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The importance of cephalopods in the diet of fish on the northwest European shelf

C. J. Barrett [1],*, P. Barry [1], E. MacLeod [1,2], S. Stott [1], R. Vieira [1] and V. Laptikhovsky [1]

[1]Cefas, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK
[2]Marine Scotland Science, Scottish Government | Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK
*Corresponding author: tel: +(0)1502 562244; e-mail: christopher.barrett@cefas.co.uk

Cephalopods are universal to the world's oceans and prey to many fish species. On the northwest European shelf, integrated ecosystem assessments are rapidly evolving into the preferred method for holistically assessing stocks, but cephalopods appear to be an overlooked component, perhaps because their roles in ecosystems have seldom been quantified in recent years. We have analysed historical fish stomach records and revisited literature at local and regional level to determine the importance of cephalopods to the diets of 26 ecologically important finfish. We conclude that, in contrast to most other large marine ecosystems, cephalopods found in the Greater North Sea and the Celtic Seas regions appear to contribute only a small fraction to the diets of ecologically important finfish (found in the stomachs of ~14% of specimens among some species, but generally only 1–3% in most species), though their role as predator may be important and require further investigation. Based on our findings, cephalopods may not represent a key component for integrated ecosystem assessments, though as squid populations have been shown to expand throughout the North Sea in recent years, regular monitoring is encouraged to identify the point where their inclusion into such models may be necessary.

Keywords: Celtic Sea, cephalopoda, finfish, fish stomach analysis, integrated ecosystem analysis, North Sea.

Introduction

Cephalopods are important elements in marine food webs as they are consumed by ecologically important predators, including fish (Smale, 1996), whales (Clarke, 1996), seabirds (Croxall and Prince, 1996), and seals (Klages, 1996). Cephalopods' role in food webs is particularly relevant in most large, temperate shelf ecosystems, where they are an important component of the diet of numerous fish species, representing up to a half of their diet by numbers and occurring in ~50–90% of fish stomachs examined. Examples include the southern hake *Merluccius hubbsi* (Laptikhovsky *et al*., 2010) and southern moonfish *Lampris immaculatus* (Jackson *et al*., 1998) in the southwest Atlantic; the swordfish *Xiphias gladius* in the Mediterranean (Salman, 2004); yellowfin tuna *Thunnus albacares* (Manooch and Mason, 1983) in the Gulf of Mexico; and warehou *Hyperoglyphe antarctica* (Laptikhovsky *et al*., 2020) in the southern Atlantic. To date, the role of cephalopods in food webs has been better understood in the temperate waters of the northeast Pacific and southernmost African waters (Smale, 1996), southwest Atlantic (Laptikhovsky *et al*., 2010), northwest Pacific (Sakurai *et al*., 2013; Katugin *et al*., 2013), and in the northwest Atlantic, south of Newfoundland (Hanlon *et al*., 2013). In the northwest Atlantic, there is a large contribution made to the food web by two squid species *Doryteuthis pealeii* and especially *Illex illecebrosus* in the trophic structure of shelf and slope ecosystems (O'Dor, 1983; Summers, 1983; Vovk, 1985; Brodziak, 1998; Moustahfid *et al*., 2009; O'Dor and Dawe, 2013). Meanwhile, in the northeast Atlantic, the importance of cephalopods as prey to predatory fishes has so far been relatively poorly researched (Pierce *et al*., 2010).

Within the northeast Atlantic region, there is evidence to suggest a recent increased abundance of cephalopods on the northwest European shelf. In recent years, ommastrephid and loliginid squid numbers have grown throughout the North Sea (Van der Kooij *et al*., 2016). Specifically, the shortfin squid (*Illex coindetii*) has begun reproducing in the North Sea and has also entered the Baltic Sea (Oesterwind and Schaber, 2020; Oesterwind *et al*., 2020). Elsewhere on the northwest Atlantic, on the US shelf, strong evidence of the latter was found: Hunsicker *et al*. (2010) calculated the cephalopod component as indirectly supporting ~15% of marine fisheries landings weight and ~20% landed value, with some areas seeing this contribution rise to 55% of landing tonnage and 70% of the fisheries' value. Hunsicker *et al*. (2010) believed ~75% of these contributions were made through cephalopods serving as a supply of prey items to commercially important finfish.

The area of interest encompassed in this study is defined as the Celtic Zoogeographic Province of the High Boreal Zoogeographic Zone (Nesis, 2003) and includes waters around the United Kingdom and Ireland, English Channel, and North Sea. Based on the aforementioned evidence, we address the question: Do squid and other cephalopods play a similarly large role as prey species in supporting predatory fish species on the northeast Atlantic European shelf? A comprehensive list of predators was compiled for all commercially important cephalopod species of the northeast Atlantic (Jereb *et al*., 2015), but to what extent cephalopods are important prey remains undefined. For this study, we aim to build upon the level of knowledge about squids in European shelf waters (Pierce *et al*., 2010) and their contribution to the diet of ecologically important finfish, by examining available information on both

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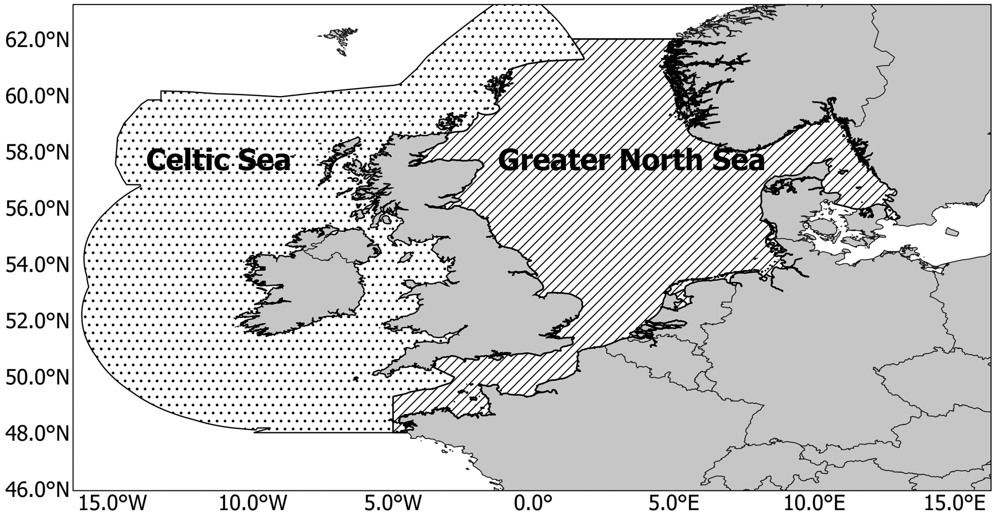

Figure 1. The study area covering the North Sea and the Celtic Sea.

stomach contents and previous studies published in relevant literature.

While ICES stock assessments are primarily carried out for single species, there has been a move in recent years towards integrated ecosystem assessments (IEAs), which provide a holistic view of an ecosystem, rather than focussing only on a single fish species (Punt *et al.*, 2020). IEAs are complex enough to accommodate prey–predator relationships between species. IEAs can factor in cumulative impacts from pressures such as anthropogenic activities and climate change (Mollmann *et al.*, 2014), and so are useful when identifying appropriate management options (McLeod and Leslie, 2009). Currently, due to their life-history complexities (Xavier *et al.*, 2015), cephalopods are not stock assessed in northwest European shelf waters (though several stocks are assessed in areas such as Japan, the southwest Atlantic shelf, and the western coast of the United States) and are omitted from regular ecosystem assessments. To address these potential gaps in coverage, this study aims to (1) characterize the importance of cephalopods in the diet of ecologically important finfish of the European shelf seas, and (2) determine whether and particularly which cephalopod groups should be considered for inclusion in fisheries IEAs.

Material and methods

Choice of species

Data on cephalopods as prey items were not considered for all finfish within the study area, which is next to impossible considering local biodiversity (195 species in North Sea alone without adjacent ecoregions—Froese and Pauly, 2021). To focus the study onto finfish of ecological importance, we restricted our study to finfish species that comprised the top 90% of catch weight from catches made by diverse ship-based research surveys by the Cefas/ Lowestoft Laboratory (1901–2020). Catch data used to screen out finfish with less of a role in European shelf food webs were obtained from Cefas' survey database, which covered those areas shown in Figure 1.

Material

We targeted all those species (among the top 90% of catch weight) for records of the presence of cephalopod remains in their stomachs to inform on their diet and prey selection. Data on fish diet were obtained from literature, in conjunction with data from the integrated database and portal for fish stomach records (DAPSTOM, https://www.cefas.co.uk/data-and-publications/fish-stomach-records/) (Pinnegar, 2014). This dataset includes fish stomach records from 449 research surveys from 1837 to 2012, spanning 226407 records from 254202 individual predator stomachs, from 188 predator species. Data were selected from the year 2000 onwards. In some cases, records were at the species level and in others, records were more general (e.g. "squid"). A summary of stomachs of these key species examined in DAPSTOM and from literature is provided in Table 1.

Methods

The contribution of cephalopods in the diet composition of the target finfish was quantified using traditional methods, such as relative abundance (%N; percentage of numbers of a particular prey item in respect to total number of prey) and frequency of occurrence (%O; number of stomachs that contained a specific prey item, divided by the total number of stomachs). These measurements are generally accepted as a method to provide an accurate account of dietary importance and to allow comparability across taxa and biogeographical gradients (Garvey and Whiles, 2016).

Results

Generally, cephalopod consumption by finfish in the study area was relatively low. The highest (albeit still very low) contribution to the diet of finfish by cephalopods was for mackerel (*S. scombrus*), which consumed sepiolids (*Sepiola atlantica*), and loliginids (Table 2). The widest recorded diversity of cephalopods consumed was in whiting *Merlangius merlangus,* which consumed squids, *S. atlantica*, inshore myopsid

Table 1. Summary of stomachs of key species examined in DAPSTOM and from literature.

Species	Number of stomachs from DAPSTOM	Number of stomachs from literature data
Mackerel (*Scomber scombrus*)	4 522	10 (Berge *et al.*, 2015)
		244 (Daly *et al.*, 2001)
		222 (Velasco *et al.*, 2001)
		11 068 (ICES, 1997)
Horse mackerel (*Trachurus trachurus*)	35	NA
Herring (*Clupea harengus*)	1 248	NA
Whiting (*Merlangius melangus*)	28 370	11 188 (Robb, 1981)
		543 (Robb & Hislop, 1980)
		2 364 (Hislop *et al.*, 1991)
		388 (Bromley *et al.*, 1997)
		57 610 (ICES (1997)
		1 311 (Demain *et al.*, (2011)
Haddock (*Melanogrammus aeglefinus*)	1 883	1 014 (Albert, 1991)
		816 (Daly *et al.*, 2001)
		37 646 (ICES, 1997)
		492 (Demain *et al.*, 2011)
Dab (*Limanda limanda*)	833	NA
Plaice (*Pleuronectes platessa*)	2 734	NA
Norway pout (*Trisopterus esmarkii*)	0	NA
Cod (*Gadus morhua*)	10 597	399 (Daly *et al.*, 2001)
		21 152 (ICES, 1997)
Sprat (*Sprattus sprattus*)	2 079	NA
Pilchard (*Sardina pilchardus*)	0	NA
Boarfish (*Capros aper*)	0	NA
Dogfish (*Scyliorhinus canicula*)	137	NA
Blue whiting (*Micromesistius poutasso*)	35	86 (Daly *et al.*, 2001)
Grey gurnard (*Eutrigla gurnardus*)	6 342	11 700 (ICES, 1997)
Spurdog (*Squalus acanthias*)	27	NA
Poor cod (*Trisopterus minutus*)	249	NA
Sardine (*S. pilchardus*)	0	NA
Hake (*Merluccius merluccius*)	62	NA
Sole (*Solea solea*)	95	NA
Thornback ray (*Raja clavata*)	12	545 (Holden and Tucker, 1974)
American plaice (*Hippoglossoides platessoides*)	108	543 (Ntiba and Harding, 1993)
Monkfish (*Lophius piscatorius*)	20	1 056 (Laurenson and Priede, 2005)
Redfish (*Sebastes viviparus*)	0	NA
Lemon sole (*Microstomus kitt*)	219	NA
Bib (*Trisopterus luscus*)	0	NA
Starry smooth-hound (*Mustelus asterias*)	4	640 (McCully Phillips *et al.*, 2020)

NA: cephalopods did not exist in the predators' stomachs.

squids (Loliginidae), common cuttlefish (*Sepia officinalis*), and unidentified cephalopods.

From the 26 finfish species (Table 1) studied, which represented 90% of Cefas survey catch biomass (i.e. those with available stomach contents data), 18 did not appear to include cephalopods in their diets at all. Those included horse mackerel, herring, Norway pout, sprat, pilchard, boarfish, blue whiting, spurdog, poor cod, hake, sole, monkfish, redfish, and bib (Table 2).

The highest occurrence (%O) of cephalopods was found in the stomachs of whiting, whereas in some situations, ~25% of the individuals were observed to have consumed squid (Table 3). Whilst saithe (*Pollachius virens*) did not contribute to the top 90% of survey catch weights and hence, was not considered here, relevant literature (Robb and Hislop, 1980; Robb, 1981; Nedreaas, 1985; Bromley *et al.*, 1997; Fujii, 2016) showed this predator regularly consumed *Loligo forbesii* (%O 0–14.4) and other cephalopods (%O 0–14.4; ICES, 1997). This demonstrates that species for which cephalopods are potentially important prey may not be numerous.

Apart from mackerel, pelagic predators were generally not found to have consumed cephalopods (Table 2), but there were feeding links between benthic/demersal predators and benthic/demersal cephalopods. Cuttlefish occurred in the diets of thornback ray (Holden and Tucker, 1974), American plaice (Ntiba and Harding, 1993), and starry smooth-hound (McCully Phillips *et al.*, 2020) (Table 3), whilst octopus appeared in the diets of haddock (Albert, 1991), cod (a single *Eledone* specimen; Daly *et al.*, 2001), and monkfish, where an ontogenetic dietary shift has been suggested (Laurenson and Priede, 2005) (Table 2).

Cephalopods contributed to the diets of whiting, particularly for 1-year-old fish (ICES, 1997). Cephalopod consumption was also highest in younger individuals of haddock (ICES, 1997; Demain *et al.*, 2011) with a similarly decreasing importance with age for saithe (ICES, 1997). Conversely, high proportions of cephalopods were found in the stomachs of older specimens of mackerel (ICES, 1997), and a beak was found in a large starry smooth-hound specimen (Ntiba and Harding, 1993). Separating the year into four quarters: January–March (Q1); April–June (Q2); July–September (Q3); and October–December (Q4), contributions to the diets of monkfish appeared seasonally dependent (found in 1.2%O in Q1, not recorded in Q2, found in 3.2%O in Q3, not recorded in Q4;

Table 2. Importance of cephalopods as prey for 26 finfish species, based on stomach records from 2000 to 2020 extracted from the DAPSTOM (see Pinnegar, 2014) data portal, and literature records where cephalopods were recorded as prey of finfish, either quantified as an average number of cephalopods per predator stomach (%N) or as a proportion of predators observed to have eaten cephalopods (%O).

		DAPSTOM records				Literature records			
Predator	Feeding type	Predator abundance (% of total fish in all surveys)	Cephalopod prey	Cephalopod prey numbers recorded	%N	%N	%O	Notes	Source
Mackerel (*S. scombrus*)	Pelagic	13.76	Little cuttlefish (*S. atlantica*)	66	1.45	–	–	–	–
			Loliginids	18	0.4	–	–	–	–
			Squids	–	–	–	–	Teuthoidea accounted for 1.5% of prey by weight and 1.8% of dry weight	Daly *et al.* (2001), Berge *et al.* (2015)
			Cephalopods	–	–	–	0– 79.9	Highest proportions found in older specimens	ICES (1997), Daly *et al.* (2001), Velasco *et al.* (2001)
Horse mackerel (*T. trachurus*)	Pelagic	12.33	No records	–	–	–	–	–	–
Herring (*C. harengus*)	Pelagic	11.1	No records	–	–	–	–	–	–
Whiting (*M. melangus*)	Demersal	9.1	Squids (nei)	49	0.002	0.01–6.15	0–25	*Alloteuthis subulata* (100–500 mm carapace length)	Robb and Hislop (1980), Robb (1981), Hislop *et al.* (1991), Bromley *et al.* (1997), ICES (1997), Demain *et al.* (2011)
			Little cuttlefish (*S. atlantica*)	4	0.00014	–	–	–	–
			Common squid (*Loligo vulgaris*)	149	0.005	–	–	–	–

Table 2. Continued

Predator	Feeding type	DAPSTOM records Predator abundance (% of total fish in all surveys)	Cephalopod prey	Cephalopod prey numbers recorded	%N	Literature records %N	%O	Notes	Source
			Common cuttlefish (*S. officinalis*)	23	0.0008	–	–	–	–
			Cephalopods	28	0.0009	–	3.87–11.9	–	ICES (1997)
Haddock (*M. aeglefinus*)	Demersal	8.75	Octopus	1	0.001	–	1.8	20–29 cm predator TL	Albert (1991)
			Squids	–	–	–	–	One *S. atlantica* identified from 151 haddock	Daly *et al.* (2001)
			Cephalopods	2	0.001	–	–	–	ICES (1997), Demain *et al.* (2011)
Dab (*L. limanda*)	Demersal	4.75	Squids (nei)	2	0.2	–	–	–	–
Plaice (*P. platessa*)	Demersal	4.66	Squids (nei)	1	0.04	–	–	–	–
Norway pout (*T. esmarkii*)	Demersal	3.3							
Cod (*G. morhua*)	Demersal	3.16	Squid	1	0.009	–	0.1–11.04	–	ICES (1997)
			Little cuttlefish (*S. atlantica*)	1	0.009	–	–	–	–
			Octopuses	2	0.019	–	–	1 Eledone found in the stomach of North Sea specimen	Daly *et al.* (2001)
Sprat (*S. sprattus*)	Pelagic	3.01							
Pilchard (*S. pilchardus*)	Pelagic	2.01							

Table 2. Continued

		DAPSTOM records				Literature records			
Predator	Feeding type	Predator abundance (% of total fish in all surveys)	Cephalopod prey	Cephalopod prey numbers recorded	%N	%N	%O	Notes	Source
Boarfish (*C. aper*)	Pelagic	1.72							
Dogfish (*S. canicula*)	Demersal	1.68	Curled octopus (*Eledone cirrhosa*)	1	0.007	–	–	–	–
Blue whiting (*M. poutasso*)	Benthopelagic	1.64	Squids	–	–	–	–	*L. vulgaris* listed as an important prey item but not quantified	Daly *et al.* (2001)
Grey gurnard (*E. gurnardus*)	Demersal	1.49	Little cuttlefish (*S. atlantica*)	14	0.22	–	–	–	–
			Squids (Nei)	56	0.88	–	–	–	–
			Cephalopoda	14	0.05	–	0.03–3.52	–	ICES (1997)
Spurdog (*S. acanthias*)	Demersal	1.07							
Poor cod (*T. minutus*)	Demersal	1.03							
Sardine (*S. pilchardus*)	Pelagic	0.97							
Hake (*M. merluccius*)	Demersal	0.75							
Sole (*S. solea*)	Demersal	0.6							
Thornback ray (*R. clavata*)	Demersal	0.56	Cuttlefish (*S. officinalis*)	–	–	–	1	–	Holden and Tucker (1974)
American plaice (*H. platessoides*)	Demersal	0.51	Cuttlefish (*S. officinalis*)	–	–	–	2.4	–	Ntiba and Harding (1993)

Table 2. Continued

		DAPSTOM records				Literature records			
Predator	**Feeding type**	**Predator abundance (% of total fish in all surveys)**	**Cephalopod prey**	**Cephalopod prey numbers recorded**	**%N**	**%N**	**%O**	**Notes**	**Source**
Monkfish (*L. piscatorius*)	Demersal	0.46	Squid	–	–	0–1.74	1.2–2.1	–	Laurenson and Priede (2005)
			Octopus	–	–	0.2–4.4	–	–	–
			Cephalopods	–	–	0–3.5	0–3.2	–	–
Redfish (*S. viviparus*)	Demersal	0.44							
Lemon sole (*M. kitt*)	Demersal	0.42	Squids	1	0.005	–	–	–	–
Bib (*T. luscus*)	Demersal	0.39	No records	–	–	–	–	–	–
Starry smouth-hound (*M. asterias*)	Demersal	0.37	Cuttlefish (*S. officinalis*)	–	–	0.1	0.3	–	McCully Phillips *et al.* (2020)

Grey cells = no records.

Laurenson and Priede, 2005). Results for grey gurnard were similar (ICES, 1997).

Discussion

As fast-growing and highly productive animals, many cephalopod species can rapidly reach adult size, providing a large biomass and therefore substantial calorific content to predators. Nevertheless, this study found most records of cephalopods in fish stomachs taken from the European shelf returned very low abundances (Table 2; see also Smale, 1996; Velasco *et al*., 2001). This contrasts with several studies on cephalopods in fish diet carried out elsewhere in the world (Table 3; see also Hunsicker *et al*., 2010; Queirós *et al*., 2021).The data we present provide an updated baseline of the cephalopod role in marine food webs in European shelf waters for the first time since the ICES 'Year of the Stomach' in 1981–1982 (Hislop *et al*., 1991) and can now be viewed in comparison with other worldwide studies that have been carried out in the intervening years (Table 3).

Based on our DAPSTOM records (Table 2), it would be plausible to assume that cephalopods have a minor contribution to the diet of the range of ecologically important finfish, but these records are dependent on the time of year of sampling and the age of the predator. Some fish may be more dependent on cephalopod prey at certain times of the year e.g. monkfish and gurnard. On the other hand, cephalopods might be more important in the diet of younger fish, e.g. haddock and saithe (ICES, 1997; Demain *et al*., 2011) or older fish, e.g. mackerel (ICES, 1997). Further, feeding relationships are conditional on the functional role of the predator, type of cephalopod prey, and type of habitat. For instance, we identified a clear relationship between benthic-feeding finfish and benthic cephalopods (see also Hislop *et al*., 1991) with relatively high numbers of octopus species in their diet, while demersal predators in Scotland feed on abundant loliginid squids early in the year (Table 2), coinciding with the squid's seafloor breeding period (Boyle and Pierce, 1994). While a large proportion of finfish species examined during the literature review exhibited either an absence or low abundance of cephalopods in their stomachs (Table 2), this may not represent the true picture of feeding relationships throughout the year. One plausible scenario is that previous studies failed to investigate the relationship between target species and cephalopods due to the expected negligible contributions.

For example, a study of demersal fish predators in the Bay of Biscay (Lusitanian Zoogeographic Province—Nesis, 2003) found that cephalopods made up just 0.66% of the total number of prey items, in line with our findings for the Celtic Zoogeographic Province. While some fish species exhibit a high occurrence of cephalopod in stomachs (~14%O in whiting, ~30%O in saithe, and ~80%O in mackerel: Pierce and Santos, 1996), these data might be seasonally dependent and in this case were taken in the first quarter of the year, during the peak of both *Loligo* species spawning, and would be influenced by post-spawning mortality when large senile and dead squid become an easy target for predation and scavenging, respectively.

As the predator fish grow larger, their diet may diversify with extending size range of prey, and among other changes, they become able to hunt larger cephalopods. In the southern Bay of Biscay, Velasco *et al*. (2001) found that for small predatory finfish (<50 cm total length (TL)), the proportion of cephalopod prey did not reach 1.5% of total volume; however, for larger fish (>50 cm in length), this proportion reached 8% (Velasco *et al*., 2001).

There are also difficulties in comparing cephalopod vs. fish as prey items when analysing stomach contents, due to the different digestion rates of fish vs. cephalopod flesh. Soft tissue or calcareous remains such as the fish skeleton are either dissolved quickly or ejected faster than cephalopod remains such as beaks (Clarke *et al*., 2002). While useful for cephalopod identification, often to family level, beaks can be retained long after digestion, giving a biased measurement of recent feeding on cephalopods (Santos *et al*., 2001). A further uncertainty that hindered our confidence in stomach records interpretation was that cephalopod prey were often recorded only to a high taxonomic level, such as "squid" or even "cephalopod", due to the difficulty of identification from digested remains alone.

The extent that cephalopods contribute to the diet of predators can vary according to the geographical region as even if predators are the same/similar, the cephalopod availability might be very different; Hunsicker *et al.* (2010) estimated cephalopods may support ~15% of marine fisheries landings by weight and 20% by value off the northeastern Unites States (Hunsicker *et al*., 2010). Such geographical differences are highlighted in Table 3, where contributions of cephalopods to the diets of some fish in the Celtic Sea and the North Sea are compared to their importance in diet of analogous predators in the different parts of the world. Table 3 highlights the contributions of cephalopods to the diets of some of the aforementioned finfish in the Celtic Sea and the North Sea, compared to their importance in different parts of the world, either to the same finfish species or to ecologically equivalent species.

Aside from the factors already discussed (depth, seasonality, and life cycle stage) that can influence finfish predation on squid, the differences in the reliance of fish populations from different parts of the world on cephalopod food supply may be a result of external factors such as geological processes, with the unique situation in the European shelf seas related to the relatively recent formation of this basin. We hypothesize that the glacial retreat, the resulting formation of new ecosystems, and new types of vertical and horizontal water circulation were accompanied by gradual penetration of fish and cephalopods into warmed shelf seas. Under this scenario, a higher efficiency of metabolism and lower demands in energy (food supply) provided fish species the unique conditions to colonize new areas. Local populations of cephalopods persisting from the glacial phase were relatively low in number and importance, as they are nowadays in both the Arctic and the Antarctic (Chesnais *et al*., 2019). Thus, observed differences in food webs between the Acadian Zoogeographic Province (northwest Atlantic) and the symmetrical Celtic Zoogeographic Province (northeast Atlantic) could be related to the distribution of the ice sheet during the recent glaciation that was covering large areas of Europe and eastern North America (Menzies, 2018). These shelf seas are relatively recently established in their new function, and the North Sea is the youngest of these shelf areas, simultaneously exhibiting the lowest importance of cephalopods in fish diets. Such intensive glaciation likely never developed in the Pacific area, South Africa, and Australia, and was relatively limited around southern South America, where cephalopod roles in food webs are incomparably higher (Xavier *et al*., 2018). This situation

Table 3. Contributions of cephalopods to the diets of finfish species in the Celtic Sea and the North Sea, compared to those in the same species or ecologically equivalent species in other marine regions.

Species	Celtic Sea and North Sea		Ecological equivalent	Other areas where cephalopods are important		Reference
	%N	%O		%N	%O	
Mackerel (*S. scombrus*)	0–1.45	0–79.9	*S. scombrus* (NE Atlantic)	N/A	N/A	Olaso *et al.* (2005)
Horse mackerel (*T. trachurus*)	N/A	N/A	*T. trachurus* (Aegean Sea)	0.91—Cephalopoda	N/A	Bayhan and Sever (2009)
Herring (*C. harengus*)	N/A	N/A	*C. harengus* (Norwegian Sea)	N/A	N/A	Prokopchuk and Sentyabov (2006)
Whiting (*M. merlangus*)	0.00014–6.15	0–25	*M. merlangus* (southeastern Mediterranean)	N/A	N/A	Mazlum and Bilgin (2014)
Haddock (*M. aeglefinus*)	0.001	1.8	*Merlanogrammus aeglefinus* (Barents Sea)	N/A	N/A	Jiang and Jørgensen (1996)
Dab (*L. limanda*)	0.2	N/A	*Platichthys flesus* (Atlantic Ocean)	N/A	N/A	Vinagre *et al.* (2008)
Plaice (*P. platessa*)	0.04	N/A	*P. flesus* (Atlantic Ocean)	N/A	N/A	Vinagre *et al.* (2008)
Norway pout (*T. esmarkii*)	N/A	N/A	*T. esmarkii* (west Norwegian fjord)	N/A	0.37—Cephalopoda	Mattson (1981)
Cod (*G. morhua*)	0.001–0.019	0.1–11.04	*G. morhua* (Faroe Bank)	N/A	N/A	Magnussen (2011)
Sprat (*S. sprattus*)	N/A	N/A	*S. sprattus* (Baltic Sea)[a]	N/A	N/A	Cardinale *et al.* (2003)
Pilchard (*S. pilchardus*)	N/A	N/A	*S. pilchardus* (Mediterranean)	N/A	N/A	Costalago *et al.* (2015)
Boarfish (*C. aper*)	N/A	N/A	*C. aper* (Aegean and Ionian Seas)	N/A	N/A	Vagenas *et al.* (2020)
Lesser spotted dogfish (*S. canicula*)	0.007	0	*S. canicula* (Bay of Biscay)	Mean 6.1 (%Volume)	0	Velasco *et al.* (2001)
Blue whiting (*M. poutasso*)	0	0	*M. poutasso* (Mediterranean)	N/A	N/A	Mir-Arguimbau *et al.* (2020)
Grey gurnard (*E. gurnardus*)	0.22	0.03–3.52	*E. gurnardus* (Mediterranean)	N/A	N/A	Montanini *et al.* (2010)
Spurdog (*S. acanthias*)	0.88	0	*S. acanthias* (Patagonian shelf)	7.7–10.8—only squid *Doryteuthis gahi*, plus other cephalopods	12.7–19.5—only squid *D. gahi*, plus other cephalopods	Laptikhovsky *et al.* (2010)
Poor cod (*T. minutus*)	0.05	0	*T. minutus* (Mediterranean)	0.083 *Alloteuthis media*, 1.832 *Sepiola* sp.	0	Morte *et al.* (2001)
Sardine (*S. pilchardus*)	N/A	N/A	*S. pilchardus* (Mediterranean)	N/A	N/A	Nikolioudakis *et al.* (2012)
Hake (*M. merluccius*)	N/A	N/A	*Meluccius hubbsi* (Falkland shelf)	43.3—only squid *D. gahi*, plus other cephalopods	89.4—only squid *D. gahi*, plus other cephalopods	Laptikhovsky *et al.* (2010)
Sole (*S. solea*)	0	1	*S. solea*, *Solea senegalensis* (Portugal)	N/A	N/A	Cabral (2000)
Thornback ray (*R. clavata*)	0	2.4	*R. clavata* (Adriatic)	*Sepietta oweniana* 2.3, *Sepiola rondoletii* 2, *Illex coindetii* 1.6, *Sepiola elegans* 1.2, *Eledone* sp. 0.7, non-identified cephalopods 2.8	*S. oweniana* 4.2, *S. rondoletii* 4, *I. coindetii* 3, *S. elegans* 2.5, *E.* sp. 1.5, non-identified cephalopods 5	Šantić *et al.* (2012)
American plaice (*H. platessoides*)	N/A	N/A	*H. platessoides* (southern Grand Bank, Newfoundland)	N/A	N/A	Zamarro (1991)
Monkfish (*L. piscatorius*)	0.5–4.4	0.7–1.2	*L. piscatorius* (Bay of Biscay)	Mean 8.04 (%Volume)	0	Velasco *et al.* (2001)

Table 3. Continued

Species	Celtic Sea and North Sea		Ecological equivalent	Other areas where cephalopods are important		Reference
	%N	%O		%N	%O	
Redfish (*S. viviparus*)	N/A	N/A	*Sebastes mentella* (Barents Sea)	0	3.26—Cephalopoda	Dolgov and Drevetnyak (2011)
Lemon sole (*M. kitt*)	0.005	0	*Microstomus pacificus* (Pacific)	N/A	N/A	Pearcy and Hancock (1978)
Bib (*T. luscus*)	N/A	N/A	*Phycis phycis* (Portuguese continental close)	Length group 25–40.5	Length group 25–42.6	Silva *et al*. (2017)
Starry smooth hound (*M. asterias*)	0.08–0.1	0.29–0.3	*Mustelus mustelus* (western Mediterranean)	0	0.79—*S. officinalis*, 0.79—*Alloteuthis mediterranea*, 1.58—*L. vulgaris*	Morte *et al*. (1997)

[a] Most sprat diet literature from the Baltic where cephalopods do not occur except for in the very western approaches.

appears paradoxical given that Cephalopoda are known to quickly react to environmental changes and occupy vacant niches faster than fish, e.g. *Octopus vulgaris* off northwest Africa (Balguerias *et al*., 2000). The real evolutionary reason for such a "mishap" in the Celtic ecoregion is difficult to guess. One possible explanation is that all dominating cephalopod species (*Loligo* spp., *Alloteuthis* spp., *S. officinalis*, and *E. cirrhosa*) are also similarly common in two southerner, and consequently, warmer zoogeographic provinces: Lusitanian and Mediterranean (Nesis, 2003). In contrast to this, the predominating fish species in the studied area are mostly sheer Celtic (e.g. cod, haddock, plaice, and herring) with very few whose distribution extends over these three provinces (e.g. whiting and sprat). Fish probably were omnipresent in the expanding and collapsing North Sea and the English Channel and established ecosystem relations in which newcomers from the south—cephalopods—found it difficult to compete.

The process of increasing cephalopod abundances in ecosystems has become apparent in the northwest Atlantic due to the Gulf Stream, particularly south of Newfoundland, where *D. pealeii* and *I. illecebrosus* have become key species in areas where ice sheet coverage had been relatively restricted. The absence of such a warming current along eastern shores of Europe slowed this process down. Noticeably, during climate-related changes in recent decades and the resulting increase of water temperatures, the abundance of squids in seas around the United Kingdom has increased, and, consequently, a distribution range expansion has been observed throughout the North Sea (Van der Kooij *et al*., 2016). In coming decades, modelling studies predict that on the European shelf, habitat suitability for several cephalopod species, notably European squid *L. vulgaris* and veined squid *L. forbesii*, will greatly increase (more than for many finfish species examined: Defra, 2013; Jones *et al*., 2015). While the current contribution is moderate only, the role of cephalopods in the diet of predatory fish is likely to increase, as is possible predation by cephalopods. Therefore, we recommend that monitoring programmes consider cephalopods as potential key prey species expected to rise in importance. To better understand their abundance and distribution dynamics, as well as the impacts that changes in predator–prey interactions might have on the wider ecosystem under a changing climate, warrants proper inclusion in IEAs in the future.

Data availability statement

The data underlying this article are available in the DAPSTOM at https://www.cefas.co.uk/data-and-publications/fish-stomach-records/.

Author contributions

CB and VL conceived the ideas and designed the methodology and analyses. All co-authors participated in data extraction and analyses. SS produced Figure 1. RV and PB quality checked and amended the final manuscript draft. This manuscript is submitted with the approval of all the authors.

Conflict of interest statement

The authors have no competing interests to declare.

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References

Albert, O. T. 1991. Distribution and Trophic Ecology of Haddock *Melanogrammus aeglefinus* in the Norwegian Deep. ICES Document CM 1991/G: 45 Demersal Fish Committee. 15pp.

Balguerías, E., Quintero, M. E., and Hernández-González, C. L. 2000. The origin of the Saharan Bank cephalopod fishery. ICES Journal of Marine Science, 57: 15–23.

Bayhan, B., and Sever, T. M. 2009. Food and feeding habits of the Atlantic horse mackerel *Trachurus trachurus,* from the Aegean Sea. Zoology in the Middle East, 46: 47–54.

Berge, J., Heggland, K., Lønne, O. J., Cottier, F., Hop, H., Gabrielsen, G. W., Nøttestad, L. *et al.* 2015. First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. Arctic, 68: 54–61.

Brodziak, J. 1998. Revised biology and management of long-finned squid (*Loligo pealei*) in the northwest Atlantic. California Cooperative Oceanic Fisheries Investigations Report, 39: 61–70.

Bromley, P. J., Watson, T., and Hislop, J. R. G. 1997. Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting

(*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea. ICES Journal of Marine Science, 54: 846–853.

Boyle, P. R., and Pierce, G. J. 1994. Fishery biology of northeast Atlantic squid: an overview. Fisheries Research, 21: 1–15.

Cabral, H. N. 2000. Comparative feeding ecology of sympatric *Solea solea* and *S. senegalensis*, within the nursery areas of the Tagus estuary, Portugal. Journal of Fish Biology, 57: 1550–1562.

Cardinale, M., Casini, M., Arrhenius, F., and Håkansson, N. 2003. Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources, 16: 283–292.

Chesnais, T. D. l., Fulton, E. A., Tracey, S. R., and Pecl, G. T. 2019. The ecological role of cephalopods and their representation in ecosystem models. Reviews in Fish Biology and Fisheries, 29: 313–334.

Clarke, M. R. 1996. The role of cephalopods in the world's oceans: general conclusion and the future. Philosophical Transactions of the Royal Society B: Biological Sciences, 351: 1105–1112.

Clarke, M., Allcock, L., and Begoña Santos, M. 2002. Estimating cephalopod biomass: workshop report. Bulletin of Marine Science, 71: 47–65.

Costalago, D., Garrido, S., and Palomera, I. 2015. Comparison of the feeding apparatus and diet of European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters: ecological implications. Journal of Fish Biology, 86: 1348–1362.

Croxall, J. P., and Prince, P. A. 1996. Cephalopods as prey. I. Seabirds. Philosophical Transactions of the Royal Society B: Biological Sciences, 351: 1023–1043.

Daly, H. I., Pierce, G. J., Santos, M. B., Royer, J., Cho, S. K., Stowasser, G., Robin, J-P. *et al.* 2001. Cephalopod consumption by trawl caught fish in Scottish and English Channel waters. Fisheries Research, 52: 51–64.

DEFRA. 2013. Economics of climate resilience: natural environment—sea fish. Department for Environment, Food and Rural Affairs (DEFRA), February 2013, 101pp.

Demain, D. K., Gallego, A., Jaworski, A., Priede, I. G., and Jones, E. G. 2011. Diet and feeding niches of juvenile *Gadus morhua, Melanogrammus aeglefinus* and *Merlangius merlangus* during the settlement transition in the northern North Sea. Journal of Fish Biology, 79: 89–111.

Dolgov, A. V., and Drevetnyak, K. V. 2011. Feeding of Three Species from the Genus *Sebastes* in the Barents Sea. ICES Document CM 2011/A: 26. Session A. Joint ICES/PICES Theme Session on Atlantic redfish and Pacific rockfish: comparing biology, ecology, assessment and management strategies for *Sebastes* spp. 13pp.

Froese, R., and Pauly, D. (Ed) 2021. FishBase. www.fishbase.org, version (08/2021) (last accessed 4 January 2022).

Fujii, T. 2016. Potential influence of offshore oil and gas platforms on the feeding ecology of fish assemblages in the North Sea. Marine Ecology Progress Series, 542: 167–186.

Garvey, J. E., and Whiles, M. 2016. Trophic Ecology, 1st edn. CRC Press, Boca Raton. 393pp.

Hanlon, R., Buresch, K., Staudinger, M., and Moustahfid, H. 2013. *Doryteuthis pealeii*, longfin inshore Squid. *In* Advances in Squid Biology, Ecology and Fisheries. Part I: Myopsid squids, pp. 205–240. Ed. by Rosa R., O'Dor R., and Pierce. G. NOVA Science Publishers Inc., Hauppauge, NY. 349pp.

Hislop, J. R. G., Robb, A. P., Bell, M. A., and Armstrong, D. W. 1991. The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. ICES Journal of Marine Science, 48: 139–156.

Holden, M. J., and Tucker, R. N. 1974. The food of *Raja clavata* Linnaeus 1758, *Raja montagui* Fowler 1910, *Raja naevus* Müller and Henle 1841 and *Raja brachyura* Lafont 1873 in British waters. ICES Journal of Marine Science, 35: 189–193.

Hunsicker, M. E., Essington, T. E., Watson, R., and Sumaila, U. R. 2010. The contribution of cephalopods to global marine fisheries: can we have our squid and eat them too? Fish and Fisheries, 11: 421–438.

ICES. 1997. Database report of the Stomach Sampling project 1991. ICES Cooperative Research Report, 219. 422pp.

Jackson, G. D., George, M. J. A., and Buxton, N. G., 1998. Distribution and abundance of the squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in the Falkland Islands region of the South Atlantic. Polar Biology, 20, 161–169.

Jereb, P., Allcock, A. L., Lefkaditou, E., Piatkowski, U., Hastie, L. C., and Pierce, G. J. (Eds) 2015.*Cephalopod biology and fisheries in Europe: II. Species Accounts*. ICES Cooperative Research Report, 325. 360pp.

Jiang, W., and Jørgensen, T. 1996. The diet of haddock (*Melanogrammus aeglefinus* L.) in the Barents Sea during the period 1984–1991. ICES Journal of Marine Science, 53: 11–21.

Jones, M. C., Dye, S. R., Pinnegar, J. K., Warren, R., and Cheung, W. W. L. 2015. Using scenarios to project the changing profitability of fisheries under climate change. Fish and Fisheries, 16: 603–622.

Katugin, O. N., Shevtsov, G. A., Zuev, M. A., Didenko, V. D., Kulik, V. V., and Vanin, N. S. 2013. Advances in Squid Biology, Ecology and Fisheries. Part II: Oegopsid Squids. NOVA Science Publishers Inc., Hauppauge, NY. 293pp.

Klages, N. T. W. 1996. Cephalopods as prey. II. Seals. Philosophical Transactions of the Royal Society B: Biological Sciences, 351: 1045–1052.

Laptikhovsky, V., Arkhipkin, A., and Brickle, P. 2010. Squid as a resource shared by fish and humans on the Falkland Islands' shelf. Fisheries Research, 106: 151–155.

Laptikhovsky, V., Bell, J. B., Benedet, R., Glass, J., Glass, W., Green, R., Robson, G. R. *et al.* 2020. Feeding habits of bluenose warehou, *Hyperoglyphe antarctica* (Carmichael, 1819) (Centrolophidae) at seamounts of the southern Atlantic. Deep Sea Research Part I: Oceanographic Research Papers, 156: 103–182.

Laurenson, C. H., and Priede, I. G. 2005. The diet and trophic ecology of anglerfish *Lophius piscatorius* at the Shetland Islands, UK. Journal of the Marine Biological Association of the United Kingdom, 85: 419–424.

McCully Phillips, S. R., Grant, A., and Ellis, J. R. 2020. Diet composition of starry smooth-hound *Mustelus asterias* and methodological considerations for assessing the trophic level of predatory fish. Journal of Fish Biology, 96: 590–600.

McLeod, K. L., and Leslie, H. M. 2009. Ecosystem-Based Management for the Oceans. Island Press, Washington DC. 363pp.

Magnussen, E. 2011. Food and feeding habits of cod (*Gadus morhua*) on the Faroe Bank. ICES Journal of Marine Science, 68: 1909–1917.

Manooch, C. S., and Mason, D. L. 1983. Comparative food studies of yellowfin tuna, *Thunnus albacares*, and blackfin tuna, *Thunnus atlanticus* (Pisces: Scombridae) from the southeastern and Gulf coasts of the United States. Brimleyana, 9, 33–52.

Mattson, S. 1981. The food of *Galeus melastomus*, *Gadiculus argenteus thori*, *Trisopterus esmarkii*, *Rhinonemus cimbrius*, and *Glyptocephalus cynoglossus* (Pisces) caught during the day with shrimp trawl in a West-Norwegian fjord. Sarsia, 66: 109–127.

Mazlum, R. E., and Bilgin, S. 2014. Age, growth, reproduction and diet of the whiting, *Merlangius merlangus euxinus* (Nordmann, 1840), in the southeastern Black Sea. Cahiers de Biologie Marine, 55: 463–474.

Menzies, J. 2018. Glacial Geomorphology. *In* Reference Module in Earth Systems and Environmental Sciences, pp. 1–16. Elsevier, San Diego.

Mir-Arguimbau, J., Navarro, J., Balcells, M., Martín, P., and Sabatés, A. 2020. Feeding ecology of blue whiting (*Micromesistius poutassou*) in the NW Mediterranean: the important role of Myctophidae. Deep-Sea Research Part I: Oceanographic Research Papers, 166: 103404

Möllmann, C., Lindegren, M., Blenkner, T., Bergström, L., Casini, M., Diekmann, R., Flinkman, J. *et al.* 2014. Implementing ecosystem-based fisheries management: from single-species to integrated ecosystem assessment and advice for Baltic Sea fish stocks. ICES Journal of Marine Science, 71: 1187–1197.

Montanini, S., Staioni, M., and Vallisneri, M. 2010. Diet of the grey gurnard, *Eutrigla gurnardus* in the Adriatic Sea, north-eastern Mediterranean. Cybium, 34: 367–372.

Morte, M. S., Redón, M. J., and Sanz-Brau, A. 1997. Feeding habits of juvenile *Mustelus mustelus* (Carcharhiniformes, Triakidae) in the western Mediterranean. Cahiers de Biologie Marine, 38: 103–107.

Morte, M. S., Redón, M. J., and Sanz-Brau, A. 2001. Feeding habits of *Trisopterus minutus capelanus* (Gadidae) off the eastern coast of Spain (western Mediterranean). Marine Ecology, 22: 215–229.

Moustahfid, H., Tyrrell, M. C., and Link, J. S. 2009. Accounting explicitly for predation mortality in surplus production models: an application to longfin inshore squid. North American Journal of Fisheries Management, 29: 1555–1566.

Nedreaas, K. H. 1985. Food and feeding habits of young Saithe on the coast of western Norway. Fiskeridirektoratets skrifter, Serie Havundersøkelser, 18: 263–301.

Nesis, K. N. 2003. Distribution of recent Cephalopoda and implications for Plio–Pleistocene events. Berliner Paläobiologische. Abhandlungen, 3: 199–224

Nikolioudakis, N., Isari, S., Pitta, P., and Somarakis, S. 2012. Diet of sardine *Sardina pilchardus*: an 'end-to-end' field study. Marine Ecology Progress Series, 453: 173–188.

Ntiba, M. J., and Harding, D. 1993. The food and feeding habits of the long rough dab, *Hippoglossoides platessoides* (Fabricius 1780) in the North Sea. Netherlands Journal of Sea Research, 31: 189–199.

O'Dor, R. K. 1983. *Illex illecebrosus*. *In* Cephalopod Life Cycles, 1 , pp. 175–199. Ed. by Boyle P. R., Academic Press, London.

O'Dor, R. K., Dawe, E. G. and G., Pierce, 2013. *Illex illecebrosus*, northern Short-Finned Squid In Advances in Squid Biology, Ecology and Fisheries. Part II. pp. 73–108. Ed. by Rosa R., and O'Dor. R. K. Nova Science Publishers Inc., Hauppauge, NY.

Oesterwind, D., Bobowski, B. T. C., Brunsch, A., Laptikhovsky, V., van Hal, R., Sell, A. F., and Pierce., G. J. 2020. First evidence of a new spawning stock of *Illex coindetii* in the North Sea (NE-Atlantic). Fisheries Research, 221: 105384.

Oesterwind, D., and Schaber, M. 2020. First evidence of *Illex coindetii* in the Baltic Sea and Kattegat. Thalassas: An International Journal of Marine Sciences, 36: 143–147.

Olaso, I., Gutiérrez, J. L., Villamor, B., Carrera, P., Valdés, L., and Abaunza, P. 2005. Seasonal changes in the north-eastern Atlantic mackerel diet (*Scomber scombrus*) in the north of Spain (ICES Division VIIIc). Journal of the Marine Biological Association of the United Kingdom, 85: 415–418.

Pearcy, W.G., and Hancock, D. 1978. Feeding habits of dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; and pacific sanddab, *Citharichthys sordidus*, in a region of diverse sediments and bathymetry off Oregon. Fish Bulletin, 76: 641–651.

Pierce, G. J., Allcock, L., Bruno, I., Bustamante, P., González, Á., Guerra, Á., Jereb, P. *et al*. 2010. Cephalopod biology and fisheries in Europe. ICES Cooperative Research Report, 303. 175pp.

Pierce, G. J., and Santos, M. B. 1996. Trophic interactions of squid *Loligo forbesii* in Scottish Waters. In Aquatic Predators and their Prey, pp. 58–64. Ed. by Greenstreet S., and Tasker. M. Fishing News Books, Cambridge, MA . 208pp.

Pinnegar, J. K. 2014. DAPSTOM—An Integrated Database & Portal for Fish Stomach Records. Version 4.7. Centre for Environment, Fisheries & Aquaculture Science, February 2014, 39pp.

Prokopchuk, I., and Sentyabov, E. 2006. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. ICES Journal of Marine Science, 63: 117–127.

Punt, A. E., Dunn, A., Elvarsson, B. Þ., Hampton, J., Hoyle, S. D., Maunder, M. N., Methot, R. D. *et al*. 2020. Essential features of the next-generation integrated fisheries stock assessment package: a perspective. Fisheries Research, 229: 105617.

Queirós, J. P., Ramos, J. A., Cherel, Y., Franzitta, M., Duarte, B., Rosa, R., Monteiro, F. *et al*. 2021. Cephalopod fauna of the Pacific Southern Ocean using Antarctic toothfish (*Dissostichus mawsoni*) as biological samplers and fisheries bycatch specimens. Deep Sea Research Part I: Oceanographic Research Papers, 174: 103571.

Robb, A. P. 1981. Observations on the food and diel feeding behaviour of pelagic O-group gadoids in the northern North Sea. Journal of Fish Biology, 18: 183–194.

Robb, A. P., and Hislop, J. R. G. 1980. The food of five gadoid species during the pelagic O-group phase in the northern North Sea. Journal of Fish Biology, 16: 199–217.

Sakurai, Y., Kidokoro, H., Yamashita, N., Yamamoto, J., Uchikawa, K., and Takahara, H. 2013. *Todarodes pacificus*, Japanese Common Squid. *In* Advances in Squid Biology, Ecology and Fisheries: Part II-Oegopsid Squids, pp. 249–275. Ed. by Rui R., Ron O. D., and Graham P., Nova Science Publishers Inc., Hauppauge, NY. 281pp.

Salman, A. 2004. The role of cephalopods in the diet of swordfish (*Xiphias gladius* Linnaeus, 1758) in the Aegean sea (eastern Mediterranean). Bulletin of Marine Science, 74: 21–29.

Šantić, M., Rada, B., and Pallaoro, A. 2012. Diet and feeding strategy of thornback ray *Raja clavata*. Journal of Fish Biology, 81: 1070–1084.

Santos, M. B., Clarke, M. R., and Pierce, G. J. 2001. Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. Fisheries Research, 52: 121–139.

Silva, A. R., Vieira, A. R., Sequeira, V., Paiva, R. B., Gordo, L. S., and Neves, A. 2018. Diet and feeding strategy of the forkbeard *Phycis phycis* (Pisces: Phycidae) from the Portuguese continental coast. Journal of the Marine Biological Association of the United Kingdom, 98: 1757–1765.

Smale, M. J. (1996). Cephalopods as prey. IV. Fishes. Philosophical Transactions of the Royal Society B: Biological Sciences, 351: 1067–1081.

Summers, W. C. 1983. *Loligo pealei*. *In* Cephalopod life cycles, 1, pp. 115–142. Ed. by Boyle P. P., Academic Press, London. 475pp.

Vagenas, G., Karachle, P. K., Dogrammatzi, A., and Tsikliras, A. C. 2020. Age, growth and feeding habits of boarfish (*Capros aper*) in the Aegean and Ionian Seas (Greece). Marine Biology Research, 16: 585–592.

Van der Kooij, J., Engelhard, G. H., and Righton, D. A. 2016. Climate change and squid range expansion in the North Sea. Journal of Biogeography, 43: 2285–2298.

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

Vinagre, C., Cabral, H., and Costa, M. J. 2008. Prey selection by flounder, *Platichthys flesus*, in the Douro estuary, Portugal. Journal of Applied Ichthyology, 24: 238–243.

Vovk, A. N. 1985. Feeding spectrum of the long-finned squid (*Loligo pealei*) in the northwest Atlantic and its position in the ecosystem. NAFO Scientific Council Studies, 8: 33–38.

Xavier, J. C., Allcock, A. L., Cherel, Y., Lipinski, M. R., Pierce, G. J., Rodhouse, P. G. K., Rosa, R. *et al*. 2015. Future challenges in cephalopod research. Journal of the Marine Biological Association of the United Kingdom, 95: 999–1015.

Xavier, J. C., Cherel, Y., Allcock, L., Rosa, R., Sabirov, R. M., Blicher, M. E., and Golikov, A. V. 2018. A review on the biodiversity, distribution and trophic role of cephalopods in the Arctic and Antarctic marine ecosystems under a changing ocean. Marine Biology, 165: 93.

Zamarro, J. 1991. Feeding behaviour of the American plaice (*Hippoglossoides platessoides*) on the southern Grand Bank of Newfoundland. Netherlands Journal of Sea Research, 29: 229–238.

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