* (2020) argue that this is a direct consequence of this genus' oceanic lifestyle, coupled with the absence of directed fisheries in most of its range, which makes its collection in some localities a chance phenomenon. For the endemic Mediterranean predators (*R. polystigma, T. belone* and *T. capelanus*), there is no doubt that the prey were ingested within the distribution range of the predator. And it could be the same for all the species with an Atlantic-Mediterranean distribution. However, only in the case of Mediterranean endemic predators it is possible to establish the Mediterranean origin of the prey.

Some Mediterranean cephalopod predators can be considered true teuthivorous, while others are opportunistic, occasional predators of cephalopods. For example, *S. coeruleoalba* is by far the most frequent cetacean in the western Mediterranean. Its strandings along the Catalan coast account for more than 60% of the total of those that occur along the coasts of the northwestern Mediterranean (Duguy *et al.,* 1988). Its diet, based on fish, cephalopods and crustaceans, has been compared between the western (Alessandri *et al.,* 2001; Aznar *et al.,* 2017; Blanco *et al.,* 1995; Pedà *et al.,* 2015; Würtz and Marrale, 1993) and eastern Mediterranean (Bello, 1992b, 1993; Dede *et al.,* 2016; Meissner *et al.,* 2012; Öztürk *et al.,* 2007; Pulcini *et al.,* 1992; Saavedra *et al.,* 2022) (Supplementary material). Based on the available collected data, the preferred cephalopod prey of striped dolphins may be *Onychoteuthis banksii* (Leach, 1817) (family Onychoteuthidae), which was present in the majority of the stomachs of these Mediterranean cetaceans (Table 1 and Supplementary material). Other important prey for this dolphin appear to be Ommastrephidae spp. (Alessandri *et al.,* 2001; Bello, 1992b, 1993; Blanco *et al.,* 1995; Pulcini *et al.,* 1992; Würtz and Marrale, 1993) which were identified in almost half of the stomachs analysed by Saavedra *et al.* (2022). However, this family was not reported by either Öztürk *et al.* (2007) or Dede *et al.* (2016). Aznar *et al.* (2017) detected a remarkable relative decrease of oceanic cephalopods and a significant increase of the lower shelf Ommastrephidae, i.e., *I. coindetii*, during 1990–2012 in the western Mediterranean. According to these authors, there seems to be a shift in the diets of teuthivourous over time: the habitat shift towards the increase of some neritic prey species was most likely related to the decline of top demersal predators (Aznar *et al.,* 2017). The possibility that Ommastrephidae had benefited from climate change is pointed out by some authors (Coll *et al.,* 2013; Pardo *et al.,* 2025). *Illex coindetii* was found in the stomach of several striped dolphins in the Mediterranean (Alessandri *et al.,* 2001; Pedà *et al.,* 2015; Pulcini *et al.,* 1992; Würtz and Marrale, 1993).

Striped dolphins also prey on other oceanic cephalopod families such as Brachioteuthidae, Chiroteuthidae, Enoploteuthidae and Histioteuthidae, or neritic species such as *Alloteuthis* spp. and sepiolids (Table 1 and Supplementary material). Dede *et al.* (2016) found *Chiroteuthis veranii* (Férussac, 1834), *Abralia veranyi* (Rüppell, 1844), *Histioteuthis bonnellii* (Férussac, 1835) and *H. dispar* as species with more than 50% occurrence, apart from other pelagic and mesopelagic luminous cephalopods. They also found *Pterygioteuthis giardi* Fischer, 1896 and *Chtenopteryx sicula* (Vérany, 1851) for the first time in the stomach contents of Mediterranean striped dolphins. Meissner *et al.* (2012) found that changes in the isotopic composition of Mediterranean *S. coeruleoalba* may be due to dolphin migrations away from coastal feeding grounds, some of which may be driven by migration within the Mediterranean basin, explaining the predation of these dolphins on oceanic species. Pedà *et al.* (2015) suggested a possible partitioning of cephalopod resources among the Mediterranean predatory cetaceans, which was also proposed by Dede *et al.* (2016). This partitioning may be due to the regional oceanographic and geological differences between the two Mediterranean basins (Cavazza and Wezel, 2003; Moranta *et al.,* 2008), which have been colonised by cephalopod species with partly different life histories.

*Grampus griseus* is a cosmopolitan dolphin which, according to the studies of its stomach contents, is an obligate teuthivorous predator. In fact, except in a few very rare cases, the remains recovered from its stomach consist exclusively of cephalopods, both oceanic and demersal (Luna *et al.,* 2022). This suggests that *G. griseus* feeds both in the water column and near the bottom, both inshore and offshore. In terms of bottom-dwelling cephalopods, the prey list includes both relatively shallow-water octopods (e.g., *Eledone moschata* [Lamarck, 1798]) and deep-water ones (i.e., *Pteroctopus tetracirrhus* [Delle Chiaje, 1830] and *B. sponsalis*). For the oceanic species, it is more difficult to establish the depth at which they are captured by Risso's dolphins because of their diel vertical migration. However, some species inhabit mainly deep-water layers, such as *Octopoteuthis sicula* Rüppell, 1844 and *H. bonnellii*, while others, such as *I. coindetii* and *Tremoctopus violaceus* delle Chiaje, 1830, live in shallower layers (Luna *et al.,* 2022: Figure 2).

In particular, Bello (1992a), based on the high proportion of bioluminescent prey cephalopods (86%) he found in a stranded Risso's dolphin, hypothesised that this cetacean could detect the light emitted by these cephalopods, even though they use bioluminescence to conceal themselves through a counter-illumination mechanism. In this regard, Luna *et al.* (2022) reported in their review that *G. griseus* feeds primarily on histioteuthids, which are known to be bioluminescent, in addition to several other bioluminescent cephalopods. This hypothesis is also indirectly supported by the fact that *G. griseus* is a powerful swimmer, capable of pursuing and catching any Mediterranean cephalopod, with a preference for muscular species with high energy content (see comments on the swordfish below); therefore, the high proportion of light-emitting squids in its diet could be explained by their better visibility in the darkness of deep water. This hypothesis could also explain the high proportion of bioluminescent cephalopod prey found in *S. coeruleoalba* in the eastern Mediterranean, 100% in Dede *et al.* (2016).

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

The dietary spectrum of the swordfish *X. gladius* indicates that it preys on a wide range of prey sizes. Its stomach contents include remains of both large-sized, prey-cephalopods, i.e., *T. sagittatus* (which constitutes the bulk of its diet), and small-sized ones, i.e., *H. dispar* (Bello, 1991). (Note that we describe these species as large or small regardless of the size of the prey in each individual stomach – even a *T. sagittatus* is small in its juvenile stage. In many of the papers reviewed, there is no indication of the individual prey size). Moreover, the swordfish prefer muscular, swift squids (preferentially Ommastrephidae; Bello, 1991; Carmona-Antoñanzas *et al.,* 2016; Romeo *et al.,* 2012), whose flesh has a comparatively high energy content compared to the ammonia-rich flesh of Histioteuthidae (Clarke *et al.,* 1979). On the contrary, Histioteuthidae species represent a staple food for a variety of oceanic predators in the Mediterranean. Therefore, it seems that the swordfish is not selective on the prey-item size, but rather on the type of prey, in terms of energetic content. As for the preferred depth of predation, the swordfish seems to feed in the upper layers of the water, at least at night (Bello, 1991), mainly on aggregating cephalopods. In fact, its high locomotor performance – including parameters such as speed (up to 130 km/h), acceleration, quick start and manoeuvrability (Lee *et al.,* 2009), which is also based on the presence of red muscles in its body and a heating system for the eyes and brain (Abid and Idrissi, 2006) – allows the swordfish to attack and subdue any Mediterranean oceanic cephalopod species. The most striking predatory feature of the swordfish is the use of its sword to kill or injure its prey, as documented by certain remains of histioteuthids found in fish (Bello, 1994). This peculiar predatory behaviour was later confirmed by direct underwater observation of a swordfish attacking a squid (probably an ommastrephid) in mid-water off the NW Atlantic coast (pers. comm. by Verena Tunnicliffe to G.B., supported by underwater film clip, during the *World Congress of Malacology*, Ponta Delgada, Azores, July 2013). Finally, it is worth noting that oceanic cephalopods, i.e., fast-growing animals, represent a major food source for the swordfish, a fast-growing fish (Tserpes and Tsimenides, 1995), thus contributing to an efficient transfer of energy in the food web, in which the swordfish is an apex consumer (Amaratunga, 1983; Bello, 1991).

The small spotted catshark *S. canicula* is a demersal species, found on the continental shelf and at depths of between 20 and 400 m, being more abundant between 150 and 300 m. It is a mesopredator (Navarro *et al.,* 2016) with a preference for osteichthyans, crustaceans, cephalopods and other marine molluscs (Supplementary material). It is a generalist predator (Kousteni *et al.,* 2018; Macpherson, 1977) that preys on both demersal and semi-pelagic cephalopod species (Kabasakal, 2002), with prey size and depth having a significant effect on the diet of this catshark (Valls *et al.*, 2011) (Table 1). Partial dietetic differences have been found by different authors (compare the results in Bello 1997; Kabasakal 2002; Keller *et al.,* 2017; Kousteni *et al.,* 2018; Valls *et al.,* 2011), which might be due to geographical differences in teuthofaunal composition, different life stages/depths (according to D'Onghia *et al.* (1995); Massutí and Moranta (2003), *S. canicula* juveniles and adult Mediterranean populations live on different bathymetric strata), as well as it could reflect different taxonomic expertise in identifying beaks. However, *S. canicula* consumes cephalopods at almost all stages of its growth (Cihangir *et al.,* 1997; Macpherson, 1977), and *I. coindetii* and *H. dispar* appear to predominate in its feeding spectrum; both species are known to have regular contact with the bottom (Vecchione and Roper, 1991). Therefore, these pelagic cephalopods may become available to sharks as they approach the bottom during the vertical diel movements (Kabasakal, 2002; Orsi-Relini and Würtz, 1975). It is possible that, as suggested by Orsi-Relini and Würtz (1975), for *G. melastomus*, it may detect cephalopods by their light emission. *Scyliorhinus canicula* also moves away from the bottom and reaches bioluminescent prey (i.e., most cephalopod species in its diet) in mid-water, but not far from the bottom. Furthermore, it is not certain that the sharks catch demersal sepiolids (i.e., Rossiinae and Sepiolinae) on the bottom, as these supposedly benthic squids are actually capable of leaving the bottom and swimming several tens of metres upwards (Bello and Biagi, 1995).

The blackmouth catshark *G. melastomus* is a small catshark, the deepest living one in the Mediterranean. Its prey-cephalopod spectrum overlaps to some extent with that of *E. spinax*, both in terms of habitat and body size (Fanelli *et al.,* 2009). The cephalopod remains in this fish belong to both demersal and oceanic species; thus it feeds both in the water column and near the bottom. Its preferred prey-cephalopods are small-sized ones, mainly Sepiolidae, but juveniles of large-sized species also contribute to its diet (Fanelli *et al.,* 2009). The cephalopod prey size correlates with the size of *G. melastomus*. Moreover, in those cases where the remains consisted of bitten off pieces, they always came from the posterior part of the body (either the arms or the arm crown or the arm crown + head; unlike the velvet belly, see below). These results show that *G. melastomus* pursues prey items that can be ingested whole, although in many cases it only succeeds in biting off the trailing portion of the prey (Bello, 1997). In summary, the hypothesis of a solitary prey pursuit behaviour is robustly supported.

In contrast to *G. melastomus*, the deep demersal small-sized velvet belly, *E. spinax* – although like *G. melastomus* it preys on both demersal and oceanic prey – is capable of attacking comparatively large prey, possibly carrying out group predation (Bello, 1997). This small shark shows a higher preference for cephalopod prey on slope bottoms around the Balearic Islands (Valls *et al.,* 2011).

In general, ontogenetic shifts in diet are common in sharks, which may be attributed to increased predator size and appear to be adaptations to the higher metabolic requirements of larger individuals switching to larger prey types (Carlson *et al.,* 2004; Lowe *et al.,* 1996; Macpherson, 1986). The decrease in cephalopod abundance as the catshark *G. melastomus* increases in size indicates an ontogenetic shift in diet in favour of bony fishes. In addition, the differences observed in the condition of the beaks retained in the stomach contents of *S. canicula* and *S. blainville*, and in the variation in prey species diversity according to the size of the predators, may imply differences in their foraging tactics (prey hunting vs. bottom scavenging), habitats and stomach evacuation frequency (Kousteni *et al.,* 2018).

Moreover, the existence of different feeding spectra in different demersal chondrichthyan species underlines the existence of a trophic partitioning by depth in the Mediterranean Sea (Carrassón *et al.,* 1992; Macpherson, 1977), but also by the feeding behaviour. Cephalopods from the stomachs of circalittoral specimens of *Raja clavata* Linnaeus, 1758 and *S. canicula* are typically caught on the circalittoral grounds and differ from cephalopods of *G. melastomus* and *E. spinax* caught on the upper slope (Bello, 1997). This is in line with the possible partitioning of cephalopod resources among Mediterranean cetaceans of Pedà *et al.* (2015) and Dede *et al.* (2016).

The albacore, *T. alalunga*, is a very active medium-sized tuna that migrates in the Mediterranean Sea, appearing in areas of the eastern Mediterranean in autumn-winter. It has been

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
https://doi.org/10.1017/S0025315425100775

described as an opportunistic predator that feeds on available prey species depending on both the season and the geographical area (Consoli *et al.*, 2008; Goñi *et al.*, 2011). Its predator activity is mainly directed towards diel migrating mesopelagic and, secondarily, epipelagic items. As for cephalopods in particular, they were mainly preyed upon during the evening/night when they migrate towards the upper water layers (Consoli *et al.*, 2008). In terms of prey size, no shift with predator size was observed (Consoli *et al.*, 2008). According to Bello (1991), albacore feed mainly, if not exclusively, on small-sized cephalopods: both small species (e.g., *H. dispar*) and early subadults of large species (e.g., *T. sagittatus*). This may also be inferred indirectly from data from other studies: e.g., Consoli *et al.* (2008) refer to *Paralepis* spp. as the main prey, with a maximum size of about 12 cm; Goñi *et al.* (2011) reported both small bony fishes and krill. It can therefore be concluded that *T. alalunga* is a relatively 'microphagous' predator. Finally, at least in some areas, such as the southern Adriatic Sea (eastern Mediterranean), schooling albacore represent an important mortality factor for juvenile squids (estimated prey in one autumn/winter season = 1.3 million *T. sagittatus* juveniles and 1 million *H. bonnellii* juveniles [Bello, 1991]), as well as 4 million other small-sized oceanic cephalopods.

The common dolphinfish, *C. hippurus*, is a cosmopolitan fish species found in tropical and subtropical seas, often associated with floating debris. Since early history, this species has been an important food source for people living around the Mediterranean. In this area, it is seasonal and is exploited by traditional fisheries in Malta, Tunisia, Sicily and Mallorca using attracting devices and purse nets (Massutí and Morales-Nin, 1995). Despite the local importance of *C. hippurus* in the Mediterranean, its feeding habits have been scarcely studied in this area (Benseddik *et al.*, 2015; Massutí *et al.*, 1998).

There are three species that can be considered Lessepsian or anti-Lessepsian. It is the case of two Lessepsian species, the invasive Teleostei *L. sceleratus* and *S. undosquamis*, which entered the Mediterranean Sea through the Suez Canal; and *M. helena*, an anti-Lessepsian species expanded from the Mediterranean Sea to the Indian ocean.

Among the cephalopods, *T. sagittatus* is the largest consumer of cephalopods and is also one of the most common prey species, consumed by 20 different predators (Table 1 and Supplementary material). Here is a clear example of a predator becoming prey, or vice versa, demonstrating the complex interactions that occur in food chains. *Heteroteuthis dispar* also occurs in the diet of many predators (23 of them) (Table 1 and Supplementary material), and despite its small body size, it seems to play an important role in Mediterranean food webs (Bello, 1999). According to Kousteni *et al.* (2018), *H. dispar* seems to be quite abundant on the upper slope of the Mediterranean Sea, as it is one of the most frequently found cephalopods in the diet of demersal chondrichthyans (Bello, 1997; Lefkaditou, 2007), large pelagic fishes (Bello, 1991, 1999; Salman and Karakulak, 2009) and dolphins (Orsi-Relini and Garibaldi, 2005; Orsi-Relini *et al.*, 1997), as well as in the catches of experimental mesopelagic trawls and macroplankton devices (Lefkaditou *et al.*, 1999; Roper, 1974). The presence of *H. dispar* in the stomach contents of predators coming from different depth zones corresponds to its high tendency for vertical migration (Roper, 1974). However, we must not forget the possibility of doubt raised by Clarke (1980) on the assertion of the geographical distribution of predators that can move rapidly away from their feeding grounds.

Fisheries data on abundance and biomass have not been used for comparison with the data extracted from the literature because it is very difficult to extract them from existing and reviewed articles. Often, these articles barely have a taxonomic list of cephalopod prey extracted from the stomachs of predators. It would be a phenomenal task for teuthologists to try to extrapolate (sizes, weights, abundances, biomasses, inter- and intraspecific interactions) all the valuable data buried in these papers, due to how difficult it is to extract this information and standardise it for comparison.

To conclude, as stated above, the analysis of studies on the role of cephalopods as prey species in Mediterranean food webs shows a very different picture from that derived from fisheries research, which is not surprising since many predators are efficient collectors of apparently rare species, as already pointed out by Clarke since 1977 (Clarke, 1977; see also Bello, 1996). Therefore, the present review contributes to the definition of the overall Mediterranean teuthofaunal situation (e.g., Kabasakal, 2002) on how the stomach content analysis of some chondrichthyans may give a good indication of the marine fauna in a specific area, both from an ecological and biogeographical standpoints; the outmost role of cephalopods in food webs, both demersal and pelagic, both in shallow and in deep waters; and also specific information on the behaviour and the habits of some teuthivorous predators.

**Supplementary material.** The supplementary material for this article can be found at https://doi.org/10.1017/S0025315425100775.

**Funding.** Funding for open access charge: Institut de Ciències del Mar – Consejo Superior de Investigaciones Marinas (ICM – CSIC), Barcelona (Spain).

**Conflict of interest.** The authors declare none.

**Data availability.** The data underlying the findings of this study are available from the corresponding author on reasonable request.

**Ethics declarations.** Ethical review and approval were not required for this study because this work does not contain any experimental studies with live animals.

**Compliance with ethical standards.** We did not require animal ethics approval for this research because we did not use animal samples, but only literature data. This manuscript complies with the Ethical Rules applicable to this journal.

## References

**Abid N and Idrissi M** (2006) Swordfish. *ICCAT. 2006-2016. International Commission for the Conservation of Atlantic Tuna, ICCAT Manual,* In: ICCAT Publications [on-line]. Updated 2016. [Cited 01/27/]. ISBN (Electronic Edition): 978-92-990055-0-7 Spain: 181–198. https://www.iccat.int/en/iccatmanual.html

**Alessandri C, Affronte M and Scaravelli D** (2001) Stomach content analysis of cetaceans stranded along the Italian coast. *European Research on Cetaceans* **15**, 285–288.

**Amaratunga T** (1983) The role of cephalopods in marine ecosystems. *FAO Fisheries Technical Papers* **231**, 379–415.

**Amor M, Norman M, Á R, Leite T, Gleadall I, Reid A, Perales-Raya C, Ch L, Silvey C, Vidal E, Hochberg F, Zheng X and Strugnell J** (2017) Morphological assessment of the *Octopus vulgaris* species complex evaluated in light of molecular-based phylogenetic inferences. *Zoologica Scripta* **46**, 275–288.

**Arnold S, Nos D, Sáez-Liante R and Fernández-Álvarez FÁ** (2025) Diversity in the squid family Ancistrocheiridae and description of a new family of the order Oegopsida (Cephalopoda). *Zoological Journal of the Linnean Society* **204**, zlaf074.

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/S0025315425100775

**Aznar FJ, Míguez-Lozano R, Ruiz B, Bosch De Castro A, Raga JA and Blanco C** (2017) Long-term changes (1990–2012) in the diet of striped dolphins *Stenella coeruleoalba* from the western Mediterranean. *Marine Ecology Progress Series* **568**, 231–247.

**Bello G** (1985) Preliminary note on cephalopods in the stomach content of swordfish, *Xiphias gladius* L., from the Ionian and Adriatic Seas. *Rapports et Procés-verbaux des Réunions Commission Internationale pour L'Exploration Scientifique de la Mer Méditerranée* **29**, 231–232.

**Bello G** (1991) Role of cephalopods in the diet of the swordfish, *Xiphias gladius*, from the eastern Mediterranean Sea. *Bulletin of Marine Science* **49**, 312–324.

**Bello G** (1992a) Stomach contents of a Risso's dolphin, *Grampus griseus*. Do dolphins compete with fishermen and swordfish, *Xiphias gladius*? *European Research on Cetaceans* **6**, 199–201.

**Bello G** (1992b) Stomach contents of a specimen of *Stenella coeruleoalba* (Cetacea: Delphinidae) from the Ionian Sea. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **4**, 41–48.

**Bello G** (1993) *Tremoctopus violaceus* (Cephalopoda: Tremoctopodidae) in the stomach content of a swordfish from the Adriatic Sea. *Bollettino Malacologico* **29**, 45–48.

**Bello G** (1994) *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae) in the Adriatic Sea: Evidence from predator stomach contents. *Bollettino Malacologico* **30**, 43–48.

**Bello G** (1996) Teuthophagous predators as collectors of oceanic cephalopods: The case of the Adriatic Sea. *Bollettino Malacologico* **32**, 71–78.

**Bello G** (1997) Cephalopods from the stomach contents of demersal chondrichthyans caught in the Adriatic Sea. *Vie et Milieu* **47**, 221–227.

**Bello G** (1999) Cephalopods in the diet of albacore, *Thunnus alalunga*, from the Adriatic Sea. *Journal of Molluscan Studies* **65**, 233–240.

**Bello G** (2003) The biogeography of Mediterranean cephalopods. *Biogeographia - the Journal of Integrative Biogeography* **24**, 209–226.

**Bello G, Andaloro F and Battaglia P** (2020) Non-indigenous cephalopods in the Mediterranean Sea: A review. *Acta Adriatica* **61**, 113–134.

**Bello G and Biagi V** (1995) How benthic are sepiolids? *Bulletin de l'Institut Océanographique de Monaco* **16**, 97–61.

**Benseddik AB, Besbes R, Ezzeddine-Najai S, Jarboui O and Mrabet R** (2015) Diet of dolphinfish *Coryphaena hippurus* (Coryphaenidae) from the Tunisian coast. *Cybium* **39**, 21–29.

**Bilecenoğlu M, Kaya M, Cihangir B and Çiçek E** (2014) An updated checklist of the marine fishes of Turkey. *Turkish Journal of Zoology* **38**, 901–929.

**Bingel F and Avsar D** (1988) Food items of *Saurida undosquamis* in the Northern Cilian Basin (Eastern Mediterranean). *Rapports et Procés-verbaux des Réunions Commission Internationale pour L'Exploration Scientifique de la Mer Méditerranée* **31**, 261.

**Blanco C, Aznar J and Raga JA** (1995) Cephalopods in the diet of the striped dolphin *Stenella coeruleoalba* from the western Mediterranean during an epizootic in 1990. *Journal of Zoology* **237**, 151–158.

**Boldrocchi G, Conte L, Galli P, Bettinetti R and Valsecchi E** (2024) Cuvier's beaked whale (*Ziphius cavirostris*) detection through surface-sourced eDNA: A promising approach for monitoring deep-diving cetaceans. *Ecological Indicators* **161**, 111966.

**Boyle P and Rodhouse P** (2005) Cephalopods as prey. In *Cephalopods, Ecology and Fisheries,* Boyle P and Rodhouse P (eds.). Hoboken, New Jersey: Blackwell Science Ltd., 234–258.

**Carlson JK, Goldman KJ and Lowe CG** (2004) Metabolism, energetic demand, and endothermy. In Carrier JC, Musick JA and Heithaus MR (eds), *Biology of Sharks and Their Relatives*. Boca Raton: CRC Press, 203–224.

**Carmona-Antoñanzas G, Metochis CP, Grammatopoulou E, Leaver MJ and Blanco C** (2016) The diet of the swordfish *Xiphias gladius* in the western Mediterranean Sea. *Vie et Milieu* **66**, 199–207.

**Carrassón M, Stefanescu C and Cartes JE** (1992) Diets and bathymetric distributions of two bathyal sharks of the Catalan deep sea (western Mediterranean). *Marine Ecology Progress Series* **82**, 21–30.

**Cavazza W and Wezel FC** (2003) The Mediterranean region—a geological primer. *International Union of Geological Sciences Episodes* **26**, 160–168.

**Cihangir B, Ünlüoğlu A and Tiraşin EM** (1997) Distribution and some biological aspects of the lesser spotted dogfish (Chondrichthyes, *Scyliorhinus canicula*, Linnaeus, 1758) from the northern Aegean Sea. In Hoşsu B (ed), *Mediterranean Fisheries Congress*. Yzmir, Turkey: 9–11 April 1997, 585–603.

**Clarke KR and Warwick RM** (1994) Similarity-based testing for community pattern: The two-way layout with no replication. *Marine Biology* **118**, 167–176.

**Clarke MR** (1977) Beaks, nets and numbers. *Symposia of the Zoological Society of London* **38**, 89–126.

**Clarke MR** (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Reports* **37**, 1–324.

**Clarke MR** (1996) Cephalopods as prey. III. Cetacean. *Philosophical Transactions of the Royal Society* **351**, 1053–1065.

**Clarke MR, Denton EJ and Gilpin-Brown JB** (1979) On the use of ammonium for buoyancy in squids. *Journal of the Marine Biological Association of the United Kingdom* **59**, 259–276.

**Clarke MR, Paliza R and Aguayo A** (1988) Sperm whales of the southeast Pacific. Part IV: Fatness, food and feeding. *Investigations on Cetacea* **21**, 53–195.

**Coll M, Navarro J, Olson RJ and Christensen V** (2013) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. *Deep-Sea Research Part II: Topical Studies in Oceanography* **95**, 21–36.

**Coll M, Piroddi C, Steenbeek J, Kaschner K, Ben Rais Lasram F, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R, Estrada M, Froglia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos MS, Koukouras A, Lampadariou N, Laxamana E, De La Cuadra CM L-F, Lotze HK, Martín D, Mouillot D, Oro D, Raicevich S, Rius-Barile J, Sáiz-Salinas JI, San Vicente C, Somot S, Templado J, Turón X, Vafidis D, Villanueva R and Voultsiadou E** (2010) The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats. *PLoS ONE* **5**, e11842.

**Consoli P, Romeo T, Battaglia P, Castriota L, Esposito V and Andaloro F** (2008) Feeding habits of the albacore tuna *Thunnus alalunga* (Perciformes, Scombridae) from central Mediterranean Sea. *Marine Biology* **155**, 113–120.

**Croxall JP, Prince PA and Clarke MR** (1996) Cephalopods as prey. I. Seabirds. *Philosophical Transactions of the Royal Society* **351**, 1023–1043.

**D'Onghia G, Matarrese A, Tursi A and Sion L** (1995) Observations on the depth distribution pattern of the Small-Spotted Catshark in the North Aegean Sea. *Journal of Fish Biology* **47**, 421–426.

**Das K, Lepoint G, Leroy Y and Bouquegneau JM** (2003) Marine mammals from the southern North Sea: Feeding ecology data from $\delta^{13}C$ and $\delta^{15}N$ measurements. *Marine Ecology Progress Series* **263**, 287–298.

**Das K, Lepoint G, Loizeau V, Debacker V, Dauby P and Bouquegneau JM** (2000) Tuna and dolphin associations in the North-East Atlantic: Evidence of different ecological niches from stable isotope and heavy metal measurements. *Marine Pollution Bulletin* **40**, 102–109.

**Dede A, Salman A and Tonay AM** (2016) Stomach contents of by-caught striped dolphins (*Stenella coeruleoalba*) in the eastern Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **96**, 869–875.

**Deville D, Mori S, Kawai K, Escánez A, Macali A, Lishchenko F, Braid H, Githaiga-Mwicigi J, Mohamed KS, Bolstad KSR, Miyahara K, Sugimoto C, Fernández-Álvarez FÁ and Sánchez G** (2024) Cryptic biodiversity in the commercial diamondback squid *Thysanoteuthis rhombus* Troschel 1857. *Reviews in Fish Biology and Fisheries* **34**, 293–313.

**Duguy R, Aguilar A, Casinos A, Grau E and Raga JA** (1988) Étude comparative des échouages de cétacés sur les côtes Méditerranéennes de France et d'Espagne. *Miscellania Zoologica* **12**, 339–345.

**Ebert DA and Stehman MF** (2013) Sharks, batoids, and chimaeras of the North Atlantic. In *FAO Species Catalogue for Fishery Purposes 7*. Rome: Food and Agriculture Organization of the United Nations, 56–66.

**Escánez Pérez A and Perales-Raya C** (2017) First record of an adult *Taningia danae* (Cefalopoda: Octopoteuthidae) in the Canary Islands (Central-east Atlantic). *Arquipelago – Life and Marine Sciences* **34**, 55–59.

**Fanelli E, Rey J, Torre P and Gil de Sola L** (2009) Feeding habits of blackmouth catshark *Galeus melastomus* Rafinesque, 1810 and velvet belly lantern shark *Etmopterus spinax* (Linnaeus, 1758) in the western Mediterranean. *Journal of Applied Ichthyology* **25**, 83–93.

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/S0025315425100775

**Fernández-Álvarez F, Braid H, Nigmatullin C, Bolstad K, Haimovici M, Sánchez P, Sajikumar K, Ragesh N and Villanueva R** (2020) Global biodiversity of the genus *Ommastrephes* (Ommastrephidae: Cephalopoda): An allopatric cryptic species complex. *Zoological Journal of the Linnean Society* **190**, 460–482.

**Fernández-Álvarez F, Sánchez G, Deville D, Taite M, Villanueva R and Allcock A** (2023) Atlantic Oceanic squids in the "grey speciation zone." *Integrative and Comparative Biology* **63**, 1214–1225.

**Fernández-Álvarez F, Sánchez P and Villanueva R** (2021) Morphological and molecular assessments of bobtail squids (Cephalopoda: Sepiolidae) reveal a hidden history of biodiversity. *Frontiers in Marine Science* **7**, 632261.

**Fernández-Corredor E, Francotte L, Martino I, FÁ F-Á, García-Barcelona S, Macías D, Coll M, Ramírez F, Navarro J and Giménez J** (2023) Assessing juvenile swordfish (*Xiphias gladius*) diet as an indicator of marine ecosystem changes in the northwestern Mediterranean Sea. *Marine Environmental Research.* **192**, 106190.

**Golikov AV, Ceia FR, Hoving HJT, Queirós JP, Sabirov RM, Blicher ME, Larionova AM, Walkusz W, Zakharov DV and Xavier JC** (2022) Life history of the Arctic squid *Gonatus fabricii* (Cephalopoda: Oegopsida) reconstructed by analysis of individual ontogenetic stable isotopic trajectories. *Animals* **12**, 3548.

**Golikov AV, Ceia FR, Sabirov RM, Zaripova ZI, Blicher ME, Zakharov DV and Xavier JC** (2018) Ontogenetic changes in stable isotope ($\delta^{13}$C and $\delta^{15}$N) values in squid *Gonatus fabricii* (Cephalopoda) reveal its important ecological role in the Arctic. *Marine Ecology Progress Series* **606**, 65–78.

**Gomes VC, Christidis G, Peristeraki P, Somarakis S and Tserpes G** (2025) The diet and feeding habits of *Lagocephalus sceleratus* in the eastern Mediterranean: A case study carried out off the island of Crete (southern Greece). *Mediterranean Marine Science* **26**, 97–114.

**Goñi N, Logan J, Arrizabalaga H, Jarry M and Lutcavage M** (2011) Variability of albacore (*Thunnus alalunga*) diet in the Northeast Atlantic and Mediterranean Sea. *Marine Biology* **158**, 1057–1073.

**Hartman KL** (2018) Risso's Dolphin. In Würsig B, Jgm T and Kovacs KM (eds), *Encyclopedia of Marine Mammals*. Cambridge: Academic Press, Elsevier Inc, 824–827.

**Hureau JC and Monod T** (1979) Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean (CLOFNAM). Paris, France. *United Nations Educational Scientific and Cultural Organization (UNESCO)* **1-2**, 683.

**Inoue T and Nakabo T** (2006) The *Saurida undosquamis* group (Aulopiformes: Synodontidae), with description of a new species from southern Japan. *Ichthyological Research* **53**, 379–397.

**Jereb P and Roper CFE** (eds) (2005) Cephalopods of the World. An Annotated and illustrated catalogue of species known to date. Volume 1. Chambered Nautiluses and Sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae, and Spirulidae). *FAO Species Catalogue for Fishery Purposes* **4**, 261p.

**Jereb P and Roper CFE** (2010) Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Myopsid and Oegopsid squids. *FAO Species Catalogue for Fishery Purposes* **4**, 605p.

**Jereb P, Roper CFE, Norman M and Finn J** (2016) FAO Cephalopods of the World Cephalopods of the world. An annotated and illustrated catalogue of species known to date. Volume 2. Octopods and Vampire Squids. *FAO Species Catalogue for Fishery Purposes* **4**, 370p.

**Kabasakal H** (2002) Cephalopods in the stomach contents of four Elasmobranch species from the northern Aegean Sea. *Acta Adriatica* **43**, 17–24.

**Keller S, Hidalgo M, Álvarez-Berastegui D, Bitetto I, Casciaro L, Cuccu D, Esteban A, Garofalo G, González M, Guijarro B, Josephides M, Jadaud A, Lefkaditou E, Maiorano P, Manfredi C, Marceta B, Micallef R, Peristeraki P, Relini G, Sartor P, Spedicato MT, Tserpes G and Quetglas A** (2017) Demersal cephalopod communities in the Mediterranean: A large-scale analysis. *Marine Ecology Progress Series* **584**, 105–118.

**Klages NTW and Clarke MR** (1996) Cephalopods as prey. II. Seals. *Philosophical Transactions of the Royal Society* **351**, 1045–1052.

**Kousteni V, Karachle PK, Megalofonou P and Lefkaditou E** (2018) Cephalopod prey of two demersal sharks caught in the Aegean Sea (eastern Mediterranean). *Journal of the Marine Biological Association of the United Kingdom* **98**, 81–88.

**Lankow AJ** (2022) Examining the effects of prey type and water temperature on the feeding behavior of a benthic generalist mesopredator, the California Two-Spot Octopus (*Octopus bimaculoides*). Master's thesis, University of California, Santa Cruz.

**Lee HJ, Jong YJ, Chang LM and Wu WL** (2009) Propulsion strategy analysis of high-speed swordfish. *Journal of the Japan Society for Aeronautical and Space Sciences* **52**, 11–20.

**Lefkaditou E** (2007) Review of cephalopod fauna in Hellenic waters. In Papaconstantinou C, Zenetos A, Vassilopoulou V and Tserpes G (eds), *State of Hellenic Fisheries*. Vol. II. 4 Athens: HCMR Publications, 62–69.

**Lefkaditou E, Papaconstantinou C and Anastasopoulou A** (1999) Juvenile cephalopods collected in the midwater macroplankton over a trench, in the Aegean Sea (northeastern Mediterranean). *Israel Journal of Zoology* **45**, 395–405.

**Lordan C, Warnes S, Cross TF and Burnell GM** (1996) The distribution and abundance of cephalopod species caught during demersal trawl surveys west of Ireland and in the Celtic Sea. *Irish Fisheries Investigations* **8**. Marine Institute. https://oar.marine.ie/handle/10793/801 (accessed June 2025).

**Lowe CG, Wetherbee BM, Crow GL and Tester AL** (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes* **47**, 203–211.

**Luna A, Rocha F and Perales-Raya C** (2021) A review of cephalopods (Phylum: Mollusca) of the canary current Large marine ecosystem (Central-East Atlantic, African coast). *Journal of the Marine Biological Association of the United Kingdom* **101**, 1–25.

**Luna A, Sánchez P, Chicote C and Gazo M** (2022) Cephalopods in the diet of Risso's dolphin (*Grampus griseus*) from the Mediterranean Sea: A review. *Marine Mammal Science* **38**, 725–741.

**Macpherson E** (1977) Estudio sobre relaciones tróficas en peces bentónicos de la costa catalana. *PhD thesis*. Universidad Autónoma de Barcelona, Spain.

**Macpherson E** (1986) Diet in skates off Namibia. *Collection of Scientific Papers of the International Commision of SE Atlantic Fisheries* **13**, 99–112.

**Marchessaux G, Mangano MC, Bizzarri S, M'rabet C, Principato E, Lago N, Veyssiere D, Garrido M, Scyphers SB and Sarà G** (2023) Invasive blue crabs and small-scale fisheries in the Mediterranean Sea: Local ecological knowledge, impacts and future management. *Marine Policy* **148**, 105461.

**Massutí E, Deudero S, Sánchez P and Morales B** (1998) Food and feeding habits of dolphin-fish (*Coryphaena hippurus*) in western Mediterranean waters. *Bulletin of Marine Science* **63**, 329–341.

**Massutí E and Morales-Nin B** (1995) Seasonality and reproduction of dolphin-fish (*Coryphaena hippurus*) in the Western Mediterranean. *Scientia Marina* **59**, 357–364.

**Massutí E and Moranta J** (2003) Demersal assemblages and depth distribution of elasmobranchs from the continental shelf and slope off the Balearic Islands (western Mediterranean). *ICES Journal of Marine Science* **60**, 753–766.

**Meissner AM, Macleod CD, Richard P, Ridoux V and Pierce G** (2012) Feeding ecology of striped dolphins, *Stenella coeruleoalba*, in the north-western Mediterranean Sea based on stable isotope analyses. *Journal of the Marine Biological Association of the United Kingdom* **92**, 1677–1687.

**Moranta J, Quetglas A, Massutí E, Guijarro B, Ordines F and Valls M** (2008) Research trends on demersal fisheries Oceanography on the Mediterranean. In Rades CV and Tilesman EB (eds), *Oceanography in the Mediterranean. Advances in Environmental Research*, Vol. 1. New York: Nova Science Publishers, Inc, 17–57.

**Navarro J, Cardador L, Ám F, Bellido JM and Coll M** (2016) Differences in the relative roles of environment, prey availability and human activity in the spatial distribution of two marine mesopredators living in highly exploited ecosystems. *Journal of Biogeography* **43**, 440–450.

**Navarro J, Coll M, Somes CJ and Olson RJ** (2013) Trophic niche of squids: Insights from isotopic data in marine systems worldwide. *Deep Sea Research Part II: Topical Studies in Oceanography* **95**, 93–102.

**Oesterwind D, Hofstede R, Harley B, Brendelberger H and Piatkowski U** (2010) Biology and meso-scale distribution patterns of North Sea cephalopods. *Fisheries Research* **106**, 141–150.

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/S0025315425100775

**Orsi-Relini L and Garibaldi F** (2005) Mesopelagic cephalopods biodiversity in the cetacean sanctuary as a result of direct sampling and observations on the diet of the Cuvier's beaked whale, *Ziphius cavirostris*. *Biologia Marina Mediterrana* **12**, 106–115.

**Orsi-Relini L, Garibaldi F and Poggi R** (1997) Note sull'alimentazione del grampo in Mar Ligure. *Convegno Nazionale sui Cetacei* **3**, *Napoli, Italy, 5-6 dicembre 1997*

**Orsi-Relini L and Würtz M** (1975) Osservazioni sull'alimentazione di *Galeus melastomus* (Chondrichthyes: Scyliorhinidae) dei fondi batiali liguri. *Quaderni di Laboratorio dell´Instituto di Tecnologia della Pesca e del Pescato* **2**, 17–36.

**Öztürk B, Salman A, Öztürk AA and Tonay A** (2007) Cephalopod remains in the diet of striped dolphins (*Stenella coeruleoalba*) and Risso's dolphins (*Grampus griseus*) in the eastern Mediterranean Sea. *Vie et Milieu* **57**, 53–59.

**Pardo M, FÁ F-Á, Varela JL, Navarro J, Medina A, Gómez-Vives MJ, Sbragaglia V, Bellido JM, Coll M and Giménez J** (2025) Long-term trophic ecology of Juvenile Atlantic Bluefin Tuna in the Western Mediterranean Sea. *Estuarine, Coastal and Shelf Science* **109471**.

**Pedà C, Battaglia P, Scuderi A, Voliani A, Mancusi C, Andaloro F and Romeo T** (2015) Cephalopod prey in the stomach contents of odontocete cetaceans stranded in the western Mediterranean Sea. *Marine Biology Research* **11**, 593–602.

**Perales-Raya C, Bartolomé A, Hernández-Rodríguez E, Carrillo M, Martín V and Fraile-Nuez E** (2020) How old are giant squids? First approach to aging *Architeuthis* beaks. *Bulletin of Marine Science* **96**, 357–374.

**Pulcini M, Carlini R and Würtz M** (1992) Stomach contents of striped dolphin (*Stenella coeureoalba*, Meyen, 1933) from the south-central Tyrrhenian coast. *European Research on Cetaceans* **6**, 194–196.

**Quetglas A, Ordines F, González M, Zaragoza N, Mallol S, Valls M and De Mesa A** (2013) Uncommon pelagic and deep-sea cephalopods in the Mediterranean: New data and literature review. *Mediterranean Marine Science* **14**, 69–85.

**Riad R** (2020) Taxonomical studies on the cephalopods (Cephalopoda: Mollusca) inhabiting both the Egyptian Mediterranean and the Red Sea waters. *Jordan Journal of Natural History* **7**, 64–92.

**Romeo T, Battaglia P, Pedà C, Perzia P, Consoli P, Esposito V and Andaloro F** (2012) Pelagic cephalopods of the central Mediterranean Sea determined by the analysis of the stomach content of large fish predators. *Helgoland Marine Research* **66**, 295–306.

**Roper CFE** (1974) Vertical and seasonal distribution of pelagic cephalopods in the Mediterranean Sea: Preliminary report. *American Malacological Bulletin* **39**, 27–30.

**Roscian M, Herrel A, Zaharias P, Cornette R, Fernández V, Kruta I, Cherel Y and Rouget I** (2022) Every hooked beak is maintained by a prey: Ecological signal in cephalopod beak shape. *Functional Ecology* **36**, 2015–2028.

**Saavedra C, García-Polo M, Giménez J, Mons JL, Castillo JJ, Fernández-Maldonado C, De Stephanis R, Pierce GJ and Santos MB** (2022) Diet of striped dolphins (*Stenella coeruleoalba*) in southern Spanish waters. *Marine Mammal Science* **38**, 1566–1582.

**Salman A** (2002) New report of the loliginid squid *Sepioteuthis lessoniana* Lesson, 1830 in the Mediterranean. *Israel Journal of Zoology* **48**, 249–250.

**Salman A and Karakulak S** (2009) Cephalopods in the diet of albacore, *Thunnus alalunga*, from the eastern Mediterranean. *Journal of the Marine Biological Association of the United Kingdom* **89**, 635–640.

**Sánchez P** (1985) On *Teuthowenia megalops* (Prosch, 1849) (Cephalopoda, Cranchiidae) in the Mediterranean Sea. *Investigacion Pesquera* **49**(2), 315–318.

**Sánchez-Márquez A, Navarro J, Kaliontzopoulou A, Farré M, Taite M, Escolar Ó, Villanueva R, Allcock L and Fernández-Álvarez FÁ** (2022) Unravelling the phylogenetic and ecological drivers of beak shape variability in cephalopods. *Reviews in Fish Biology and Fisheries* **33**, 221–239.

**Santos M, Pierce G, Herman J, López A, Guerra A, Mente E and Clarke M** (2001) Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): A review with new information on the diet of this species. *Journal of the Marine Biological Association of the United Kingdom* **81**, 687–694.

**Smale MJ and Clarke MR** (1996) Cephalopods as prey. IV. Fishes. *Philosophical Transactions of the Royal Society* **351**, 1067–1081.

**Tserpes G and Tsimenides N** (1995) Determination of age and growth of swordfish, *Xiphias gladius* L., 1758, in the eastern Mediterranean using anal-fin spines. *Fish Bulletin* **93**, 594–602.

**Valls M, Quetglas A, Ordines F and Moranta J** (2011) Feeding ecology of demersal elasmobranchs from the shelf and slope off the Balearic Sea (western Mediterranean). *Scientia Marina* **75**, 633–639.

**Van Heezik Y and Seddon P** (1989) Stomach sampling in the yellow-eyed Penguin (*Megadyptes antipodes*): Erosion of Otoliths and Squid Beaks. *Journal of Field Ornithology* **60**, 451–458.

**Vecchione M and Roper CFE** (1991) Cephalopods observed from submersibles in the western North Atlantic. *Bulletin of Marine Science* **49**, 433–445.

**Velasco F, Olaso I and Sánchez F** (2001) The role of cephalopods as forage for the demersal fish community in the southern Bay of Biscay. *Fisheries Research* **52**, 65–77.

**Villanueva R, Perricone V and Fiorito G** (2017) Cephalopods as predators: A short journey among behavioral flexibilities, adaptions, and feeding habits. *Frontiers in Physiology* **8**, 598.

**Whitehead H, Macleod C and Rodhouse P** (2003) Differences in niche breadth among some teuthivorous mesopelagic marine mammals. *Marine Mammal Science* **19**, 400–406.

**WoRMS Editorial Board** (2025) World Register of Marine Species. Available from https://www.marinespecies.orgatVLIZ. (Accessed 2025-02-11).

**Würtz M and Marrale D** (1993) Food of striped dolphin, *Stenella coeruleoalba*, in the Ligurian Sea. *Journal of the Marine Biological Association of the United Kingdom* **73**, 571–578.

**Würtz M and Palumbo F** (1985) Notes on the role of cephalopods in the Bathyal Foodwebs of the Ligurian Sea. *Rapports et Procés-verbaux des Réunions Commission Internationale pour L'Exploration Scientifique de la Mer Méditerranée* **29**, 227–230.

**Xavier J, Clarke M, Magalhães M, Stowasser G, Blanco C and Cherel Y** (2007) Current status of using beaks to identify cephalopods: III international workshop and training course on cephalopod beaks, Faial Island, Azores, April 2007. *Arquipélago: Life and Marine Sciences* **24**, 41–48.

**Xavier J, Golikov A, Queirós J, Perales-Raya C, Rosas-Luis R, Abreu J, Bello G, Bustamante P, Capaz J, Dimkovikj V, González A, Guímaro H, Guerra-Marrero A, Gomes-Pereira J, Kubodera T, Laptikhovsky V, Lefkaditou E, Lishchenko F, Luna A, Liu B, Pierce G, Pissarra V, Reveillac E, Romanov E, Rosa R, Roscian M, Rose-Mann L, Rouget I, Sánchez P, Sánchez-Márquez A, Seixas S, Souquet L, Varela J, Vidal E and Cherel Y** (2022) The significance of cephalopod beaks as a research tool: An update. *Frontiers in Physiology* **13**, 1038064.

**Zaragoza N, Quetglas A, Hidalgo M, Álvarez-Berastegui D, Balbín R and Alemany F** (2015) Effects of contrasting oceanographic conditions on the spatiotemporal distribution of Mediterranean cephalopod paralarvae. *Hydrobiologia* **749**, 1–14.

Downloaded from https://www.cambridge.org/core. IP address: 193.191.134.1, on 16 Sep 2026 at 12:46:33, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms. https://doi.org/10.1017/S0025315425100775