Oceanography and Marine Biology: An Annual Review, 2009, **47**, 111-190

Taylor & Francis

CEPHALOPODS IN THE NORTH-EASTERN ATLANTIC: SPECIES, BIOGEOGRAPHY, ECOLOGY, EXPLOITATION AND CONSERVATION

L.C. HASTIE[1], G.J. PIERCE[1], J. WANG[1], I. BRUNO[2], A. MORENO[3], U. PIATKOWSKI[4] & J.P. ROBIN[5]

[1]*University of Aberdeen, School of Biological Sciences, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK*
[2]*Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, 36200 Vigo, Spain*
[3]*Instituto Nacional de Recursos Biológicos, INRB/L-IPIMAR, 1400 Lisboa, Portugal*
[4]*Leibniz-Institut für Meereswissenschaffen, Universität Kiel, 24105 Kiel, Germany*
[5]*UMR-IFREMER, Université de Caen, 14032 Caen Cedex, France*
E-mail: nhi646@abdn.ac.uk

Abstract Cephalopods play a significant role in coastal and oceanic ecosystems, both as consumers of invertebrates and small fish and as the prey of some fish, seabirds and marine mammals and other large predators. Approximately 30 species of cephalopod have been recorded in the north-eastern Atlantic and adjacent waters, including 18 teuthid (squid), seven sepiolid (bobtail), three sepiid (cuttlefish) and 10 octopod (octopus) species. A number of these are exploited commercially and support important target and by-catch fisheries in Western Europe. During the past decade, annual landings of cephalopods from the north-eastern Atlantic (International Council for the Exploration of the Sea [ICES] area) have ranged from 40,000 to 55,000 t, including substantial catches of long-fin (loliginid) squid (7000–11,000 t per annum), short-fin (ommastrephid) squid (3000–10,000 t), cuttlefish (including sepiolids; 16,000–24,000 t) and octopods (12,000–18,000 t). The most important exploited species in the north-eastern Atlantic are *Eledone cirrhosa*, *Illex coindetii*, *Loligo forbesi*, *Loligo vulgaris*, *Octopus vulgaris*, *Todarodes sagittatus*, *Todaropsis eblanae* and *Sepia officinalis*. Other species including *Alloteuthis subulata*, *Gonatus fabricii* and certain sepiolids, appear to be abundant and may be marketable. Cephalopods tend to rapidly concentrate heavy metals and other toxic substances in their tissues and this plays an important role in the bioaccumulation of these pollutants in marine predators as well as having implications for human consumption. High levels of cadmium and mercury are often recorded in cephalopod tissues. Another important environmental issue concerns the potential impact of widespread human activity on cephalopod spawning areas, particularly bottom-fishing operations but also shipping, and oil exploration and production. In contrast to many finfish species that spawn annually over a number of years, most cephalopods live only 1–2 yr and die after spawning. Therefore, failure to reproduce and recruit adequately in any given year may seriously impact the long-term viability of cephalopod stocks. Climate change is expected to have a significant effect on many species in the north-eastern Atlantic. This review provides a detailed account of the zoogeography, biology and ecology of cephalopods in the north-eastern Atlantic, on a species-by-species basis. Important economic, ecological and conservation issues affecting cephalopods in this area are also discussed.

Introduction

The Class Cephalopoda comprises three major extant divisions, of which two, the Decapoda (squid and cuttlefish) and Octopoda (octopus), are represented in the north-eastern Atlantic. They range in length from 1.5 cm in pygmy (bobtail) squid (Sepiolidae) to 20 m in giant squid (Architheuthidae). Cephalopods exhibit the highest degree of development in invertebrate nervous systems, as expressed through complex behaviour patterns, learning ability and the display of complex colour changes. In contrast to other molluscs, most cephalopods lack an external shell, are highly mobile as adults and occupy similar ecological niches to predatory fish. They are opportunistic predators, taking a wide variety of prey (cannibalism has frequently been recorded). Cephalopods are also preyed on and sustain a large number of marine predators such as fish, birds and marine mammals, especially whales (e.g., Clarke 1996, Croxall & Prince 1996, Smale 1996, Santos et al., 2001a). Their importance as prey is almost certainly greater than suggested by stock biomass alone since they are characterised by very high individual growth rates and a high production/biomass (P/B) ratio (Boyle, 2002). Many species are powerful swimmers and undertake long feeding and spawning migrations, thus influencing ecosystem functioning and community structure on a seasonal and regional basis. Cephalopods are important elements in marine food webs and interact significantly with commercially exploited finfish species. Historical evidence suggests that, in certain areas, fishing pressure has changed ecological conditions and shifts in community structures have occurred, with cephalopod stocks gradually replacing predatory fish stocks (Caddy & Rodhouse 1998). However, while squids are short-lived and often thought of as r-selected pioneer species, their life history also includes typical k-selected features. There are few if any proven examples of ecological replacement of fish by squid where fish have been overexploited. Balguerías et al. (2000) found that, although Saharan Bank fisheries were historically based on sparids and currently take mainly cephalopods, there was no evidence that ecological replacement had occurred.

Cephalopods play a significant role in marine ecosystems and are becoming an increasingly important fisheries resource in the north-eastern Atlantic (Sacau et al. 2005), previously an area identified by Caddy & Rodhouse (1998) as having relatively low exploitation of cephalopods. The main commercial squid species in U.K. waters is the long-fin squid *Loligo forbesi* (Boyle & Pierce 1994) but cuttlefish *Sepia officinalis* is currently the most commercially important cephalopod (Anonymous 2005). Since 1995, annual U.K. landings of loliginid squid have ranged from 1600 to 3200 t, making the United Kingdom the second most important fishery nation for loliginid squid within the International Council for the Exploration of the Sea (ICES) Area after France (Stowasser et al. 2004). Other species of commercial interest in U.K. waters are the squids *Alloteuthis subulata, Illex coindetii*, *Loligo vulgaris, Todarodes sagittatus,* and *Todaropsis eblanae*, and octopus, *Eledone cirrhosa*. Both *Todarodes sagittatus* and *Todaropsis eblanae* were part of a substantial fishery off Shetland and Norway in the 1980s (Joy 1989, Hastie et al. 1994) but are currently of relatively minor commercial importance (Stowasser et al. 2004). Large numbers of the oceanic squid *Gonatus fabricii* may also sporadically occur in fishing hauls. This species is of considerable ecological interest as the main prey of large predators such as sperm whales (Santos et al. 1999, 2002, Bjørke, 2001) and is attracting interest as a potential commercial resource in Norway and Greenland.

Cephalopods tend to contain high levels of metals in their tissues. This is a natural phenomenon, but higher concentrations are expected to occur in polluted waters. The concentration of heavy metals and other toxic substances by cephalopods plays an important role in the bioaccumulation of these pollutants in marine predators (Koyama et al. 2000). Accumulation rates in cephalopod species appear to be rapid (Craig 1996) and various studies of cephalopods reported high levels of cadmium (Caurant & Amiard-Triquet 1995, Bustamante et al. 1998, Koyama et al. 2000, Stowasser et al. 2005) and, to a lesser extent, mercury (Frodello et al. 2000). Inputs of pollutants to the marine environment include discharges associated with oil production operations, industrial emissions and river discharges (Sheahan et al. 2001, Ridgway et al. 2003). Trace elements such as heavy metals and radionuclides contained in these discharges can accumulate in coastal and deeper waters, leading to an increase of metal and radioactive burdens in biota and thus increasing contaminant loads for human consumption (Kunisaki, 2000, Bustamante et al. 2000, 2003, Betti et al. 2004, Stowasser et al. 2005).

Sampling of cephalopods tends to be opportunistic, whether from commercial fisheries or research catches, reflecting the relatively low importance attached to these species by European fishery managers and governments, despite the growing economic value of cephalopod fishing. Consequently, reports of spatial and temporal variation in distribution, abundance and life history parameters need to be viewed with some caution. Differences may be local and short-lived, reflecting the known plasticity and environmental sensitivity of life history parameters, but may also be an artefact of inadequate sampling.

Another important environmental issue concerns the potential impact of widespread human activity, particularly extensive bottom-fishing operations, shipping, oil exploration and production, for example on cephalopod spawning areas. In contrast to many finfish species that spawn annually over a number of years, most cephalopods live only 1–2 yr and die after spawning. Therefore, failure to reproduce and recruit adequately in any given year may seriously impact the long-term viability of cephalopod stocks and populations (Caddy 1995).

Given the ecological and economic importance of cephalopods, their tendency to bioaccumulate heavy metals and other contaminants and the potential vulnerability of the many species to large-scale seabed operations are clearly very important environmental issues. Many finfish stocks are at all-time low levels and interest in cephalopods as a fishery resource has never been greater (e.g., the current interest in directed squid fishing in U.K. coastal waters where squid have previously been landed mainly as a by-catch; Young et al. 2006). The purpose of the following review therefore is to provide information on the distribution, biology, ecology, exploitation and conservation of common cephalopod species found in the north-eastern Atlantic, with particular emphasis on species found in U.K. waters.

The cephalopod fauna of the north-eastern Atlantic

Of a global total of 786 recognised species of living cephalopods, approximately 30 have been recorded in the north-eastern Atlantic. Seven teuthid (squid), one sepiolid (bobtail), one sepiid (cuttlefish) and two octopod (octopus) families are represented. The current taxonomic classifications of these are summarised in Table 1, although it should be noted that molecular taxonomic studies continue to lead to changes in the accepted taxonomic status of many cephalopods. In general terms, north-eastern Atlantic cephalopods can be arranged in the following groupings: long-fin squids (four spp.), short-fin squids (four spp.), other squids (ten spp.), bobtails (seven spp.), cuttlefishes (three spp.) incirrate (non-fin) octopods (five spp.) and cirrate (finned) octopods (five spp.).

Long-fin squids (family Loliginidae)

Long-fin or loliginid squids belong to the suborder Myopsina and are characterised by a membrane of tissue over their eyes. They are typically small- to medium-sized squid and a number of species are suitable for human consumption and are of commercial importance. Loliginid squid are associated with coastal environments. The eye membrane is thought to have a protective function for living in shallow, turbid waters. All other squid families belong to the suborder Oegopsina and are characterised by having 'naked' eye pores. Two genera and four species of loliginid squid are found in the north-eastern Atlantic.

Alloteuthis media

Biogeographic distribution The European common squid *Alloteuthis media* (Linnaeus, 1758) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental

Table 1 Classification of cephalopods found in the north-eastern Atlantic: Phyllum Mollusca (Linnaeus, 1758), Class Cephalopoda (Cuvier, 1797), Subclass Coleoidea (Bather, 1888)

Superorder	Order	Suborder	Family	Subfamily	Genus	Species
Decapodiformes (Young et al., 1998)	Teuthida (Naef, 1916)	Myopsina (Orbigny, 1841)	Loliginidae (Lesueur, 1821)		*Alloteuthis* (Wulker, 1920)	*media* (Linnaeus, 1758)
						subulata (Lamarck, 1798)
					Loligo (Lamarck, 1798)	*forbesi* (Steenstrup, 1857)
						vulgaris (Lamarck, 1798)
		Oegopsina (Orbigny, 1845)	Architeuthidae (Pfeffer, 1900)		*Architeuthis* (Steenstrup, 1857)	*dux* (Steenstrup, 1857)
			Cranchiidae (Prosch, 1847)	Taoniinae (Pfeffer, 1912)	*Galiteuthis* (Joubin, 1898)	*armata* (Joubin, 1898)
					Teuthowenia (Chun, 1910)	*megalops* (Prosch, 1847)
			Gonatidae (Hoyle, 1886)		*Gonatus* (Gray, 1849)	*fabricii* (Lichtenstein, 1818)
			Histioteuthidae (Verrill, 1881)		*Histioteuthis* (Orbigny, 1841)	*bonnellii* (Ferussac, 1834)
						reversa (Verrill, 1880)
			Ommastrephidae (Steenstrup, 1857)	Illicinae (Posselt, 1891)	*Illex* (Steenstrup, !880)	*coindetii* (Verany, 1839)
				Ommastrephinae (Posselt, 1891)	*Ommastrephes* (Orbigny, 1834)	*bartramii* (Lesueur, 1821)

		Todarodinae (Adam, 1960)	*Todarodes* (Steenstrup, 1880)	*sagittatus* (Lamarck, 1798)
			Todaropsis (Girard, 1890)	*eblanae* (Ball, 1841)
	Onychoteuthidae (Gray, 1849)		*Onychoteuthis* (Lichtenstein, 1818)	*banksii* (Leach, 1817)
Sepiolida (Fioroni, 1981)	Sepiolidae (Leach, 1817)	Rossinae (Appellof, 1898)	*Rossia* (Owen, 1834)	*glaucopis* (Lovern, 1845) *macrosoma* (Chiaie, 1830)
			Neorossia (Boletzky, 1971)	*caroli* (Joubin, 1902)
		Sepiolinae (Appellof, 1898)	*Rondeletiola* (Naef, 1921)	*minor* (Naef, 1912)
			Sepietta (Naef, 1912)	*neglecta* (Naef, 1912) *oweniana* (Orbigny, 1839)
			Sepiola (Leach, 1817)	*atlantica* (Orbigny, 1839) *aurantiaca* (Jatta, 1896)
Sepiida (Zittel, 1895)	Sepiidae (Keferstein, 1866)		*Sepia* (Linnaeus, 1758)	*elegans* (Blainville, 1827) *officinalis* (Linnaeus, 1758) *orbignyana* (Ferussac, 1826)

(continued on next page)

Table 1 (continued) Classification of cephalopods found in the north-eastern Atlantic: Phyllum Mollusca (Linnaeus, 1758), Class Cephalopoda (Cuvier, 1797), Subclass Coleoidea (Bather, 1888)

Superorder	Order	Suborder	Family	Subfamily	Genus	Species
Octopodiformes (Young et al., 1998)	Octopoda (Leach, 1818)	Incirrina (Grimpe, 1916)	Octopodidae (Orbigny, 1840)	Bathypolypodinae (Robson, 1928)	*Bathypolypus* (Grimpe, 1921)	*arcticus* (Prosch, 1847)
					Benthoctopus (Grimpe, 1921)	*piscatorum* (Verrill, 1879)
				Eledoninae (Grimpe, 1921)	*Eledone* (Leach, 1818)	*cirrhosa* (Lamarck, 1798)
				Allopsidae (Verrill, 1881)	*Haliphron* (Steenstrup, 1861)	*atlanticus* (Steenstrup, 1861)
				Graneledonae (Voss, 1988)	*Graneledone* (Joubin, 1918)	*verrucosa* (Verrill, 1881)
				Octopodinae (Orbigny, 1840)	*Octopus* (Cuvier, 1797)	*vulgaris* (Cuvier, 1797)
		Cirrina (Grimpe, 1916)	Cirroteuthidae (Keferstein, 1866)		*Cirroteuthis* (Eschricht, 1836)	*massyae* (Grimpe, 1920) *muelleri* (Eschricht, 1836)
					Cirrothauma (Chun, 1911)	*murrayi* (Chun, 1911)
					Grimpoteuthis (Grimpe, 1920)	*wulkeri* (Grimpe, 1920)
			Opisthoteuthidae (Verrill, 1896)		*Opisthoteuthis* (Verrill, 1896)	*grimaldi* (Joubin, 1903)
			Stauroteuthidae (Grimpe, 1916)		*Stauroteuthis* (Verrill, 1879)	*syrtensis* (Verrill, 1879)

shelf areas and is widely distributed in the eastern Atlantic, from the north-western coast of Africa (21°N) to the North Sea (60°N) (Guerra 1992). It is most common south of 50°N, in the Bay of Biscay, English Channel and throughout the Mediterranean. *Alloteuthis media* and its congener *A. subulata* are thought to be sympatric throughout much of their geographic range (Roper et al. 1984). In U.K. waters, these species are particularly abundant in the English Channel (Rodhouse et al. 1988) and Irish Sea (Nyegaard, 2001).

Biology and ecology It has been suggested that *Alloteuthis media* and the very similar *A. subulata* may be intraspecific forms rather than true, separate species (Laptikhovsky et al. 2002). However, these types are highly sympatric, with overlapping ranges and they do not appear to be simply due to minor differences between separate populations. *Alloteuthis subulata* is usually distinguished from *A. media* by its exceptionally long tail and fins that are more than 50% of the mantle length (ML) in males (Nesis 1987). Recent morphometric and genetic information supports a sister-species relationship between *A. media* and *A. subulata* as well as significant genetic differentiation between Atlantic and Mediterranean *A. media* (Anderson et al. 2008). At present, however, there is little information about their population structures, for example, whether *A. subulata* forms a single, continuous, mixed population across its range or is divided into a number of smaller, discrete population units with limited gene flow between them.

Alloteuthis subulata

Biogeographic distribution The European common squid *Alloteuthis subulata* (Lamarck, 1798) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from the north-western coast of Africa (20°N) to the North Sea (60°N). It also occurs throughout the Mediterranean (Roper et al. 1984). *Alloteuthis subulata* lives in shelf waters, particularly in the North Sea (Grimpe 1925, Steimer 1993), the Kattegat and the western Baltic Sea (Herrmann et al. 2001, Hornborg, 2005). In U.K. waters, *A. subulata* is often found in abundance in the English Channel (Rodhouse et al. 1988) and Irish Sea (Nyegaard, 2001). It occurs from the coastline to a possible maximum depth of 500 m (Guerra 1982), but primarily between 20 and 120 m (Roper et al. 1984). In Portuguese waters, it is often found in abundance at depths of 20–200 m (Moreno 1990, 1995). Within the western Mediterranean, it is usually recorded in depths of 30–280 m (González & Sánchez, 2002). In some parts of its range, *A. subulata* is thought to be migratory. For example, in the North Sea, juveniles are thought to leave the area at an age of about 3 mo in November and return the following spring at a length of about 5 cm ML. In this area, males and females move inshore in early summer but are absent during winter (Yau 1994). However, in other areas (e.g., English Channel), this species can be found year-round (Rodhouse et al. 1988).

Biology and ecology In Portuguese waters, progressive maturation in *Alloteuthis subulata* occurs from winter to late spring, with the males maturing slightly earlier than the females (Moreno 1990, 1995). Maturation commences at 3–4 cm mantle length (ML) in both sexes. Lengths at maturity (i.e., the length at which 50% of animals are mature, ML_{50}) of 7.7–8 cm and 7–7.5 cm have been reported for males and females respectively (Moreno, 1995). The maximum size at maturity of female *A. subulata* is about 12 cm ML (Yau 1994).

A potential fecundity of 1,200–19,000 eggs per female (average 6000 eggs, size range 8–12 cm ML) has been reported. Nyegaard (2001) observed a batch count of about 150 mature eggs laid per session, thus indicating that female *A. subulata* may spawn intermittently and produce up to 40 separate batches of eggs. The number of batches produced may depend on condition and mortality during the spawning season (Nyegaard 2001).

Table 2 Main predators of *Alloteuthis subulata*

Predators	Source
Whales	
Bottlenose whale (*Hyperoodon ampullatus*)	Santos et al. 2001a
Bottlenose dolphin (*Tursiops truncatus*)	Santos et al. 2001b, 2005a
Common dolphin (*Delphinus delphis*)	González et al. 1994, Meynier 2004, Santos et al. 2004
Harbour porpoise (*Phocoena phocoena*)	Santos et al. 2005b
Fishes	
Hake (*Merluccius merluccius*)	Daly et al. 2001
Squids	
Veined squid (*Loligo forbesi*)	Pierce et al. 1994c, Rocha et al. 1994
European squid (*Loligo vulgaris*)	Pierce et al. 1994c, Rocha et al. 1994

There may be several distinct spawning events each year. For example, in the English Channel, there are three spawning groups of female *A. subulata* that spawn in spring, summer and autumn, with two recruitment events in spring and summer. The pattern in adult males is more complex, with no regular pattern observed (Rodhouse et al. 1988). In the Irish Sea, spawning occurs mainly in spring and summer, with only a possible minor event in autumn (Nyegaard 2001). In the North Sea, the spawning season is restricted to June–July, with hatchlings appearing in plankton samples towards the end of July (Yau 1994). In early summer, male and female *A. subulata* arrive together inshore. Spawning probably occurs earlier off the west coast of Scotland than in the North Sea (Yau 1994).

Alloteuthis subulata is an important species in coastal ecosystems since it appears to be an abundant predator of small fish species and is itself preyed on by a number of larger marine animals. The main prey of *A. subulata* is reported to be clupeid fish and crustaceans (Nyegaard 2001). Nyegaard (2001) showed that, although *A. subulata* was associated with the distribution of its main prey species, the squid at stations with high prey abundance did not seem to have been more frequently engaged in feeding activity than those at other stations (based on stomach fullness). This could indicate that *A. subulata* feeds in the pelagic zone rather than close to the bottom. Indeed both sandeel and sprat, which are important prey of *Alloteuthis*, undertake vertical migrations and were found in higher abundances in the pelagic zone than near the bottom during the day in the North Sea (Pedersen 1999). The observed co-occurrence of *Alloteuthis* and its prey near the seabed may thus be due to other factors.

A number of marine mammals, fish and larger squid species are reported to prey on *A. subulata* (Table 2). It is the most commonly recorded cephalopod species in stomach contents of demersal fish in U.K. waters (Hislop et al. 1991, Daly et al. 2001) and is also an important item in the diet of demersal fish in Spanish waters (Velasco et al. 2001).

Loligo forbesi

Biogeographic distribution The veined squid *Loligo forbesi* (Steenstrup, 1856) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental shelf areas and is distributed in the north-eastern Atlantic from the Azores (20°N) to the Faroes and the north-western coast of Norway (63°N). It also occurs in the North Sea between Scotland and Norway and to a lesser extent the Mediterranean (Roper et al. 1984). It is relatively rare south of the Bay of Biscay (45°N). In U.K. waters, *L. forbesi* is often relatively abundant in the English Channel (Holme 1974), Irish Sea (Collins et al. 1995b), off Rockall Bank and the Scottish west coast (Pierce et al. 1994a) and in the Moray Firth (Young et al. 2006). Since the early 1990s, there has been a dramatic decline in catches of *L. forbesi* off the Iberian Peninsula (Chen et al. 2006). At the same time, abundance in northern waters (around Scotland) has increased. According to Chen et al. (2006), this apparent northerly shift in the range of *L. forbesi* may be associated with increasing seawater temperatures.

The main population in U.K. waters is distributed over the continental shelf and shelf edge, mostly 50–250 m in depth and within about 200 km of the coast (Pierce et al. 1994b). Mangold-Wirz (1963) described the vertical distribution of *L. forbesi* as between 15 and 150 m in the North Sea and eastern Atlantic and 150 and 400 m in the Mediterranean. Moreno et al. (1994) reported *L. forbesi* to occur in depths of 100–200 m in Portuguese waters. At Rockall, survey catches were mostly in shallow waters less than 150 m (Pierce et al. 1998). Recent data collected in U.K. waters showed that the depth distribution seemed to be correlated to season, with squid predominantly found in deeper waters along the shelf edge (100–200 m) at the beginning and the end of the spawning season (November and March) while during the peak of spawning most squid were caught in waters shallower than 50 m (Stowasser et al. 2005). The maximum recorded depth for the species is 700 m but in the Azores the fished population occurs in water depths greater than 1000 m (Martins 1982, Salman & Laptikhovsky 2002). Where its distribution overlaps with that of its congener *L. vulgaris*, it tends to be in slightly deeper water and at greater depths than the other species.

Migratory patterns are known but relatively poorly understood. Generally, this squid moves inshore during winter months for breeding where populations are at their most highly aggregated and where they may be targeted for fishing. Pierce et al. (1994c, 1998) found the spatial pattern of abundance of *L. forbesi* for the North Sea and the north-eastern Atlantic to vary with season, with highest abundances in coastal waters occurring in October and November and most landings from offshore waters (Rockall, north-eastern Atlantic) occurring in July and August. Horizontal migrations of *L. forbesi* are also known to occur in the southern range of its distribution, in spring–summer to shallow waters of the north, and in autumn–winter to deeper waters of the south (Holme 1974, Roper et al. 1984, Sims et al. 2001). Holme (1974) found *L. forbesi* to hatch in the western English Channel and migrate eastwards, appearing in trawls off Plymouth around May. After a few months of rapid growth in the English Channel and the southern North Sea (some summer spawning), squid moved back to the western English Channel to spawn and die during the following December–January.

Recent studies on temporal trends in abundance of *L. forbesi* showed that both the timing of migration into the English Channel and winter abundance in the North Sea are influenced by sea-surface temperature (SST) (Pierce et al. 1998, Waluda & Pierce 1998, Sims et al. 2001, Pierce & Boyle 2003). Its distribution in the North Sea in winter seemed also to be strongly correlated to sea bottom temperatures and to a lesser extent salinity (i.e., more squid in more saline waters), generally not being found in temperatures below 8.5°C (Pierce et al. 1998). Peak squid abundances in the English Channel occurred when bottom temperature measured 13°C independent of time of year (Sims et al. 2001). Zuur & Pierce (2004) found strength of the North Atlantic Oscillation (NAO) and SST to be key factors influencing squid abundance. It was concluded that both the inflow of Atlantic water (with associated nutrients, prey organisms and squid) and favourable growth conditions (i.e., temperature) are important in determining abundance. Georgakarakos et al. (2002) found a positive correlation between loliginid landings and SST in nutrient-rich areas. Pierce et al. (2008a) have recently reviewed cephalopod-environment interactions.

Morphometric and genetic studies of *L. forbesi* have found no evidence of distinct inshore stocks (Pierce et al. 1994d, Brierley et al. 1995, Collins et al. 1997a, 1999, Shaw et al. 1999). There is some evidence that the offshore population found on Rockall Bank may be distinct from the coastal population. By contrast, the unique morphometric and genetic characteristics exhibited by exploited Azorean *L. forbesi* stock indicate that they belong to a highly isolated population, based on an introductory event up to 1 million yr ago (Shaw et al. 1999). Based on allozyme data, Brierley et al. (1995) suggested that the Azorean population should be regarded as a separate subspecies.

Biology and ecology *Loligo forbesi* is an annual, semelparous species (Holme, 1974) showing extended breeding seasons with one, two or several pulses of recruitment. *Loligo forbesi* in Scottish waters spawns mainly from December to February, although breeding animals are also recorded in May. Two main pulses of recruitment appear in April and August to November, with small numbers of recruits present throughout most of the year (Lum-Kong et al. 1992, Boyle & Pierce 1994, Pierce et al. 1994b, Collins et al. 1997a). Early work on *L. forbesi* in the English Channel by Holme (1974) indicated the existence of distinct winter and summer breeding populations of *L. forbesi* in U.K. waters. Examination of Scottish fishery data suggests that since the 1970s, the summer breeding population has declined in Scottish waters and the winter population now dominates and breeds later than was previously the case (Pierce et al. 2005).

Loligo forbesi is a relatively large loliginid squid. It matures over a range of sizes, with males achieving a larger maximum size than females (although some males mature at much smaller sizes). In U.K. waters, maximum lengths and weights of 61 cm ML and 2.87 kg for males and 42 cm ML and 1.54 kg for females, respectively, have been recorded (unpublished data). The largest *L. forbesi* have been caught around the Azores, with reported maximum values of 94 cm ML and 8.31 kg for males and 46 cm ML and 2.18 kg for females (Martins 1982), although the Azores population may belong to a distinct subspecies (Brierley et al. 1995). A number of techniques have been used to determine the growth characteristics of *L. forbesi*, including observations of captive squid in aquaria (Forsythe & Hanlon 1989), length-frequency analyses (Pierce et al. 1994a), statolith increment estimations (Collins et al. 1995a) and gladius increment estimations (Hughes 1998). Daily statolith increments in *L. forbesi* have been validated by aquarium-based studies (Hanlon et al. 1989) and supported by length-frequency analyses of fishery data (Collins et al. 1995a). The growth pattern of *L. forbesi* is influenced by a number of factors, including sex, maturation, season and reproduction (Hughes 1998, Smith et al. 2005). Although precise age determinations of cephalopods are difficult, it is generally accepted that *L. forbesi* lives for a maximum of 9–23 mo (Rocha & Guerra 1999, Cordes 2002).

Modal progression analyses of length-frequency data have revealed the presence of two or three size modes at maturity in males (Holme 1974, Boyle & Ngoile 1993, Pierce et al. 1994a, Boyle et al. 1995, Collins et al. 1995a). Boyle et al. (1995) suggested three possible models that could explain these: squid of mixed growth, squid of mixed age or squid of mixed stock. Temperature is known to influence development time of squid embryos (von Boletzky 1987). A development time of 75 days at 12.5°C has been reported for *L. forbesi* (Hanlon et al. 1989). Boyle et al. (1995) suggested that *L. forbesi* eggs may be held in stasis over winter in low temperatures (8–10°C), thus generating two cohorts from a single breeding population in Scottish waters. By analogy with other loliginids, male squid maturing at a small size may become 'sneakers' on the spawning grounds (Hanlon & Messenger 1998).

The two recruitment periods identified for Scottish waters produce distinctive microcohorts of two or three different size classes in female and male squid, respectively (Collins et al. 1997a, 1999). Genetic evidence exists for separate offshore (Rockall and Faroe banks) and shelf stocks in Scottish waters (Shaw et al. 1999). Mature squid are recorded throughout Scottish waters in winter and eggs of *L. forbesi* have been recorded in trawls off Shetland (Lum-Kong et al. 1992) and are regularly found on creel lines along the Scottish mainland coastline. Although spawning grounds have not yet been documented it has been suggested from the analysis of spatial patterns in fishery data that *L. forbesi* move from the West Coast of Scotland into the North Sea to spawn (Waluda & Pierce 1998, Pierce et al. 2001). However, a more comprehensive recent analysis by Viana (2007) suggests that the pattern is considerably more complicated. Two general, seasonal migrations of *L. forbesi* in Scottish waters were apparent, a movement inshore during summer/autumn and offshore during winter/spring. One subpopulation may in fact reside in inshore waters, whereas another appears to migrate offshore during winter/spring. Squid abundance appeared to be closely related to SST, bottom depth and distance offshore, with optimal values of 11°C, 200 m and 30 km, respectively, reported for *L. forbesi* (Viana 2007). Potential spawning areas have been modelled based on survey and market sample data on squid distribution and size at maturity data (Stowasser et al. 2005).

Loligo forbesi has an annual reproductive cycle and is semelparous (Lum-Kong et al. 1992, Pierce et al. 1994a, Collins et al. 1995a). It exhibits intermittent, terminal spawning, in which the females lay eggs in batches and die shortly after spawning (Rocha et al. 2001). However, an extended spawning pattern, with different seasonal peaks has been reported (Roper et al. 1984, Lum-Kong et al. 1992, Boyle & Ngoile 1993, Guerra & Rocha 1994, Moreno et al. 1994, Pierce et al. 1994a, Boyle et al. 1995, Collins et al. 1995a). The timing of peak spawning activity varies across its range and secondary peaks have been observed in some areas (Pierce et al. 1994a). Depending on the area and season, one or more associated pulses of recruitment occur. In the North Atlantic, concentrations of *L. forbesi* are usually found west of Scotland and Ireland in autumn and gradually shift from offshore to inshore waters as spawning progresses. By the following spring (January to March), the highest abundances are found in the Minch and Moray Firth areas and further south along the east coast of England. In summer, mature specimens are only found in the English Channel (Stowasser et al. 2005). It is not clear how long an individual squid can remain in spawning condition and it is likely that extended seasonal peaks represent a series of microcohorts maturing out of phase with each other, while secondary peaks may indicate distinct winter and summer breeding populations.

Although they are a short-lived species, fecundity in loliginid squids is surprisingly low, with female *L. forbesi* apparently producing only a few thousand eggs in their lifetime (Boyle et al. 1995). Mature females exhibit permanent oocyte maturation, with several types of oocytes found at various stages of development (Ngoile 1987, Collins et al. 1995a). The potential fecundity of *L. forbesi* females is estimated to range from 1,000 to 23,000 eggs (Boyle at al. 1995). A weakly positive relationship between size (ML) and fecundity has been reported for this species, although small mature females may have relatively more oocytes than larger females (von Boletzky 1987, Hanlon et al. 1989, Guerra & Rocha 1994, Boyle et al. 1995, Collins et al. 1995a). Fecundity does not appear to be related to the timing of maturity during the spawning season (Guerra & Rocha 1994).

The eggs of *L. forbesi* are relatively large and contain large quantities of yolk (von Boletzky 1987, Hanlon et al. 1989). They are usually packed together in layers of gelatinous substances produced by the oviducal and nidamental glands and wrapped into finger-like egg strings (Lum-Kong et al. 1992). The number of egg strings in a cluster is variable and a cluster may contain egg strings deposited by one or several females. Even egg strings deposited by single females may be multipaternal since they could be fertilised by different males (Shaw & Boyle 1997). Clusters of egg strings are typically attached to submerged, fixed substrata, including macrophytes, shells, rock crevices and various types of fishing gear. Records of egg clusters of *L. forbesi* originate primarily from shallow, inshore areas. Collins et al. (1995a) recovered egg clusters from static fishing gear over rocky ground at 10–50 m depth off the south coast of Ireland. Lum-Kong et al. (1992) and Martins (1997) found egg clusters attached to creel lines in Scottish waters and Holme (1974) reported egg clusters attached to fishing boats, rope moorings and crab pots off the coast of Devon. Along the west coast of Scotland, egg clusters of *L. forbesi* were found on creels set on both muddy and rocky grounds, at 40–110 m depth (Craig 2001). Along the Moray Firth, egg clusters have been found on moorings and piers as shallow as 2 m depth.

There are also, however, a small number of records from deeper, offshore waters. Egg clusters were found in the Celtic Sea, between France and Ireland, at depths of 135–507 m (Lordan & Casey 1999). Salman & Laptikhovsky (2002) reported egg clusters in the Aegean Sea at 720–740 m depth. In other parts of the Mediterranean, *L. forbesi* eggs have been found at 150–200 m depth (lo Bianco 1909). According to Lum-Kong et al. (1992), however, most spawning may occur in relatively deep waters since the majority of spawning squid reported are usually captured by commercial fleets working offshore. The lack of egg data could be due to non-reporting or the possibility that spawning squid prefer areas of rocky substrata that are inaccessible to demersal trawling (Holme 1974, Lordan & Casey 1999).

The rate of development and timing of hatching of *L. forbesi* are influenced by egg size and water temperature (Paulij et al. 1990, Gowland et al. 2002). Size at hatching is inversely related to temperature and is significantly reduced at 16°C compared to 8°C. The duration of the embryonic phase decreases as temperature increases, for example, 140 days at 8°C, 60 days at 12°C and 36 days at 16°C (Martins 1997, Gowland et al. 2002). The possibility that eggs may remain unhatched for several months could give rise to a complex pattern of 12-, 18- and 24-mo life cycles as discussed in Boyle & von Boletzky (1996). The incidence of deformities in hatchlings is reported to increase at extreme temperatures (Martins 1997, Gowland et al. 2002), indicating a small temperature range for normal hatching development. Craig (2001) found hatchlings to emerge from egg strings over several days, but only during hours of darkness. Detailed descriptions of the embryonic stages of *L. forbesi* are provided by Segawa et al. (1988).

Loligo forbesi is a highly mobile, opportunistic predator that will attack and consume any potential prey that it can overcome. A large number of prey species, including various polychaetes, molluscs, crustaceans and fish have been identified in *L. forbesi* stomachs (Table 3). Across its geographical range, fish was found to be the main prey type, with crustacean, cephalopod and polychaete species present in the diet to varying degrees. The most prominent fish species present in the diet belong to families Gadidae, Clupeidae, Ammodytidae and Gobiidae (Collins et al. 1994, Rocha et al. 1994, Collins & Pierce 1996, Pierce & Santos 1996). Pierce et al. (1994c) observed that crustaceans were relatively more important in the diet of small squid whilst larger squid preyed predominantly on fish. In Spanish waters, cephalopods also become a larger component of the diet, as the squid grow larger (Rocha et al. 1994). Cannibalism in *L. forbesi* appears to be limited to large squid (>15 cm ML) feeding on much smaller squid (2–5 cm ML) (Collins & Pierce 1996).

The same broad prey taxa are important in the diet of *L. forbesi* throughout its geographic range (Pierce et al. 1994c). However, regional differences in the prey composition of the diet have been identified. For example, in Scottish waters, whiting (*Merlangius merlangus*), *Trisopterus* spp. and sandeels (Ammodytidae) were the principal prey species (Pierce et al. 1994c) whereas in Irish waters, sprat (*Sprattus sprattus*) and *Trisopterus* spp. were predominant (Collins et al. 1994). There is some evidence that prey composition may vary seasonally, probably due to changes in prey availability (Collins et al. 1994, Pierce et al. 1994c, Rocha et al. 1994, Collins & Pierce 1996). Howard (1979) observed seasonal differences in stomach emptiness, with a higher frequency of empty stomachs found in winter. Gaard (1987) noted that *L. forbesi* probably feeds mainly by day since stomach fullness was greatest and the state of digestion was less when squid were caught in the evening.

Recent investigations using fatty acid and stable isotope analyses indicates that *L. forbesi* is mainly associated with the benthic food web and that prey type and prey variability changed with body size (Stowasser et al. 2005). Captive rearing studies have shown that *L. forbesi* paralarvae feed predominantly on copepods, juvenile mysids and palaemonid larvae (Forsythe & Hanlon 1989, Hanlon et al. 1989).

Loligo forbesi is itself included in the diets of a number of marine predators. Large demersal fish and some marine mammals have been reported to prey on *L. forbesi* (Table 4). Identification of stomach contents in the majority of published reports on predatory fish and marine mammals however remains at the level of family (Loliginidae). Beaks have been identified from the stomachs of pygmy sperm whale (*Kogia breviceps*), northern bottlenose whale (*Hyperoodon ampullatus*), common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleolba*), bottlenose dolphin (*Tursiops truncatus*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), killer whale (*Orcinus orca*), long-finned pilot whale (*Globicephala melaena*) and Risso's dolphin (*Grampus griseus*; Santos et al. 2004, De Pierrepont et al. 2005). The great skua (*Catharacta skua*) is the only reported bird species from north-eastern Atlantic waters with beaks of *Loligo* sp. found in the stomach (Furness 1994). None of these species, however, were considered by the investigators to be a major cause of mortality of *Loligo* sp.

Table 3 List of identified prey types and species from *Loligo forbesi* stomach contents

		Geographic area						
Group	Taxonomic description	Northwest Spain	Ireland	Scotland	England	Faroes	Portugal	Azores
Fish	*Agonus cataphractus*		•					
	Ammodytes sp.	•	•	•	•		•	
	Anthias anthias							•
	Anthias minuta	•	•	•				
	Argentina sp.		•	•			•	
	Argentina sphyraena	•	•					
	Atherina sp.	•						
	Belone belone							•
	Boops boops							•
	Callionymus sp.	•	•	•	•		•	
	Callionymus lyra							•
	Callionymus maculatus	•	•	•	•	•		
	Capros aper		•	•				
	Cepola macrophthalma		•					
Crustacea	Amphipoda							•
	Brachyura	•						•
	Caridea	•						
	Copepoda			•				
	Calanoidea	•		•				
	Crangonidae		•					
	Crustacea	•	•	•	•	•	•	•
	Decapoda Natantia							•
	Dichelopandalus bonnieri		•					
	Euphasiacea	•		•				•
	Gnathia sp. (larvae)		•					
	Hippolytidae	•						
	Maia sp.							•
	Meganyctiphanes norvegica		•					
	Mysidacea	•						
	Nephrops norvegicus		•					
	Oplophoridae		•					
	Paguridae		•					
	Palaemonidae		•					
	Pandalidae			•				
	Pasiphaea sivado		•					
	Processidae	•						
Mollusca	*Alloteuthis* sp.	•						
	Alloteuthis subulata	•		•				
	Bivalvia	•						
	Cephalopoda	•	•	•	•	•	•	•
	Eledone cirrhosa	•						
	Loliginidae		•					
	Loligo forbesi	•		•	•			
	Loligo sp.	•						
	Loligo vulgaris	•						

(continued on next page)

Table 3 (continued) List of identified prey types and species from *Loligo forbesi* stomach contents

		Geographic area						
Group	Taxonomic description	Northwest Spain	Ireland	Scotland	England	Faroes	Portugal	Azores
	Octopodidae		•	•				•
	Octopus vulgaris	•						
	Sepioidea							
	Sepiolidae		•	•				
	Teuthoidea							•
Polychaeta	*Nereis pelagica*		•					•
	Nereis sp.							
	Polychaeta			•				
	Sternaspid							•
Chaetognatha	*Sagitta* sp.							•

Source: Compiled from Martins 1982, Collins et al. 1994, Pierce et al. 1994c, Rocha et al. 1994, Stowasser et al. 2004.

Table 4 Reported predators of *Loligo forbesi*

Type/species	Geographic area	References
Demersal fish		
Gadus morhua	Scotland	Daly et al. 2001
Lophius piscatorius	Scotland	Daly et al. 2001
Seals		
Halichoerus grypus	Scotland	Pierce et al. 1991
Phoca vitulina	Scotland	Brown & Pierce 1998
Cetaceans		
Phocoena phocoena	Netherlands	Santos et al. 2005b
Physeter macrocephalus	Scotland, Denmark	Santos et al. 1999
	Iceland, Norway	Santos et al. 2002

Loligo vulgaris

Biogeographic distribution The European squid *Loligo vulgaris* (Lamarck, 1798) is a neritic, demersal species occurring in subtropical/temperate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from South Africa (20°S) to north-western Scotland (57°N). It also occurs in the southern North Sea and the Mediterranean (Roper et al. 1984). It is most abundant in waters between southern Portugal (36°N) and the English Channel (52°N); in this area there appears to be a gradual increase in abundance with decreasing latitude (Cunha et al. 1995). It is also found in Madeiran waters (Clarke & Lu 1995). It is widely distributed in the Mediterranean, particularly in the Catalan Sea (Sánchez & Martin 1993), the Adriatic (Flamigni & Giovanardi 1984), Greek seas (Lefkaditou et al. 2001) and the Levantine Basin (Ruby & Knudsen 1972). In U.K. waters, it is moderately abundant only in the English Channel (Robin & Boucaud-Camou 1993). It is relatively scarce in the Irish Sea and southern North Sea, although it often appears in mixed catches with *L. forbesi* during late spring and summer. In Scottish waters it is typically very rare, with only one or two individual *L. vulgaris* appearing sporadically in samples from *L. forbesi* catches during certain years (Pierce et al. 1994a).

Loligo vulgaris is typically a benthic spawner and attaches egg clusters to hard substrata. At other times, it is more pelagic in behaviour, for example hunting in the water column in the circum-littoral and upper bathyal regions (Worms 1983). Off the Portuguese coast and in the Mediterranean, it occurs in shallow waters (<100 m deep) (Sánchez & Martin 1993, Cunha et al. 1995, Salman et al. 1997, Sánchez et al. 1998). Smaller numbers are also found over the continental slope (200–300 m), especially near coasts with steep bottom slopes in Algerian waters (Mangold-Wirz 1963) and the Ionian Sea (Lefkaditou et al. 2001).

In the North Sea, *L. vulgaris* usually appears in small numbers in late spring–summer, occasionally reaching the Kattegat and western Baltic (Jaekel 1937, Muus 1959, Hornborg 2005). Large population fluctuations have been reported in some areas (Amaratunga 1983) and changes in SST may be involved (Chen et al. 2006). Adult and juvenile squid inhabit waters with temperatures ranging from 12.5 to 20°C and are often associated with relatively low salinities (Mangold-Wirz 1963). In the North Atlantic this species has been reported at salinities of 30–36‰ (Tinbergen & Verwey 1945) and it has also been found in brackish conditions in the Sea of Marmar (Unsal et al. 1999) and the River Tagus estuary (unpublished data). However, in the Mediterranean, it has also been recorded in much higher salinities of 37.7–38.15‰ (Salat et al. 1978), indicating that it may be able to adapt to local conditions.

Biology and ecology *Loligo vulgaris* is an annual, semelparous species (Mangold 1987) showing extended breeding seasons with one, two or several pulses of recruitment, depending on locality. At the northern and eastern edges of its range, in the North Sea, English Channel and central Mediterranean, the spawning period is relatively short (Tinbergen & Verwey 1945, Moreno et al. 2002, Sifner & Vrgoc 2004). Further south and west, *L. vulgaris* spawns throughout the year, in Atlantic waters between north-western Spain and Africa (Baddyr 1988, Coelho et al. 1994, Guerra & Rocha 1994, Moreno et al. 1994, Rocha 1994, Bettencourt et al. 1996, Villa et al. 1997, Raya et al. 1999, Moreno et al. 2002) and the western Mediterranean (Mangold-Wirz 1963, Worms 1983). The timing of spawning also varies with locality. In the English Channel, *L. vulgaris* spawns in winter (November to April, peaking in February; Moreno et al. 2002). In Portuguese waters and on the Saharan Bank, it spawns all year but with two peak periods, in autumn–winter and late spring (Moreno et al. 1994). Further east, in the Adriatic and Greek seas, this species spawns during winter–spring (January to May and November to May, respectively) peaking in April (Mangold-Wirz 1963, Worms 1983).

Loligo vulgaris is a relatively large loliginid squid, very similar in size and appearance to *L. forbesi*. It also matures over a range of sizes, with males generally growing bigger than females (although again, some males mature at small sizes). In the north-western Atlantic, maximum lengths of 55 cm ML for males and 37 cm ML for females have been recorded (unpublished data). The largest *L. vulgaris* have been caught off the West African coast, with reported maximum values of 64 cm ML for males and 54 cm ML for females (Raya et al. 1999).

The reproductive system of *L. vulgaris* is identical to that of *L. forbesi*; a detailed description is provided by van Oordt (1938). Fertilisation is internal; during mating, the male seizes a female by the head and transfers spermatophores to a buccal receptacle via the penis and hectocotylus. Oogenesis is asynchronous and mature ovaries exhibit polymodal oocyte size distribution, indicating a reproductive strategy of ‘intermittent terminal spawning’, where oocyte maturation and egg-laying occur as a number of discrete events during an extended spawning season (Rocha 1994). During spawning, female *L. vulgaris* secrete a protective mucous coating around their eggs, forming egg strings 6–16 cm long (Worms 1983). Female squid are known to lay egg strings close to others, forming ‘clusters’ containing up to 40,000 eggs, probably as a result of visual or chemical stimuli (Mangold-Wirz 1963). The sizes of mature oocytes of *L. vulgaris* appear to vary according to location, with the largest values (2.3–2.8 mm) found in Galician and north-western Mediterranean waters (Mangold-Wirz 1963, Guerra & Rocha 1994, Sifner & Vrgoc 2004) and the smallest values (1.9–2.2 mm) found off southern Portugal and the North African coasts (Coelho et al. 1994, Laptikhovsky 2000). The potential fecundity of female *L. vulgaris*, based on the total numbers of developing and mature oocytes in the ovary and oviducts, ranges from 10,000 to 42,000 eggs (Baddyr 1988, Coelho et al. 1994, Guerra & Rocha 1994, Laptikhovsky 2000). Maximum fecundity, based on mature oocytes only, is reported to be only about 7000 eggs per individual (Worms 1983) but this could be an underestimate if several egg batches mature sequentially.

Egg clusters are found throughout the year, but more frequently between June and August, during a peak in spawning activity, with some geographic variation (Baddyr 1988, Villa et al. 1997). They are typically attached to hard substrata in shallow water (6–120 m depth) over sand and silt bottoms (Worms 1983, Baddyr 1988). There are no confirmed records of *L. vulgaris* eggs in U.K. waters, although spawning is thought to occur in the English Channel. Further south, confirmed records in northern French, Galician and Portuguese waters (15–80 m depth) were reported by Pereira et al. (1998). Fixed egg clusters of *L. vulgaris* have been reported as shallow as 2 m (Villa et al. 1997).

The rate of embryonic development of *L. vulgaris* is influenced by water temperature and oxygen content (Worms 1983). For example, development times of 40–45 days at 12–14°C, 30 days at 17°C and 26–27 days at 22°C have been reported (Mangold-Wirz 1963, von Boletzky 1979). Photoperiod also appears to impact embryonic development, with most embryos hatching after a fixed light period ends (Paulij et al. 1990). Sen (2004) reported a 100% hatching success rate for a 12-h light plus 12-h dark regime but only a 52% success rate for a 24-h light regime. However, the duration of embryonic development did not appear to be affected by photoperiod.

There are no confirmed records of *L. vulgaris* paralarvae in U.K. waters, although they are likely to be included in the *Loligo* sp. collected in plankton samples in the English Channel (Collins et al. 2002). They have not been found in the cooler neritic waters around Scotland, in the northern North Sea or the Rockall Trough area (Yau 1994). Further south, records of *L. vulgaris* paralarvae from samples off Galicia and Portugal have been reported (Moreno & Pereira 1998, Piatkowski 1998, González et al. 2005, Moreno et al. 2009). They appear to overwinter offshore, move inshore during summer (Moreno & Sousa Reis 1995, Moreno et al. 2009) and undergo diurnal vertical migrations, appearing near the surface during the night (Sousa Reis 1989). SST ranges of 11–20°C have been reported for *L. vulgaris* paralarvae (Mangold-Wirz 1963, Moreno & Sousa Reis 1995, Moreno & Pereira 1998), with optimum values at 13–15°C (Moreno et al. 2009).

The early juvenile stages of *L. vulgaris* feed mainly on planktonic crustaceans, particularly copepods, mysids, euphausids and shrimp larvae (Nigmatullin 1975, Worms 1983). As the squid grow larger, fish become a greater proportion of the overall diet (Rocha et al. 1994). Adult *L. vulgaris* also prey, to a lesser degree, on polychaetes, cephalopods and crustaceans (Coelho et al. 1994, Guerra & Rocha 1994, Pierce et al. 1994c, Rocha et al. 1994). The ranges of observed prey species and types of *L. vulgaris* are similar to those reported for *L. forbesi* (Pierce et al. 1994c, Rocha et al. 1994). There is also evidence that the prey composition of *L. vulgaris* may vary seasonally due to changes in prey availability (Rocha et al. 1994).

Short-fin squids (family Ommastrephidae)

Short-fin or flying squids (ommastrephids) belong to the Suborder Oegopsina and are characterised by lacking a membrane of tissue over their eyes. Ommastrephid squids are typically medium-sized, muscular, powerful swimmers and have high-quality flesh suitable for human consumption. A number of species are of commercial importance. They are typically oceanic, deep-water squids although a few species sometimes venture occasionally into shallow waters. Many ommastrephid species exhibit diurnal vertical migratory behaviour, inhabiting deep waters during the day and moving to surface waters to feed at night. Four genera and four species of ommastrephid squid are found in the north-eastern Atlantic.

Illex coindetii

Biogeographic distribution The broadtail short-fin squid *Illex coindetii* (Verany, 1839) is an oceanic, benthopelagic species occurring in subtropical/temporate, offshore and coastal waters and continental slope areas and is widely distributed in the eastern Atlantic to 30°W and from South Africa (17° S) to the North Sea (60°N) (Clarke 1966, Lu 1973). It is quite common in the Mediterranean (Mangold & von Boletzky 1987) and Galician waters (González et al. 1994) and is also found in the western Atlantic Ocean, from the Caribbean Sea (9°N) to the eastern seaboard of North America (37°N). The limit of its southern distribution is undefined (Roper et al. 1984). In U.K. waters, *I. coindetii* is often found in the Celtic Sea, south-west of Cornwall (Arvanitidis et al. 2002).

Illex coindetii occurs over a considerable depth range, from surface waters down to greater than 800 m. The optimal depth range, where maximum concentrations of this squid have been observed, is reported to be 100–400 m and 100–600 m depending on locality (Sánchez et al. 1998). It is usually found close to soft (mud/sand/detritic) bottoms, often covered by *Funiculina* sp., in the lower sublittoral and upper bathyal zones (Mangold-Wirz 1963, Roper et al. 1984). The occurrence of *I. coindetii* has also been associated with decapod crustaceans, for example *Parapenaeus longirostris*, certain fish species, including *Merluccius merluccius* and *Micromesistius poutassou* (Jereb & Ragonese 1991a, Rasero et al. 1996, Dawe & Brodziak 1998) and another short-fin squid, *Todaropsis eblanae* (Mangold-Wirz 1963, Rasero et al. 1996). Adult squid are known to undergo diurnal vertical migrations in the water column, from close to the seabed during daylight hours to just below the surface at night (Ragonese & Bianchini 1990, Sánchez et al. 1998). The distribution and abundance of *I. coindetii* in certain areas appears to be influenced by particular hydrographic conditions and frontal zone movements (Jereb et al. 2001).

Biology and ecology In the wild, *Illex coindetii* exhibits extended spawning periods, ranging from a few days to several weeks, and it is considered to be an 'intermittent spawner' (González et al. 1996a). Variable seasonal peaks in maturation and spawning activity occur, depending on locality. For example, in the Mediterranean, maturity peaks in spring and autumn are apparent (Sánchez et al. 1998, Belcari et al. 1999), whereas in the north-eastern Atlantic, a summer (July–August) peak has been observed (González et al. 1996a). According to Hernández-Garcia (2002), water temperature is the main factor influencing the timing of reproduction. Correlations between the timing of peak spawning activity and environmental conditions (e.g., temperature, food availability) have also been observed in populations of *I. coindetii* in the Mediterranean (Arvanitidis et al. 2002).

Illex coindetii is a relatively small ommastrephid squid. It matures over a range of sizes, with females generally growing larger than males. Unusually large specimens (>25 cm ML) are occasionally reported in the Atlantic (Roper & Mangold 1998) and Mediterranean (Arvanitidis et al. 2002). Across its range, however, the majority of mature *I. coindetii* are typically far smaller (<20 cm ML). Estimates of longevity based on length-frequency and statolith analyses indicate maximum life spans of 6–18 mo for this species, depending on locality (Sánchez 1982, González et al. 1994b, Jereb & Ragonese 1995, Arkhipkin 1996).

Fecundity in ommastrephid squids is relatively high. Female *I. coindetii* are typical in this respect, being capable of producing 50,000–200,000 mature eggs. A maximum of 800,000 oocytes was reported by Sánchez et al. (1998). The eggs are relatively small, ranging from 0.8 to 1.3 mm (von Boletzky et al. 1973, Hernández-Garcia 2002). Although egg masses of *Illex* spp. have never been found in nature, observations of the closely related *I. illecebrosus* 'spawning' in captivity, producing gelatinous egg masses whilst swimming in open water (Durward et al. 1980, O'Dor & Balch 1985), indicate that species of the genus *Illex* may be pelagic spawners. According to O'Dor & Balch (1985), the gel coating appears to function as a buoyancy mechanism, regulating the sinking rate of the eggs in accordance with ambient conditions, particularly temperature. As a result, *Illex* eggs could be suspended in the mesopelagic zone for days, perhaps maintaining them at optimal temperatures for embryonic development, a possible explanation for why ommastrephid eggs are seldom found in nature (O'Dor & Balch 1985). The eggs of *I. illecebrosus* require temperatures above 13°C for successful embryonic development (O'Dor et al. 1982).

The diet of *Illex coindetii* includes various fish, crustacean and cephalopod species, in decreasing order of importance. The main components are usually related to local prey abundance and availability, but they are also influenced by the size of the feeding squids. Crustaceans are relatively more important in the diet of smaller squid, with cephalopods and fish becoming increasingly important as the squids grow larger (Castro & Hernández-García 1995). Small, juvenile squids exhibit a larger proportion of euphausids in the diet, an indication of pelagic feeding, whereas adult squid seem to take both pelagic and benthic species (Castro & Hernández-García 1995). Prey species taken include myctophids, anchovies, pearlside, blue whiting and mackerel (Sánchez 1982, Ovcharov et al. 1985, Chesalin 1987, Rasero et al. 1996, Lordan et al. 1998, Sánchez et al. 1998, Lelli et al. 2005). *Illex coindetii* is also cannibalistic, particularly at high densities (Dawe 1988) and where fish and other prey species are scarce (Dawe & Brodziak 1998). *I.coindetii* is in turn preyed on by a number of marine mammal species, including *Delphinus delphis*, *Tursiops truncatus* and *Stenella coeruleoalba* (González et al. 1994, Santos et al. 2004, 2005a).

Ommastrephes bartramii

Biogeographic distribution The red flying squid *Ommastrephes bartramii* (Lesueur, 1821) is an oceanic, mesopelagic species occurring in temperate/subtropical coastal waters and continental slope areas. It has a discontinuous, circumglobal distribution, being absent from the tropics. In the South Atlantic, it is found at 14–27°S off Africa (Roeleveld 1989) and at 27–45°S off South America (Brunetti et al. 1999). In the North Atlantic, it is found at 44–65°N, as far north as Iceland, although it is rarely caught in the North Sea and the Mediterranean (Roper et al. 1984). It appears to be particularly abundant in the eastern Atlantic off North Africa, between the Azores and the Canary Islands (Pinchukov 1975).

Although *O. bartramii* is very widely distributed, reproduction has only been reported in, and may be limited to, warm equatorial and subtropical waters, between 40°S and 25°N, with squids migrating elsewhere to feed (Aleksandronetz et al. 1983). Zuev et al. (1976) suggested a thermal range of 14–17°C for this species. It is believed to undergo considerable diurnal vertical migrations, from 560 to 1050 m depth during hours of daylight to less than 100 m depth at night (Moiseev 1987, 1991). Upwards migration speeds of 5 $m.min^{-1}$, and overall migration times of up to 2.5 h have been reported, depending on the starting depth (Moiseev 2001). During the night, *O. bartramii* appears to avoid shallow waters above seamounts (Moiseev 2001) and tends to group together in small shoals of fewer than 30 individuals (Zuev & Nigmatullin 1975).

Biology and ecology *Ommastrephes bartramii* is a medium-sized ommastrephid squid. Females generally mature at greater than 40 cm ML and can reach 69 cm, growing much larger than males (36 cm). Very little biological information is available on *O. bartramii* in the North Atlantic. Based on research on Pacific stocks, it appears that *O. bartramii* is an annual species and that females grow faster than males (Yatsu et al. 1997, Yatsu 2000).

Reproduction in *O. bartramii* is an annual event, with timing depending on location. For example, spawning occurs in late summer/early autumn in the Atlantic and in spring in the North Pacific. There are no confirmed records of *O. bartramii* egg masses in nature. Sakurai et al. (1995) developed an artificial fertilization technique for observing embryonic development in *O. bartramii*. Females are thought to produce more than 300,000 eggs, arranged in floating ribbons. The eggs and newly hatched rynchoteuthis paralarvae measured about 1 mm (ML) (Nigmatullin 1987). The latter inhabit open water 0–250 m deep (Zuev & Nesis 1971). Excellent descriptions of *O. bartramii* paralarvae were provided by Young & Hirota (1990).

Nigmatullin (1987) suggested five developmental changes in the ecological niche of *O. bartramii* (Table 5). *O. bartramii* is considered to be an important food resource for a number of marine

Table 5 Developmental and ecological changes in *Ommastrephes bartramii*

Size (mantle length, cm)	Developmental stage	Habitat	Prey
0.1	Egg mass	Plankton	N/A
0.1–0.8	Paralarva	Plankton	Macroplankton
1.0–2.5	Juvenile	Plankton	Mesozooplankton
3.0–8.0	Juvenile	Micronekton	Macrozooplankton
>15.0	Subadult/adult	Necton	Fish and squid

Source: From Nigmatullin 1987.

predators, including large fish (Bello 1991, 1996, Carrassòn et al. 1992), seabirds (den Hartog & Clarke 1996) and marine mammals (Carlini et al. 1992, Clarke et al. 1993, Hernández-Garcia 2002).

Todarodes sagittatus

Biogeographic distribution The European flying squid *Todarodes sagittatus* (Lamarck, 1798) is a neritic and oceanic, pelagic species occurring in temperate/subarctic/arctic, deep offshore, coastal waters and continental slope areas and is widely distributed in the eastern Atlantic to 40°W and the Arctic Ocean to 13°S (Guerra 1992). It is also found in the North Sea and is common in the Mediterranean (Roper et al. 1984). *Todarodes sagittatus* is found in both shallow coastal and deep oceanic environments. It has been recorded from surface waters to estimated depths of 4500 m (Collins et al. 2001) although most specimens have been caught in waters less than 1000 m deep (Roper et al. 1984). In common with other ommastrephids, it is known to undergo considerable diurnal vertical migrations, occurring at depths down to 2500 m during hours of daylight to surface waters at night (Mangold-Wirz 1963, Clarke 1966, Korzun et al. 1979, Nesis 1987). Significant strandings of this species sometimes occur at various beaches (Berdar & Cavallaro 1975). Spawning depths of 70–800 m have been reported for *T. sagittatus* in Portuguese waters (Anonymous 2005).

In the northern Atlantic, *T. sagittatus* is known to undergo extensive seasonal feeding and spawning migrations (Shimko 1989). Between early June and December, large aggregations of these squid appear around Iceland and the Faroe Islands and off the north-western coast of Norway (Wiborg 1972, Sundet 1985). It is often caught in deep waters west of Scotland and Ireland (Boyle et al. 1998, Lordan et al. 2001) but less commonly in shallow coastal waters. In certain years, however, huge aggregations of this species have been observed in the North Sea, around Shetland and just off the Scottish coast (Stephen 1944, Joy 1990). Large-scale strandings of *T. sagittatus* also occur during these events (Berdar & Cavallaro 1975). By late December, the squid have started migrating into the deeper, offshore waters of the continental slope where they overwinter and spawn. Elsewhere, migratory patterns are highly variable, depending on the geographic area. For example, in fishing grounds around Madeira and elsewhere in the eastern central Atlantic, *T. sagittatus* are only caught in large numbers between March and May (Borges & Wallace 1993, Piatkowski et al. 1998, Arkhipkin et al. 1999). However, no evidence of similar migrations of this species has been found in the Mediterranean (Quetglas et al. 1998a).

Biology and ecology *Todarodes sagittatus* is generally considered to be an annual species (Rosenberg et al. 1990, Arkhipkin et al. 1999), although a 2-yr life cycle has also been suggested (Lordan et al. 2001). Breeding seems to be protracted, with two peaks occurring, in spring and in autumn (Wiborg & Beck 1984, Roper et al. 1984, Rosenberg et al. 1990, Lordan et al. 2001). According to Borges & Wallace (1993), there is evidence of at least two *T. sagittatus* populations coexisting in north European waters. In years of abundance, *T. sagittatus* moves inshore during summer and autumn, when it is caught in large numbers (Wiborg & Gjøsæter 1981, Sundet 1985, Joy 1989, Lordan et al. 2001). Catches in northern coastal waters are made up mainly of immature female specimens, which suggests that inshore migration is mainly carried out by females, probably for feeding (Wiborg et al. 1982, Sundet 1985, Joy 1989, Borges & Wallace 1993, Boyle et al. 1998).

Todarodes sagittatus is a medium- to large-sized ommastrephid squid. It is reported to reach 75 cm ML, with females growing larger than males (Roper et al. 1984). Confirmed maximum sizes of 49 and 64 cm in the North Atlantic and 39 and 60 cm in the Mediterranean have been reported for this species (Cuccu et al. 2005). According to Nesis (1987), individual *T. sagittatus* larger than 50 cm ML may be at least 2 yr old.

Age at maturity in this species is thought to be 12–15 mo. Annual spawning events of *T. sagittatus* are thought to occur in deep waters adjacent to the continental slopes. These occur in late winter–spring in north European waters, around March–April in the Bay of Biscay, mainly between October and December in Portuguese waters and September–November in the western Mediterranean (Roper et al. 1984, Piatkowski et al. 1998, Quetglas et al. 1998a, Arkhipkin et al. 1999, Lordan et al. 2001). Females always outnumber males in fished samples. Mature males are relatively scarce but are usually found throughout the year, while mature females are more abundant but only found during the spawning season. Female *T. sagittatus* may produce 12,000–18,000 eggs (Laptikhovsky & Nigmatullin 1999).

Todarodes sagittatus is an opportunistic and aggressive, highly mobile squid that will consume any potential prey it can overpower. Its diet is typically composed of fish, crustaceans and cephalopods, in decreasing order of importance. Cannibalism is also relatively common in this species. In the North Atlantic, *T. sagittatus* feeds voraciously on a variety of small fish, particularly young herring (*Clupea harengus*) and cod (*Gadus morhua*) (Brieby & Jobling 1985, Joy 1990, Piatkowski et al. 1998, Quetglas et al. 1998a. *Todarodes sagittatus* is itself preyed on by a number of fish and marine mammal species (Table 6).

Todaropsis eblanae

Biogeographic distribution The lesser flying squid *Todaropsis eblanae* (Ball, 1841) is a neritic, demersal species occurring in subtropical/temporate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from South Africa (40°S) to the North Sea (61°N). It has also been reported in the Mediterranean (Mangold-Wirz 1963, Quetglas et al. 2000). A distinct population also occurs in the Indo-Pacific region (Nesis 1979), off the south coast of Australia (Lu 1982, Roper et al. 1984). *Todaropsis eblanae* appears to be primarily a benthic species, associated with soft (mud-sand) bottoms, mainly in the lower sublittoral and upper bathyal zones of the continental shelf (Clarke 1966). Unlike other ommastrephid species, there is no evidence that it regularly ascends to the surface or approaches shorelines. It occurs in waters of 9–18°C and depths of 20–780 m (Guerra 1992). In Italian waters, a depth range of 30–700 m has been reported (Belcari et al. 1999).

Todaropsis eblanae is commonly caught in Galician waters (González et al. 1994), in the Celtic Sea, south-west of Ireland (Lordan et al. 1998), in Portuguese waters and in the Bay of Biscay (Robin et al. 2002). In some years, it can be very widespread and abundant in the north-eastern Atlantic, second only to *Loligo forbesi* in overall squid catches (Stephen 1944, Lordan et al. 2001). Further north, this species is relatively scarce, although huge aggregations do occur infrequently in the northern North Sea, around Shetland and just off the Scottish coast (Stephen 1944, Hastie et al. 1994). These historical phenomena may be linked to hydrographical anomalies such as incursions of high-salinity Atlantic seawater into the North Sea (Hastie et al. 1994).

Biology and ecology *Todaropis eblanae* is a relatively small ommastrephid squid. It is thought to live for 1–2 yr and matures over a range of sizes, with females generally growing larger than males. Maximum sizes of 22 and 29 cm ML have been reported for males and females, respectively (Robin et al. 2002). Estimates of size at maturity for this species range from 12 to 13 cm ML for males and from 14 to 20 cm ML for females, depending on the locality (González et al. 1994, Hastie et al. 1994). Total potential fecundity estimates of female *T. eblanae* range from 28,000 eggs in Scottish

Table 6 Recorded marine predators of selected cephalopod species found in U.K. waters

	Predator[a]	*Alloteuthis subulata*	*Loligo forbesi*	*Loligo vulgaris*	*Illex coindetii*	*Ommastrephes bartramii*	*Todarodes sagittatus*	*Todaropsis eblanae*	*Architeuthis* spp.	*Brachioteuthis riisei*	*Galiteuthis* spp.	*Gonatus* spp.	*Gonatus fabricii*	*Histioteuthis* spp.	*Histioteuthis bonnellii*	*Histioteuthis reversa*	*Onychoteuthis* spp.	*Teuthowenia* spp.	*Teuthowenia megalops*	*Neorossia* spp.	*Redeletiola* spp.	*Rossia macrosoma*	*Sepiola atlantica*	*Sepia officinalis*	*Sepia elegans*	*Eledone cirrhosa*	*Haliphron atlanticus*	*Octopus vulgaris*
Cephalopods																												
Loligo forbesi	X	X	X																						X		X	
Loligo vulgaris	X	X	X																					X				
Illex coindetii	X	X		X		X	X					X									X				X			
Onychoteuthis banksii								X																				
Todarodes sagittatus						X																						
Fishes																												
Alepisaurus ferox							X	X																				
Beryx splendens						X																						
Centroscymnus coelolepis					X	X		X																				
Conger conger				X																							X	
Coryphaenoides armatus												X																
Echiichthys vipera			X																									
Gadus morhua		X										X													X			
Galeus melastomus						X																						
Heptranchias perlo				X																								
Isurus oxyrinchus								X																				
Lamna nasus						X							X															
Lophius piscatorius		X																							X			
Melanogrammus aeglefinus																									X			
Merluccius merluccius	X																											
Micromesistius poutassou				X																								
Molva molva																									X			
Muraena helena																											X	

(continued on next page)

Table 6 Recorded marine predators of selected cephalopod species found in U.K. waters

	Predator[a]	*Alloteuthis subulata*	*Loligo forbesi*	*Loligo vulgaris*	*Illex coindetii*	*Ommastrephes bartramii*	*Todarodes sagittatus*	*Todaropsis eblanae*	*Architeuthis* spp.	*Brachioteuthis riisei*	*Galiteuthis* spp.	*Gonatus* spp.	*Gonatus fabricii*	*Histioteuthis* spp.	*Histioteuthis bonnellii*	*Histioteuthis reversa*	*Onychoteuthis* spp.	*Teuthowenia* spp.	*Teuthowenia megalops*	*Neorossia* spp.	*Redeletiola* spp.	*Rossia macrosoma*	*Sepiola atlantica*	*Sepia officinalis*	*Sepia elegans*	*Eledone cirrhosa*	*Haliphron atlanticus*	*Octopus vulgaris*
Mustelus mustelus			X																				X					
Phycis blennoides				X																								
Pollachius virens				X																								
Prionace glauca						X	X	X															X		X			
Reinhardtius hippoglossoides												X																
Sebastes marinus												X																
Seriola lalandi							X																					
Seriola dumerili			X									X																
Sphyrna zygaena								X																				
Somniosus spp.								X																				
Thunnus alalunga						X		X																				
Thunnus albacares				X																								
Torpedo spp.			X																									
Xiphias gladius			X	X	X	X		X																				
Zeus capensis							X																					
Birds																												
Calonectris diomedea					X																							
Diomedea spp.								X																				
Fratercula arctica												X																
Fulmarus glacialis												X																
Phoebetria fusca								X																				

Mammals																												
Arctocephalus pusillus																						X						
Balaenoptera musculus											X																	
Cysophora cristata											X																	
Delphinus delphis	X		X	X		X	X			X		X									X			X		X		
Globicephala macrorhynchus						X																						
Globicephala melas			X	X		X					X										X			X		X		
Grampus griseus						X	X														X	X		X		X		
Halichoerus grypus		X																										
Hyperoodon ampullatus	X					X	X				X																	
Kogia breviceps		X			X	X			X					X	X													
Monachus monachus																						X						
Monodon monoceros											X																	
Phoca groenlandica						X					X																	
Phoca vitulina		X																						X				
Phocoena phocoena	X	X	X																		X			X				
Physeter macrocephalus		X			X	X		X			X	X	X	X				X						X	X	X		
Pseudorca crassidens					X																							
Stenella attenuata								X																				
Stenella coeruleoalba						X																						
Tursiops truncatus	X		X	X		X	X																	X		X		
Ziphus cavirostris					X	X					X																	

Sources: Grimpe 1925, Hjort & Ruud 1929, Grieg 1930, Nesis 1965, Scott & Tibbo 1968, Dexter 1969, Clarke & Stevens 1974, Macalaster 1976, Wiborg 1980, Martins 1982, Sánchez 1982, Amaratunga 1983, Bergström & Summers 1983, Kristensen 1984, Clarke & Pascoe 1985, Ovcharov et al. 1985, Chesalin 1987, Dawe 1988, Lydersen et al. 1989, Bello 1991, 1996, Castley et al. 1991, Hislop et al. 1991, Carrasson et al. 1992, Falk et al. 1992, Clarke et al. 1993, Clarke & Goodall 1994, González et al. 1994, Pierce et al. 1994c, Rocha et al. 1994, Castro & Hernández-Garcia 1995, Hernandez-Garcia 1995, Matallanas et al. 1995, den Hartog & Clarke 1996, Klages 1996, Pierce & Santos 1996, Rasero et al. 1996, Clarke & Pascoe 1997, Martin & Christiansen 1997, Potelov et al. 1997, Hanlon & Messenger 1998, Lordan et al. 1998, MacNaughton et al. 1998, Sánchez et al. 1998, Hjelset et al. 1999, Santos et al. 1999, 2001a, 2002, 2004, 2006a, Brown et al. 2001, Daly et al. 2001, Velasco et al. 2001, López 2002, Hernandez-Garcia 2002, Salman et al. 2002, Cherel & Duhamel 2004, Garthe et al. 2004, Lelli et al. 2005, De Pierrepont et al. 2005,

[a] Not all predator species found in north-eastern Atlantic waters.

waters (Hastie et al. 1994) to 275,000 eggs in west African waters (Laptikhovsky & Nigmatullin 1999). Up to 10,000 mature eggs, ranging in size from 0.8 to 2.5 mm, have been observed in individual female squids (Mangold-Wirz 1963). The reported maximum number of eggs spawned ranges from 13,200 to 34,400 per female (Hastie et al. 1994, Laptikhovsky & Nigmatullin 1999).

Spent females are rarely found in the wild, indicating that *T. eblanae* is a terminal spawner. Annual spawning events, between spring and autumn (possibly peaking in summer), have been reported in the North Atlantic and Mediterranean (Mangold-Wirz 1963, González et al. 1994, Hastie et al. 1994, Arkhipkin & Laptikhovsky 2000, Robin et al. 2002).

The diet of *T. eblanae* includes, in decreasing order of importance, fish, crustaceans and other cephalopods. Cannibalism has also been reported in this species (Rasero et al. 1996, Lordan et al. 1998). *Todaropis eblanae* is itself preyed on by a number of fish and marine mammals (Table 6).

Other squid species

In addition to the commercially important ommastrephid squids, there are a number of other oegopsid species of various sizes found in the north-eastern Atlantic. At present, none of these are exploited commercially, although certain species are widespread and abundant, suitable for human consumption and are considered to have fishery potential. Five families, six genera and seven species of squid in this category are found in the north-eastern Atlantic:

Architeuthis dux

Biogeographic distribution The giant squid *Architeuthis dux* (Steenstrup, 1857) and its congeners are oceanic, cosmopolitan mesopelagic species found in relatively high abundance in subtropical/temporate, deep, offshore waters in the Atlantic and Indo-Pacific (Roper et al. 1984). Very few specimens of *Architeuthis* spp. in good condition have ever been found and consequently little is known about their taxonomy, biology and ecology. Based on 34% of verified worldwide reports (115 specimens), it is assumed that they are relatively abundant in the north-eastern Atlantic (Guerra et al. 2004). In U.K. and Irish waters, specimens are very occasionally caught by fishers or washed up on the coastlines of the northern North Sea, particularly Scotland (Ritchie 1918, 1920, 1922, Rae & Lamont 1963, Boyle 1986, Collins et al. 1997b, Collins 1998, Guerra et al. 2004a). Collins (1998) lists 25 known *Architeuthis* strandings and by-catches in the U.K. and Ireland.

Biology and ecology *Architeuthis dux* is one of the largest invertebrates known, with the only other possible contenders being other *Architeuthis* spp. and the Antarctic colossal squid *Mesonychoteuthis hamiltoni* (Robson, 1925). Maximum sizes of 6 m ML and 20 m total length (TL) have been reported for this species (Roper et al. 1984). Around the world, juvenile architeuthids are known to be predated by a number of marine mammals (notably the sperm whale *Physeter macrocephalus*, but also *Stenella attenuata*) (Clarke & Pascoe 1997, Robertson & Chivers 1997), seabirds (*Diomedea* spp., *Phoebetria fusca*) (Roper & Young 1972, Rodhouse et al. 1987), fish (*Alepisaurus ferox*, *Centroscymnus coelolepis*, *Isurus oxyrinchus*, *Prionace glauca*, *Somniosus* spp., *Sphyrna zygaena*, *Thunnus alalunga* and *Xiphias gladius*) (Roper & Young 1972, Toll & Hess 1981, Arkhipkin & Nigmatullin 1997) and other squid (*Onychoteuthis banksii*) (Arkhipkin & Nigmatullin 1997). The only confirmed predator of adult *Architeuthis* spp. is the sperm whale *Physeter macrocephalus* (Clarke & Pascoe 1997, Santos et al. 2002). Remains of large architeuthids have also been found in the stomachs of deep-water sleeper sharks (*Somniosus* spp.), although it is not known whether the squid were actively predated or already dead when scavenged on the seabed (Cherel & Duhamel 2004).

Brachioteuthis riisei

Biogeographic distribution The common arm squid *Brachioteuthis riisei* (Steenstrup, 1882) is an oceanic, cosmopolitan mesopelagic species found in deep, cool waters in all oceans except the

North Pacific and Gulf of Mexico. It is also present in the Mediterranean (Yau 1994). Larval and juvenile *Brachioteuthis* spp. are relatively common in plankton samples taken from waters west of Ireland (Collins et al. 2001). A depth range of 0 to 3000 m is reported for this species, with paralarvae found in the upper 200 m and subadults and adults occurring much deeper (Zuev & Nesis 1971, Clarke & Stevens 1974).

Biology and ecology Roper et al. (1984) report a maximum size of 4 cm ML for this species, but this is based on a few records. Young et al. (1985) provided descriptions of the eggs and larvae of a *Brachioteuthis* sp. from Hawaiian waters. In the North Atlantic, young stages of *B. riisei* are present from May to August and in February (Massy 1909). Paralarvae and juveniles are also abundant in the Rockall Trough area during May–June, indicating that hatching occurs throughout the year (Clarke 1966). Certain marine mammals are known to prey on *B. riisei*, including *Globicephala melaena*, *Hyperoodon planifrons* and *Ziphus cavirostris* (Clarke & Goodall 1994, Santos et al. 2001a). Remains of *B. riisei* have also been found in the stomachs of stranded pygmy sperm whales (*Kogia breviceps*) (Santos et al. 2006a).

Galiteuthis armata

Biogeograpic distribution The armed cranch squid *Galiteuthis armata* (Joubin, 1898) is an oceanic, bathypelagic species found in subtropical/temperate waters of the Atlantic, from Florida and the Gulf of Guinea (11° N) to Rockall Trough (60° N). It is also found in the Mediterranean but appears to be absent from the North Sea (Yau 1994). It has been recorded in Atlantic waters west of Scotland (Russell 1909).

Biology and ecology Roper et al. (1984) reported maximum sizes of 8 cm ML and 39 cm total length TL for this species, but these are based on a few records. Certain marine mammals are known to prey on *G. armata*, including *Globicephala melaena*, *Hyperoodon planifrons* and *Ziphus cavirostris* (Clarke & Goodall 1994, Santos et al. 2001a). Remains of galiteuthid squid have been found in the stomachs of sperm whales (Clarke & Pascoe 1997).

Gonatus fabricii

Biogeographic distribution The boreoatlantic armhook squid *Gonatus fabricii* (Lichtenstein, 1818) is an oceanic, mesopelagic species found in subarctic/arctic, deep offshore waters of the Arctic and North Atlantic, from Newfoundland Basin to the Norwegian Sea. The recorded southerly limits of this species are considered to be around 40°N in the western Atlantic, on the eastern seaboard of North America and 55°N in the eastern Atlantic, west of Scotland (Roper et al. 1984). It is found over a considerable depth range, from surface waters at night to depths of 3000 m during daylight hours (Kristensen 1983). According to Collins et al. (2001), juvenile *G. fabricii* are very common in plankton samples taken from waters around the United Kingdom.

Biology and ecology *G. fabricii* is a relatively small semelparous oegopsid, with males and females reaching maximum lengths of 35 and 38 cm ML, respectively (Roper et al. 1984). Maturity in both sexes occurs at about 20 cm ML. The potential fecundity of female *G. fabricii* is estimated to be approximately 10,000 eggs per individual (Bjørke & Gjøsæter 2004). Females undergo considerable morphological degeneration before spawning, including tentacle loss, arm sucker loss and swelling of arm and mantle tissues; they appear to lose ability for active locomotion and their swollen bodies may act as gelatinous floats for their egg masses that remain attached (Bjørke et al. 1997, Arkhipkin & Bjørke 1999, Bjørke & Gjøsæter 2004). In the Norwegian Sea and off Greenland, spawning occurs pelagically, possibly at great depths, between late winter and summer and hatching events occur from late March to July (Kristensen 1984, Bjørke & Gjøsæter 2004).

Juvenile *Gonatus fabricii* feed on planktonic invertebrates, including copepods, euphausids, amphipods, pteropods and chaetognaths. When the squid reach 2.5 cm ML, they develop characteristic tentacle hooks and fish become an important dietary component. Adult *G. fabricii* are apparently capable of overcoming prey larger than themselves and their diet includes, in decreasing order of importance, crustaceans, fish (*Mallotus villosus*, *Sebastes marinus*) and other cephalopods. Cannibalism has also been reported in this species (Nesis 1965, Wiborg 1980, Kristensen 1984).

Gonatus fabricii is an abundant food source that is exploited by a large number of marine predators in the Arctic and North Atlantic (see Bjørke 2001 for a review). These include several species of whale (*Globicephala melaena*, *Hyperoodon ampullatus*, *Monodon monoceros*, *Physeter macrocephalus*, *Ziphius cavirostris*) (Hjort & Ruud 1929, Grimpe 1925, Nesis 1965, Santos et al. 1999, 2001a, 2002), seals (*Cysophora cristata*, *Phoca groenlandica*) (Potelov et al. 1997, Lydersen et al. 1989), seabirds (*Fratercula arctica*, *Fulmaris glacialis*) (Falk et al. 1992, Garthe et al. 2004), fish (*Coryphaenoides armatus*, *Gadus morhua*, *Histiobranchus bathybius*, *Sebastes marinus*, *Seriola dumerili*, *Reinhardtius hippoglossoides*) (Grimpe 1925, Nesis 1965, Matallanas et al. 1995, Martin & Christiansen 1997, Dawe & Brodziak 1998) and other squid (*Illex illecebrosus*) (Amaratunga 1983) (Table 6). In certain offshore areas of the North Atlantic, particularly around the Faroes and Norwegian Sea, puffins (*Fratercula arctica*) have been observed feeding almost exclusively on *G. fabricii* (Falk et al. 1992).

Gonatus steenstrupi

Biogeographic distribution The Atlantic gonate squid, *Gonatus steenstrupi* (Kristensen, 1981) is an oceanic, mesopelagic species found in boreal/subarctic, deep offshore waters of the North Atlantic, from Newfoundland Basin and the Bay of Biscay (40°N) to south-eastern Greenland and Iceland (65°N). It is found off the west coast of the British Isles but appears to be absent from the North Sea (Roper et al. 1984).

Biology and ecology *Gonatus steenstrupi* is very similar in morphology and biology to its congener *G. fabricii* and the two species co-occur in many areas and are often confused. Falcon et al. (2000) provided valuable descriptions of the early life stages of both species. These species are highly sympatric, with overlapping ranges and a considerable amount of further research is required to distinguish them properly.

Histioteuthis bonnellii

Biogeographic distribution The umbrella squid *Histioteuthis bonnellii* (Férussac, 1835) is an oceanic, mesopelagic species found in subtropical/temperate/subarctic waters of the Atlantic, from the west coast of Africa (20°S) to Greenland (65°N). It is also present in the southern Indian Ocean (30°S) and the Mediterranean, but is absent from the Gulf of Mexico and Caribbean Sea (Yau 1994). It is widely distributed in northern waters (Clarke 1966) and has been recorded off the Irish coast (Collins et al. 1997b). A depth range of 240–2200 m has been reported for this species, with mature specimens typically occurring below 1000 m (Yau 1994).

Biology and ecology Roper et al. (1984) reported a maximum size of 33 cm ML for this species, but this is based on a few records. A large mature female specimen, measuring 23 cm ML, was caught off the west coast of Ireland (Collins et al. 1997b). *Histioteuthis bonnellii* is preyed on by various species of whale (*Physeter macrocephalus*, *Hyperoodon ampullatus*, *Ziphius cavirostris*) and fish (*Prionace glauca*, *Xiphias gladius*) (Bello 1991, Hernández-Garcia 1995, Santos et al. 2001a). Sperm whales and porbeagle sharks (*Lamna nasus*) are known to feed on several histioteuthid squid species (Clarke & Pascoe 1997, Clarke & Roper 1998, Cherel & Duhamel 2004). Remains of *Histioteuthis bonnellii* have been found in the stomachs of stranded pygmy sperm whales (*Kogia breviceps*) (Santos et al. 2006a).

Histioteuthis reversa

Biogeographic distribution The reverse jewel squid *Histioteuthis reversa* (Verrill, 1880) is an oceanic, mesopelagic species found in moderately warm waters of the Atlantic, from South Africa (45° S) to south of Iceland and Newfoundland Bank (52° N). It is also present in the southern Indian Ocean (to 30° S) and the Mediterranean. It is absent from the Gulf of Mexico and rare in the Caribbean Sea (Yau 1994). According to Voss (1969), *H. reversa* occurs in greatest abundance over deep bottom slopes, near land masses and oceanic ridges.

Biology and ecology Little is known about the biology and ecology of *Histioteuthis reversa*. In the North Atlantic, young specimens (2–4 cm ML) were captured near the continental shelf, indicating spawning over the continental slope (Clarke 1966). Remains of *H. reversa* have been found in the stomachs of stranded pygmy sperm whales and sperm whales (Santos et al. 2006a,b).

Onychoteuthis banksii

Biogeographic distribution The common clubhook squid *Onychoteuthis banksii* (Leach, 1817) is an oceanic, epipelagic species with a circumglobal distribution in deep, tropical, subtropical and temperate waters, between 45°S and 65°N (Roper et al. 1984). It has not been recorded in the Mediterranean. In U.K. waters, it has been caught in the North Sea, off the Scottish coast and near the Isle of Man in the Irish Sea. According to Arkhipkin & Nigmatullin (1997), *O. banksii* is one of the most abundant epipelagic squid species found in the oceans. Paralarvae and juveniles occur mainly near the surface (<30 m), whereas larger adults are generally found 30–150 m deep (Degner 1925, Arkhipkin & Nigmatullin 1997) and are occasionally encountered as deep as 4000 m (Clarke 1966).

Biology and ecology A maximum size of 30 cm ML is reported for *Onychoteuthis banksii* (Roper et al. 1984), but this is based on a few records. The larvae are abundant in the eastern Atlantic, particularly from January to March (Roper et al. 1984). There are no records of predation on this species in U.K. waters, although specimens have been found in the stomachs of blue sharks (*Prionace glauca*) caught in Irish waters (MacNaughton et al. 1998). In other parts of the world, *O. banksii* is apparently predated by petrels (*Pteroderma* spp.) (Imber et al. 1995), fur seals (*Arctocephalus* spp.) (Klages 1996) and dolphins (*Stenella* spp.) (Fiscus 1993).

Teuthowenia megalops

Biogeographic distribution The Atlantic cranch squid *Teuthowenia megalops* (Prosch, 1847) is an oceanic, bathypelagic species found in deep, cool subarctic waters of the North Atlantic, from the Canary Islands (24°N) to Greenland (66°N). It is absent from the North Sea and Mediterranean (Yau 1994). It is reported to be widely distributed and abundant (Nesis 1987). Juvenile *T. megalops* have been recorded in plankton samples off the west coasts of Ireland, Scotland and northern Portugal (Collins et al. 2001, Santos et al. 2001c, Moreno et al. 2009).

Biology and ecology According to Nixon (1983), the lifespan of *T. megalops* is probably 2–3 yr and it can reach a size of 35 cm ML. No eggs of this species have been found in the wild. A potential fecundity of 70,000–80,000 eggs is reported based on a few preserved specimens (Nixon 1983). Hatching probably occurs at greater than 1000 m deep, followed by ontogenetic ascent (Yau 1994). Paralarvae of *T. megalops* (<1 cm ML) have been found at 1000 m and larger specimens (1–6 cm ML) at 200–300 m. There is some evidence of diel vertical migrations for juvenile and adult *T. megalops* (Yau 1994). A peak in abundance of paralarvae occurred in spring (May–June) in the Rockall Trough and in winter (February–March) in northern Portugal. Remains of *T. megalops* have been recovered from the stomachs of large fish (*Prionace glauca*, *Xiphias gladius*) (Hernández-Garcia 1995, MacNaughton et al. 1998) and stranded whales (*Globicephala melaena*, *Hyperoodon ampullatus*, *Physeter macrocephalus*, *Ziphius cavirostris*) (Clarke & Goodall 1994, Santos et al. 2001a, 2002) (Table 6).

Sepiolids

Bobtails (sepiolids), also known as dumpling or stubby squids, are a group of small-sized decapods closely related to cuttlefishes. They tend to have shorter, round mantles and possess no cuttlebone. Bobtails have a symbiotic relationship with bioluminescent bacteria that help to conceal their silhouettes from below by matching the amount of light hitting their mantles from above. In U.K. waters, sepiolids are considered to be too small to exploit and are often overlooked in catches, although certain species may be very abundant (Stephen 1944). During deep-water benthic surveys in the north-eastern Atlantic, Collins et al. (2001) found that sepiolids were predominant in cephalopod catches taken from upper continental slope stations (150–500 m deep) Four sepiolid genera and eight species are found in the north-eastern Atlantic: *Neorossia caroli, Rondeletiola minor, Rossia glaucopis, Rossia macrosoma, Sepietta neglecta, Sepietta oweniana, Sepiola atlantica* and *Sepiola aurantiaca*.

Neorossia caroli

Biogeographic distribution The carol bobtail *Neorossia caroli* (Joubin, 1902) is a deep-water, benthic species found in the eastern Atlantic, from the equator to 40–50°N (Roper et al. 1984, Nesis 1987). Further north, in U.K. waters it is very rare, although significant numbers have been caught in 400–1540 m in the Porcupine Seabight, south-west of Ireland (Collins et al. 2001).

Biology and ecology There is very little published information available about the biology and ecology of *N. caroli*. A maximum size of 6 cm ML has been reported for this species (Roper et al. 1984, Collins et al. 2001).

Rondeletiola minor

Biogeographic distribution The lentil bobtail *Rondeletiola minor* (Naef, 1912) is a neritic, nectobenthic species occurring in moderately warm, shallow coastal waters and continental shelf areas in the eastern Atlantic and Mediterranean. Its geographic range has not been determined (Roper et al. 1984). It is common in the Mediterranean and in Portuguese waters (Nesis 1987, Villanueva 1995). Further north, in U.K. waters it is very rare, although significant numbers have been caught in 150–280 m in the Porcupine Seabight, south-west of Ireland (Collins et al. 2001). It is typically found over muddy bottom substrata, at depths of 80–100 m (Roper et al. 1984).

Biology and ecology Very little is known about the biology and ecology of *R. minor*. It is a very small sepiolid species, with a maximum size of about 2 cm ML reported (Reid & Jereb 2005).

Rossia glaucopis

Biogeographic distribution The stout bobtail *Rossia glaucopis* (Lovén, 1845) is a neritic, nectobenthic species occurring in cool, coastal waters and continental shelf areas of the Arctic and North Atlantic, off Greenland, Iceland and Sptizbergen. It is found over a considerable depth range, from 10 to 1500 m, but is most common at a depth of 120 m (Yau 1994). The southerly limit of *R. glaucopis* appears to be around the northern North Sea (60°N) and it is rarely found in Scottish waters (Yau 1994).

Biology and ecology A maximum size of 4 cm ML has been reported for this species (Yau 1994). The eggs of *R. glaucopis* are relatively large (~7 mm diameter) and are laid singly but attached in clusters to empty shells, stones and other hard substrata. Hatchlings measure about 5–6 mm ML. In Scottish waters, juveniles appear in plankton samples from spring to autumn, with peak abundances in the spring, although data are scarce (Yau 1994). Adult *R. glaucopis* are hardly ever found in U.K. waters, the last confirmed record from Scottish waters being 1926 (Yau 1994).

Rossia macrosoma

Biogeographic distribution The stout bobtail *Rossia macrosoma* (delle Chiaje, 1829) is a neritic, nectobenthic species occurring in moderate and cool, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Senegal (15°N) to Greenland and the Norwegian Sea (65°N). It is also found in the North Sea (Nesis 1987) and the Mediterranean (Villanueva 1995). It has been found in waters all around the United Kingdom (Nesis 1987), although in Scottish waters it is apparently more common on the west coast than the east coast, at around 50 m deep (Yau 1994). It is usually found over sand-mud substrata (Roper et al. 1984). A maximum depth of 515 m was reported by Collins et al. (2001).

Biology and ecology Current knowledge of *R. macrosoma* is largely based on observations made in the western Mediterranean and laboratory studies. It is a relatively large sepiolid, sometimes exceeding 8 cm ML, but usually less than 6 cm ML (Jereb & Roper 2005). Longevity is apparently 1–1.5 yr (von Boletzky & von Boletzky 1973). Mangold-Wirz (1963) reported seasonal spawning migrations to shallow inshore waters, with an extended spawning season from March to November. Migrations are apparently partitioned by size, with the largest individuals arriving first in spring, followed by smaller individuals in summer (Jereb & Roper 2005). Maturation begins at 3 cm ML (age 7 mo) and 3.5 cm ML (age 8 mo) for males and females, respectively. The eggs, which measure 7–8 mm, are laid in clusters of 30–40 and covered by a violet-red coat. These are usually deposited on bivalve shells or other hard substrata on the seabed. Embryonic development lasts about 45 days at 16°C (Mangold-Wirz 1963). In Scottish waters, juvenile *R. macrosoma* are found in the summer and early autumn (Yau 1994). *R. macrosoma* preys on decapod shrimps such as *Leander serratus* but does not appear to feed on mysids or crabs (von Boletzky & von Boletzky 1973). Unlike other sepiolids, it does not bury itself in bottom substrata but prefers to sit on the surface or hide in crevices (von Boletzky & von Boletzky 1973).

Sepietta neglecta

Biogeographic distribution The elegant bobtail *Sepietta neglecta* (Naef, 1916) is a neritic, nectobenthic species occurring in moderate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Morroco (25°N) to the northern North Sea (63°N). It is also found in the Mediterranean. This species appears to prefer muddy bottom substrata, at depths of 25–500 m (Jereb & Roper 2005).

Biology and ecology *Sepietta neglecta* rarely exceeds 3 cm ML (Jereb & Roper 2005). Little is known about its biology and ecology. It is thought to spawn throughout the year and is often associated with the bobtails *Rossia macrosoma* and *Sepietta oweniana*. It closely resembles the latter species and it is often difficult to distinguish between them (Jereb & Roper 2005).

Sepietta oweniana

Biogeographic distribution The common bobtail *Sepietta oweniana* (d'Orbigny, 1841) is a neritic, nectobenthic species occurring in moderate, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Mauritania (20°N) to the Faroe Islands and

Norwegian Sea (63°N). It is also found in the North Sea and Mediterranean, in depths of 20–600 m (Mangold-Wirz 1963). In Scottish waters, it is most common in 80–90 m (Yau 1994). This species appears to prefer bottom substrata of mud or muddy sands (Mangold-Wirz 1963).

Biology and ecology *Sepietta oweniana* is a relatively large sepiolid, reaching 7 cm ML (Norman 2000). It is a short-lived species; longevity ranges from 6 to 9 mo in the Mediterranean (Mangold & Froesch 1977). However, it does appear to be a multiple spawner (Bello & Deickert 2003). In the western Mediterranean, spawning migrations of *S. oweniana* to shallow inshore waters, with an extended spawning period from March to November, have been reported (Mangold-Wirz 1963). According to Salman (1998), in the Aegean Sea peaks in spawning activity occur during April–May and October–November. In Scottish waters, spawning occurs from September to February (Yau 1994). Batch size ranges from 50 to 100 eggs per female (Bello & Deickert 2003). Embryonic development is related to temperature, taking for example, 67 days at 14°C and 84 days at 12°C. Juvenile *S. oweniana* (measuring up to 9 mm ML) have been found in plankton samples between March and September (Yau 1994).

Juvenile *S. oweniana* prey on mysids (*Praunus* spp.), amphipods and large copepods, whilst the adults prey on larger crustaceans (*Meganyctiphanes norvegica*, *Palaemon elegans*, *Crangon crangon*) (Bergström & Summers 1983, Bergström 1985). Newly hatched juveniles actively forage during the day until they reach 10 wk old at 15–18 mm ML (Bergström & Summers 1983). The adults are ambush predators, remaining buried in soft substratum and feeding during dawn and dusk (Bergström 1985). Predators of *Sapietta oweniana* include species of demersal fish (*Gadus morhua*, *Melanogrammus aeglefinus*) (Bergström & Summers 1983).

Sepiola atlantica

Biogeographic distribution The Atlantic bobtail *Sepiola atlantica* (d'Orbigny, 1839) is a neritic, nectobenthic species occurring in moderate and cool, shallow coastal waters and continental shelf areas and is distributed in the eastern Atlantic, from North Africa (20°N) to the Faroe Islands, Iceland and the Norwegian Sea (65°N). It is also found in the North Sea and is reported to be very common in U.K. waters (Yau & Boyle 1996) but is either rare or absent in the Mediterranean (Yau 1994). *S. atlantica* is found from the sublittoral zone to a depth of 150 m and is most common in clean, sandy bottoms at 50–120 m deep (Yau 1994).

Biology and ecology Although *S. atlantica* is a very common nearshore species, few studies have been carried out on this species (Yau 1994, Yau & Boyle 1996). It is a small species, with both sexes measuring less than 2 cm ML maximum (Roper et al. 1984, Yau 1994). The eggs of *S. atlantica* measure 2–3 mm (Yau & Boyle 1996) and are usually laid in clusters attached to hard surfaces on the seabed (Yau 1994). Mature females carry 40–130 ova prior to spawning (Yau & Boyle 1996). Males and females mature at about 1.3 and 1.6 cm ML, respectively. In Scottish waters, mature individuals are found from March to August, with a peak in maturity observed in June, indicating an extended spawning season (Yau & Boyle 1996). Size at hatching is unknown; a minimum size of less than 2 mm ML has been recorded in plankton samples (Yau 1994).

The main prey of *S. atlantica* are mysids and decapod shrimps, usually taken near the seabed during dawn and dusk (Yau 1994). *Sepiola atlantica* appears to be the most common cephalopod recorded in the diet of harbour porpoises (Santos et al. 2004, 2005b).

Sepiola aurantiaca

Biogeographic distribution The golden bobtail *Sepiola aurantiaca* (Jatta, 1896) is a neritic, nectobenthic species occurring in moderate, shallow coastal waters and continental shelf areas and is distributed in the eastern Atlantic and North Sea, from the French coast (45°N) to southern Norway

(60°N) (Yau 1994). It occurs in shallow to moderate depths of 0–150 m, most common around 40 m depth.

Biology and ecology A maximum size of 2 cm ML has been reported for *S. aurantiaca* (Yau 1994). The precise timing of spawning is unknown, but juveniles have been found during August–September in Scottish waters, suggesting a similar pattern to *S. atlantica*, which spawns during summer months (Yau 1994). Occasionally, large numbers of *S. aurantiaca* are caught in demersal trawls, in association with foliaceous (flustridian) bryzoans (Yau 1994).

Cuttlefishes

Cuttlefishes (Sepiida) are small- to medium-sized decapods of commercial importance. They possess a unique, internal porous structure known as cuttlebone, which is used to regulate buoyancy by adjusting its internal gas-liquid ratio. Cuttlefish have highly developed eyes capable of perceiving polarised light. One genus and three species of cuttlefish are found in the north-eastern Atlantic.

Sepia elegans

Biogeographic distribution The elegant cuttlefish *Sepia elegans* (Blainville, 1827) is a neritic, demersal species occurring in moderately warm shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Namibia (21°S) to the west coast of Scotland (55°N). It is also found in the southern North Sea and throughout the Mediterranean (Roper et al. 1984). It is a sublittoral species, inhabiting soft (sand-mud) bottoms at depths of up to 600 m, although records deeper than 400 m are rare and depth may be a limiting factor for the species (Ward & von Boletzky 1984).

Biology and ecology *Sepia elegans* is a relatively small cuttlefish, with males and females measuring up to 7 and 8 cm ML, respectively, and weighing 50–60 g (Adam 1952). Male and female *S. elegans* begin to mature at 2 and 3 cm ML, respectively (Guerra & Castro 1989). However, most of the population matures at a greater size, at an age of about 1 yr. Mature females carry about 250 eggs and spawn at temperatures of 13–18°C (Mangold-Wirz 1963). The eggs are relatively large (0.5 cm) and usually attached to hard substrata (sea fans, shells corals) on muddy bottoms (Mangold-Wirz 1963). Juvenile *S. elegans* are benthic immediately after hatching.

Mature individuals (both sexes) are present throughout the year, indicating that spawning and recruitment events may be continuous for this species, although small peaks in recruitment have been observed in some Mediterranean waters (Jereb & Ragonese 1991b). In some areas in the Mediterranean, male and female *S. elegans* overwinter in deep water (>200 m) and migrate into shallower waters in spring–summer to spawn (Mangold-Wirz 1963, Guerra 1992, Belcari 1999). However, in other areas, no seasonal migratory patterns have been observed (Jereb & Ragonese 1991b). *Sepia elegans* has also been recorded in brackish, estuarine environments of low salinities (18–25%), indicating a relatively high degree of tolerance (Guerra 1992, Unsal et al. 1999).

Sepia elegans is a small but efficient benthic predator, feeding on small fish, crustaceans and polychaetes (Reid & Jereb 2005). No size or seasonal effects on diet composition have been observed for this species (Guerra 1985, Castro & Guerra 1990), although males and females appear to have slightly different feeding rates and habits (Bello 1991).

Sepia officinalis

Biogeographic distribution The common cuttlefish *Sepia officinalis* (Linnaeus, 1758) is a neritic, demersal species occurring in moderately warm, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from the north-western coast of Africa (16°N) to the North Sea (60°N). However, it is typically found only in the southern North Sea and further south (<55°N). It also occurs throughout the Mediterranean (Roper et al. 1984). In the English Channel and Bay of Biscay, *S. officinalis* undertakes considerable seasonal migrations, wintering in deep offshore waters (<200 m) and moving inshore to shallow grounds during spring–summer to spawn (Mangold-Wirz 1963, Gi Leon 1982, Najai 1983, Wang et al. 2003). It is currently the most important exploited cephalopod in British waters, with the fishery being primarily located in the English Channel (Anonymous 2005).

Biology and ecology *Sepia officinalis* has a lifespan of up to 2 yr, depending on the timing of the reproductive cycle. It is a relatively large sepioid, with males growing larger than females and measuring up to 49 cm ML and weighing up to 4 kg. Specimens caught in the English Channel typically range from 10 to 22 cm ML. *Sepia officinalis* is semelparous and spawns intermittently, in shallow waters, typically at depths less than 30 m (von Boletzky 1983, Boucaud & Daguzan 1990, Boucaud-Camou et al. 1991). Male and females mature over considerable size ranges, at 6–14 and 11–25 cm ML, respectively. Female *S. officinalis* produce between 150 and 4000 eggs, depending on their size at maturity. Most individuals spawn during spring and summer, although there is also some winter spawning activity in the North Atlantic. Hatching follows from midsummer to autumn (von Boletzky 1983, Le Goff & Daguzan 1991, Dunn 1999). Mature males and large mature females (~18 mo old) move inshore during early spring to reproduce. These are later followed in summer by smaller mature females (14–16 mo old). Adult cuttlefish concentrate in coastal spawning grounds, mainly along both sides of the English Channel and on the French Atlantic coast.

Cuttlefish eggs are black and relatively large (measuring 12–14 mm) and are attached in grape-like clusters to various substrata fixed on the seabed. Embryonic development in this species varies with temperature and ranges from 40 to 45 days at 20°C and 90 to 90 days at 15°C. *Sepia officinalis* hatchlings range in size from 6 to 9 mm ML (von Boletzky 1983). In late autumn, juveniles migrate from inshore nursery grounds to deeper waters offshore, where they overwinter. Recent studies indicate that English Channel and Bay of Biscay cuttlefish may be genetically distinct and therefore should be considered as separate stocks (Le Goff & Daguzan 1991, Pawson 1995, Dunn 1999).

Sepia officinalis actively preys on small crabs, shrimps, demersal fishes, other cephalopods and polychaetes. Individuals change from feeding on mainly crustaceans to more fish as they grow larger. Cannibalism occurs at all sizes. Daily feeding rates range from 5 to 30% of body weight, depending on size and temperature (Castro & Guerra 1990, Guerra 1992). *Sepia officinalis* is itself consumed by a large number of marine predators. It has, for example, been found in the stomachs of cetaceans (e.g., *Grampus griseus*) (Clarke & Pascoe 1985), pinnipeds (e.g., *Monachus monachus* (Salman et al., 2002), *Arctocephalus pusillus* (Castley et al. 1991)) and sharks (e.g., *Prionace glauca*) (Clarke & Stevens 1974), *Mustelus mustelus* (Morte et al. 1997)) (Table 6).

Sepia orbignyana

Biogeographic distribution The pink cuttlefish *Sepia orbignyana* (Férussac, 1826) is a neritic, demersal species occurring in moderately warm, shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from southern Angola (17°S) to the west coast of Scotland (55°N). It is also found in the southern North Sea and throughout the Mediterranean (Roper et al. 1984). A maximum depth range of 15–565 m has been reported for this species (Belcari & Sartor 1993, Cuccu et al. 2003), although records outside the 25- to 450-m range are extremely rare (Jereb & Ragonese 1991b, Casali et al. 1998). It is particularly abundant over sand-mud bottoms at depths of 50–250 m (Mangold-Wirz 1963, Jereb & Ragonese 1991b, Casali et al. 1998).

Biology and ecology *Sepia orbignyana* is a relatively small cuttlefish, with males and females measuring up to 10 and 12 cm ML, respectively (Mangold-Wirz 1963). There have been no reports of *S. orbignyana* reproducing in U.K. waters. In the Mediterranean, the spawning period is continuous, with peaks of intense activity observed between spring and autumn (Jereb & Ragonese 1991b, Wurtz et al. 1991, Belcari & Sartor 1993). Mature female *S. orbignyana* carry around 400 eggs (Roper et al. 1984). The eggs measure 7–9 mm, are off-white or grey in colour and more elongate than those of *S. officinalis* (Mangold-Wirz 1963). Based on aquarium studies, the newly hatched juveniles measure 6 mm ML and become benthic immediately, either swimming just above the bottom or crawling over short distances (von Boletzky 1988). Recruitment appears to be continuous throughout the year, with peaks in spring–autumn (Jereb & Ragonese 1991b, Wurtz et al. 1991). Female *S. orbignyana* grow slightly faster than males, rates of 2.9 and 3.0 mm ML per month have been reported for males and females, respectively (Jereb & Ragonese 1991b). Maturation occurs at about 3.5 and 6.5 cm ML for males and females, respectively (Belcari & Sartor 1993). *Sepia orbignyana* feeds on small crustaceans and fish (Auteri et al. 1988).

Incirrate octopods

Incirrate (non-finned) octopods are highly developed, small- to large-sized cephalopods, characterised by eight arms and lacking the paired head fins, tentacles and rigid internal supporting structures found in decapods (squid, bobtails, cuttlefish). Octopus arms are usually equipped with rows of suckers. Unlike squid suckers, octopus suckers lack rings or hooks and perform as simple suction cups. Incirrate octopods dominate the benthic cephalopod fauna at depths of 500–1500 m (Collins et al. 2001). Six genera and six species of incirrate octopods are found in the north-eastern Atlantic:

Bathypolypus arcticus

Biogeographic distribution The spoonarm octopus *Bathypolypus arcticus* (Prosch, 1847) is a deep-water benthic species occurring in the cool oceanic waters of the northern Atlantic. It is known to occur over a wide geographic area, between 25 and 80°N, at depths of 250–2700 m (Collins et al. 2001). In U.K. waters, it has been recorded in Rockall Trough and the Faroe-Shetland Channel (Collins et al. 2001).

Biology and ecology *Bathypolypus arcticus* is a relatively small octopod; the largest specimens recorded are 10 cm ML, but most are less than 6 cm ML (Roper et al. 1984). In the wild, *B. arcticus* is known to feed on a wide range of invertebrates, including various bivalves, crustaceans, cumaceans, foraminiferans, gastropods, polychaetes and sipunculids (von Boletzky & Hanlon 1983). In laboratory studies, it has been maintained on a diet of polychaetes and amphipods (*Gammarus* spp.) (von Boletzky & Hanlon 1983). *Bathypolypus arcticus* is itself preyed on by a number of fish species, including *Anarhichas lupus*, *Coryphaenoides berglax*, *Gadus morhua*, *Merluccius merluccius*, *Melanogrammus aeglefinus*, *Reinhardtius hippoglossoides*, *Sebastes marinus*, *Xiphias gladius* (Grieg 1930, Scott & Tibbo 1968, Dexter 1969, Macalaster 1976) and seals (*Erignathus barbatus*, *Phoca groenlandica*) (Klages 1996, Hjelset et al. 1999).

Benthoctopus piscatorum

Biogeographic distribution The octopus *Benthoctopus piscatorum* (Verrill, 1879) (no common name) is a deep-water benthic species occurring in the cool oceanic waters of the northern Atlantic, between 39 and 78°N. It has been recorded in Scottish waters (Boyle et al. 1998), around the Faroe-Shetland channel (Russell 1922) and in the Rockall Trough (Collins et al. 2001). In the last, a depth range of 1400–2520 m was reported for this species (Collins et al. 2001).

Biology and ecology A maximum size of 4 cm ML is reported for this species (Roper et al. 1984), but this is based on limited information. Collins et al. (2001) identified three putative species of *Benthoctopus* (possibly including *B. piscatorum*) from samples taken in deep waters around Rockall Bank. Remains of *B. piscatorum* have apparently been found in the stomach contents of two predatory fish species (*Melanogrammus aeglefinus*, *Gadus morhua*) (Grieg 1930).

Eledone cirrhosa

Biogeographic distribution The curled octopus *Eledone cirrhosa* (Lamarck, 1798) is a neritic, nectobenthic species occurring in warm and cool shallow coastal waters and continental shelf areas and is widely distributed in the eastern Atlantic, from Morocco (25°N) to the Norwegian Sea (67°N). It is also found throughout the Mediterranean (Roper et al. 1984). Collins et al. (2001) reported depth records of down to 450 m, but it is generally found 50–300 m deep on a variety of seabed types, ranging from soft muds to rocky bottoms (Boyle 1983). In British waters, it appears to be very common in shallow coastal waters to the west of Scotland.

Biology and ecology *Eledone cirrhosa* is a small- to medium-sized octopus. Individuals of about 18 cm ML have been reported in the Mediterranean and occasionally in Portuguese waters (Belcari & Sartor 1999, unpublished data). Elsewhere, sizes greater than 16 cm ML are rare for this species. Females tend to grow larger than males; the latter may reach more than 13 cm ML but generally reach less than 12 cm ML. Although *E. cirrhosa* is a short-lived, semelparous species (Mangold-Wirz 1963, Guerra 1992), it exhibits considerable plasticity in its life cycle throughout its geographic range. In the North Sea, a combination of 1- and 2-yr cycles, based on individual growth and maturation rates, has been proposed (Boyle & Knobloch 1983, Boyle et al. 1988). In the Mediterranean, however, 2- and 3-yr cycles have been proposed for this species based on individual growth and maturation studies and length-frequency analyses of different local stocks (Mangold-Wirz 1963, Lefkatidou & Papaconstantinou 1995, Cuccu et al. 2003, Orsi Relini et al. 2006).

Eledone cirrhosa exhibits seasonal maturation patterns that vary with locality (Belcari et al. 1990). In the Mediterranean, sexual maturity occurs earlier (spring–summer) in western waters than further east (summer–autumn) (Belcari & Sartor 1999, Lefkatidou et al. 2000). In the North Sea, sexual maturity is observed from July to September, with spawning occurring shortly thereafter (Boyle 1983, Boyle & Knobloch 1983). In Portuguese waters spawning occurs from May to August at a mean size of 12 cm (unpublished data). Fecundity estimates for *E. cirrhosa* range from 2000 to 9000 eggs, depending on locality (Boyle et al. 1988). Few spent females have been recovered after spawning, indicating post-reproductive mortality (Mangold-Wirz 1963, Guerra 1992, Tursi et al. 1995). Fertilised eggs hatch after 3–4 mo, usually during April–July, in temperatures of 14–18°C. Young *E. cirrhosa* are less than 5 mm ML and are planktonic for several weeks before settling on the seabed (Mangold et al. 1971).

The diet of *E. cirrhosa* is composed mainly of decapod crustaceans, particularly alpheids and brachyurans (Auteri et al. 1988, Sánchez 1981, Boyle & Knobloch 1983). Cephalopod eggs and other molluscs are occasionally found in stomach contents of *E. cirrhosa*, and cannibalism has also been reported (Moriyasu 1981, Guerra 1992). A number of marine mammal and fish species are considered to be important predators of *E. cirrhosa* (Santos et al. 1999, Brown et al. 2001, Velasco et al. 2001) (Table 6). *Eledone cirrhosa* is an important component of the summer diet of harbour seals in the Moray Firth in some years (Tollit et al. 1998) as well as a prominent component of the diet of some cetaceans (e.g., *Grampus griseus* and to a lesser extent *Hyperoodon ampullatus*) (Pierce et al. 2007).

Graneledone verrucosa

Biogeographic distribution The octopus *Graneledone verrucosa* (Verrill, 1881) (no common name) is a deep-water benthic species occurring in the cool oceanic waters of the northern Atlantic, between 30°S and 62°N. It occurs in depths of 950–2500 m. It has been recorded in Scottish waters, the Faroe-Shetland Channel, Rockall Trough, Porcupine Seabight and off the coast of Norway (Grieg 1930, Boyle et al. 1998, Collins et al. 2001).

Biology and ecology Virtually nothing is known about the biology and ecology of *G. verrucosa*. A maximum size of 10 cm ML is reported for this species (Robson 1932), but this is based on a few records. There is no published information available on the prey or predators of *G. verrucosa*.

Haliphron atlanticus

Biogeographic distribution The seven-arm octopus *Haliphron atlanticus* (Steenstrup, 1861) is a cosmopolitan, deep-water, benthic species occurring in the temperate and tropical oceanic waters of the central and northern Atlantic, between the equator and 65°N (Norman 2000). Small numbers of *H. atlanticus* have been recorded off the coasts of Ireland, Shetland and Norway at depths of 100–200 m (Collins et al. 1995b, 1997b).

Biology and ecology Virtually nothing is known about the biology and ecology of *H. atlanticus*. Maximum sizes of 40 cm ML and 200 cm TL have been reported for this species (Norman 2000), but these are based on a few records. In U.K. waters, remains of *H. atlanticus* have been recovered from the stomachs of stranded sperm whales (Clarke & Pascoe 1997, Santos et al. 2002). In other parts of the world, *H. atlanticus* is sometimes predated by the wandering albatross (*Diomedea exulans*) (Xavier et al. 2003) and the Hawaiian monk seal (*Monachus schauinslandi*) (Goodman-Lowe 1998).

Octopus vulgaris

Biogeographic distribution The common octopus *Octopus vulgaris* (Cuvier, 1797) is a neritic, nectobenthic species occurring in abundance in moderately warm, shallow coastal waters (<200 m deep) and continental shelf areas of the north-eastern Atlantic and Mediterranean. It has a huge geographic range (presently undefined) and may in fact be a cosmopolitan species, with records in the South Atlantic and Pacific. Its northern limit appears to be the southern North Sea (55°N) (Roper et al. 1984).

Biology and ecology *Octopus vulgaris* is a relatively large-sized semelparous species, measuring up to 40 cm ML (with arms up to 140 cm in length) (Norman 2000). Maximum lifespans of 15–20 mo for males and 12–17 mo for females have been reported for this species, varying depending on locality (Sánchez & Obarti 1993, Domain et al. 2000). Captive *O. vulgaris* have recently been successfully reared through a complete life cycle, with excess food provided and a temperature range of 17–23°C maintained; a male and female achieved 1.6 kg in 339 days and 1.8 kg in 356 days, respectively (Iglesias et al. 2004).

The spawning season of *O. vulgaris* varies according to locality. In the north-eastern Atlantic populations, spawning extends throughout the year with peaks between February and July (Otero et al. 2005, Moreno et al. 2009). In Galician (north-western Spain) and north-western Portuguese waters, the spawning season is thought to be linked to the regional dynamics of coastal upwelling, so that hatchlings benefit from the greatest abundance of zooplankton but avoid the most advective months (Otero et al. 2005, Moreno et al. 2009). In the Mediterranean, the main spawning event occurs in June–July (Mangold 1987, Sánchez & Obarti 1993). The total potential fecundity of *O. vulgaris* is reported to be 70,000–600,000 oocytes per mature female (Silva et al. 2002). Mature eggs are oval shaped and relatively small, measuring 2.5 mm along the longest axis (Mangold-Wirz 1963). During spawning, female *O. vulgaris* attach eggs to hard substrata and care for them for considerable periods until they hatch. The duration of incubation for *O. vulgaris* eggs is temperature dependent, ranging from 20 to 30 days at 25°C to 100–120 days at 13°C (Mangold & von Boletzky 1987).

The duration of the early, planktonic, post-hatching phase is also influenced by temperature, ranging from 33 days at 25°C to 60 days at 21°C. *Octopus vulgaris* juveniles are still very small when they become benthic, typically at about 0.1 cm ML and weighing less than 0.2 g. *Octopus vulgaris* exhibits rapid, highly variable, non-asymptotic growth patterns (Alford & Jackson 1993, Domain et al. 2000) that appear to be partly influenced by temperature and diet (Forsythe & van Heukelem

1987, Aguado & García 2002). Individuals raised in aquaria can reach body weights of 0.5–0.6 kg within 6 mo of hatching (Itami et al. 1963, Imamura 1990, Villanueva 1995, Iglesias et al. 2004).

Octopus vulgaris paralarvae feed on zooplankton and the abundance of this food source is thought to be a limiting factor affecting stock recruitment success. Nevertheless, according to Iglesias et al. (2006), greater prey densities have not produced a greater number of attacks under culture conditions. Therefore, to reduce time and economise on costs, it is advisable to fit the prey quantity to the effective consumption of paralarvae. Iglesias et al. (2007) concluded that satisfactory results at around 1 mo culture were attained using *Artemia* enriched with *Nannochloropsis* sp. Adult and juvenile *Octopus vulgaris* are active hunters and prey on a wide variety of fish, crustaceans, molluscs and polychaetes. Table 7 lists recorded prey of *O. vulgaris* from the north-eastern Atlantic. A large number of different prey items have also been recorded for the Mediterranean (Guerra 1978, Sánchez & Obarti 1993, Quetglas et al. 1998b). Significant predators of *O. vulgaris* include various marine mammals, birds and other cephalopod species (Hanlon & Messenger 1998). Mammal predators include *Delphinus delphis*, *Grampus griseus*, *Globicephala melas* and *Tursiops truncatus* (Blanco et al. 2001, López 2002, Santos et al. 2004). Certain fish species, including *Trisopterus* spp., Sparidae and Serranidae are significant predators of the planktonic stages of *Octopus vulgaris*, whilst others, including *Conger conger* and *Muraena helena*, prey on the benthic juvenile and adult stages (Table 6). Available literature on the biology of the planktonic stages of *Octopus vulgaris* and other incirrate octopod species was recently reviewed by Villanueva & Norman (2008).

Cirrate octopods

Cirrate (finned) octopods are highly specialised deep-water cephalopods that are poorly understood (Collins & Villanueva 2006). They are characterised by possession of eight arms and paired head fins. They include some of the largest invertebrates in the bathyal and abyssal megafauna (Gage & Tyler 1991). Although cirrate octopods are usually found in depths greater than 300 m and dominate the benthic cephalopod fauna at depths greater than 1500 m (Collins et al. 2001, Collins & Villanueva 2006), very little is known about their biogeography, biology and ecology. A few behavioural studies of cirrate octopods, using deep-water video cameras, have been undertaken (Vecchione 1987, Vecchione & Young 1997, Villanueva et al. 1997, Villanueva 2000, Collins & Villanueva 2006). They are apparently predated by certain marine mammal species (Santos et al. 2001a,b). At present, they are not considered to be marketable and there are no known conservation issues. Four genera and five species of cirrate octopods have been recorded in the north-eastern Atlantic (Table 8).

Opisthoteuthis grimaldii

Biogeographic distribution The cirrate octopus *Opisthoteuthis grimaldii* (Joubin 1903) is an oceanic, benthic species that appears to be relatively common in deep waters west of Scotland, where it has been recorded from 210 to 2300m (Collins et al. 2001). It is a regular by-catch in benthic trawls from the 800–1200 m depth range (Daly et al. 1998, Boyle & Daly 2000).

Biology and ecology *Opisthoteuthis grimaldii* is a relatively small species, with maximum sizes of 5 cm ML and 25 cm TL reported (Collins et al. 2001), but these are based on a few records. Body weights of 0.6–3 kg are reported for mature females (Daly et al. 1998). Boyle & Daly (2000) estimated a maximum potential fecundity of about 3000 eggs per female for this species. Based on observations of female maturation patterns and egg size distributions, Boyle & Daly (2000) concluded that, west of the Hebrides, mature female *O. grimaldii* spawned continuously throughout their growth period. No seasonal differences in female maturation during spring, autumn and winter have been observed, indicating that the timing of spawning is not closely related to season (Daly et al. 1998).

Table 7 Identified prey types and species from *Octopus vulgaris* stomach contents (Nigmatullin & Ostapenko 1976, Guerra 1978)

		Geographic area	
Group	Taxonomic description	NE Atlantic	Sahara Bank
Fish	Blenniidae	•	•
	Boops boops		•
	Decapterus sp.		•
	Dentex sp.		•
	Dentex macrophthalmus		•
	D. filosus		•
	Gobiidae	•	
	Labridae	•	
	Pagellus acarne		•
	P. canariensis		•
	Sardinella sp.		•
	Serranidae	•	
	Soleidae		•
	Trachinus sp.		•
	Trachurus sp.		•
	Triglidae	•	
Crustacea	Amphipoda		•
	Atelecyclus sp.	•	
	Cancer pagurus	•	
	Carcinus maenas	•	
	Eriphia verrucosa	•	
	Inachus sp.	•	
	Isopoda		•
	Liocarcinus puber	•	
	Liocarcinus sp.	•	
	Macropodia sp.	•	
	Maia squinado	•	
	Ostracoda		•
	Pachygrapsus marmoratus	•	
	Palaemon sp.	•	
	Polybius henslowii	•	
	Stomatopoda		•
Mollusca	*Alloteuthis subulata*		•
	Cymbium sp.		•
	Ensis ensis	•	
	Loligo vulgaris		•
	Mytilus galloprovincialis	•	
	Octopus vulgaris	•	
	Octopus sp.		•
	Sepia sp.	•	•
Polychaeta	Aphroditidae		•
	Polychaeta		•

Opisthoteuthis spp. feed on a variety of small, slow-moving benthic polychaetes and crustaceans. They in turn appear to be preyed on by large fish, sharks and marine mammals (Collins & Villanueva 2006).

Table 8 Cirrate octopod species recorded in U.K. waters

Species	ML[a] (cm)	TL[a] (cm)	Area record[b]
Cirroteuthis massyae (Grimpe, 1920)	19	30	Rockall Trough
Cirroteuthis muelleri (Eschricht, 1836)	8	150	West of Shetland
Grimpoteuthis wulkeri (Grimpe, 1920)	12	40	Rockall Trough
Opisthoteuthis grimaldii (Joubin, 1903)	5	25	Rockall Trough
Stauroteuthis syrtensis (Verrill, 1879)	9	N/A	Rockall Trough

Notes: ML = mantle length; TL = total length.

[a] *Source:* Roper et al. 1984, Nesis 1987, Voss & Pearcy 1990.

[b] *Source:* Collins et al. 2001.

Other species

Virtually nothing is known about other cirrate octopod species inhabiting the deep waters of the north-eastern Atlantic. According to Collins et al. (2001), the following species often dominate cephalopod catches from waters west of Ireland and Scotland: *Opisthoteuthis massyae* (Grimpe, 1920) (870–1400 m deep), *Stauroteuthis syrtensis* Verrill 1879 (1400–3100 m), *Cirroteuthis muelleri* (Eschricht, 1836) (700–4900 m), *Cirrothauma murrayi* (Chun, 1911) (2400–4900 m), and *Grimpoteuthis wulkeri* (1800–4900 m). Reported maximum sizes of these species are provided in Table 8. Available literature on the taxonomy, ecology and behaviour of cirrate octopods around the world was recently reviewed by Collins & Villanueva (2006).

Warm-water cephalopods

Besides the 30 species listed for the north-eastern Atlantic, several other species typical of the Mediterranean and the tropical-to-subtropical eastern Atlantic have their northern distribution encroaching north-eastern Atlantic waters. Examples include the sepiolids *Sepietta obscura* (Naef 1916) and *Sepiola ligulata* (Naef, 1912) both endemic of the Mediterranean Sea (Mangold & von Boletzky 1987) and reported off the west Iberian shelf by Pereira (1996) and Guerra (1985), respectively. The deep-water octopods *Bathypolypus sponsalis* (Fischer and Fischer, 1892), *Benthoctopus ergasticus* (Fischer and Fischer, 1892), *Pteroctopus tetracirrhus* (Chiaie, 1830) and *Scaeurgus unicirrhus* (Chiaie, 1839–1841 in Férussac and D'Orbigny, 1834–1848), and the histioteuthid squids *Histioteuthis corona* (Voss and Voss, 1962), *H. hoylei* (Goodrich, 1896) and *H. meleagroteuthis* (Chun, 1910) are also recorded occasionally to the west of Iberia. On the other hand, the octopods *Octopus salutii* Verany, 1839, *Octopus defilippi* (Verany, 1851), *Opisthoteuthis calypso* (Villanueva et al. 2002) and especially *Eledone moschata* (Lamarck, 1798) are presently fairly common in Portuguese waters as well as the sepiolid *Sepiola rondeletii* (Leach, 1834) and the enoploteuthid squid *Abralia veranyi* (Rüppell, 1844) (this species only since 1998). In addition, many tropical and subtropical oceanic species, mostly cranchiids and enoploteuthids, approach the rich Iberian waters for spawning and their early stages may be found in the vicinity of the Portuguese continental shelf (listed in Moreno et al. 2009). Given that temperature is a determinant in the biogeographic distribution, many southern species are likely to advance to higher latitudes in face of global warming, resulting in the near future in important changes in the biodiversity of the north-eastern Atlantic ecosystems.

Economic importance of cephalopods in the north-eastern Atlantic

A number of north-eastern Atlantic cephalopod species are highly valued for consumption, and substantial catches of these are taken each year. During the past decade, total cephalopod landings (all species) from the north-eastern Atlantic ranged from about 41,000 to 51,000 t (Table 9). Several species are exploited, although for (Food and Agricultural Organization, FAO and International

Table 9 Total annual (tonnes) cephalopod landings (1997–2006) in the north-eastern Atlantic; categories as used in official (FAO) fishery statistics (Anonymous 2008)

	Year									
Group	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Long-fin squid	11,519	11,245	11,049	10,253	8,234	9,939	8,472	12,562	9,420	7,800
Short-fin squid	6,145	5,841	7,693	5,607	4,260	2,571	1,483	2,114	2,536	1,282
Cuttlefish	16,652	20,275	20,210	23,754	18,034	22,614	19,492	30,928	21,371	21,513
Octopods	15,801	13,043	15,718	16,500	11,461	12,831	12,191	14,195	17,906	8,999
Total	50,117	50,404	54,670	56,114	41,989	47,955	41,638	59,799	51,233	39,594

Notes: FAO = Food and Agricultural Organization.

Council for the Exploration of the Sea, ICES) fisheries statistical records, they are conveniently grouped into four broad categories: long-fin squid, short-fin squid, cuttlefish (including sepiolids) and octopods. The main species caught and marketed in Europe are *Loligo forbesi*, *L. vulgaris*, ommastrephid spp., *Sepia officinalis*, sepiolid spp., *Octopus vulgaris* and *Eledone* spp. The bulk of European catches are landed by the French, Portuguese, Spanish and U.K. fleets. These four nations, in fact, account for more than 90% of the total north-eastern Atlantic cephalopod catch.

As with all commercially exploited marine species, fishery data are imperfect. Since no quotas are set in European cephalopod fisheries, deliberate misreporting or illegal landing of catches is not a major issue. However, the low taxonomic resolution of official landings statistics, the relatively high importance of poorly recorded artisanal landings, and indeed patchy reporting of commercial landings from some ports, are issues.

Exploitation of long-fin squid

Total landings of long-fin squid (Family Loliginidae) from the north-eastern Atlantic (ICES Area) ranged from about 8,000 to 11,000 t per annum during the past decade (Table 10). The four main fishing fleets involved, based in France, Portugal, Spain and the United Kingdom, currently account for 90–95% of total landings (Figure 1a). A large portion of the total long-fin squid catch (40–50%) was landed by the French fleet. The geographical distribution of French and U.K. (1999–2002) catches is provided in Figure 2.

Table 10 Total annual long-finned squid (f. Loliginidae) landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Loligo forbesi*, *L. vulgaris* and *Alloteuthis subulata*) (Anonymous 2008)

	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Belgium	155	253	222	463	51	137	132	106	73	81
Denmark	22	48	50	20	0	0	0	0	0	0
France	4,560	4,275	5,759	5,039	4,243	5,963	5,523	6,292	5,621	5,829
Germany	4	11	6	5	0	0	58	38	24	15
Ireland	217	216	178	101	14	40	0	245	264	115
Netherlands	0	0	0	773	0	0	0	238	176	168
Portugal	1,153	1,111	375	678	899	687	236	1,526	873	96
Spain	2,253	2,186	1,728	1,371	1,489	927	748	987	872	438
Sweden	1	1	1	+	0	0	0	5	3	10
United Kingdom	3,014	3,045	2,624	1,765	539	2,184	1,775	3,125	1,514	1,351
Total (ICES)	11,379	11,146	10,943	10,215	8,234	9,939	7,527	12,562	9,420	7,100

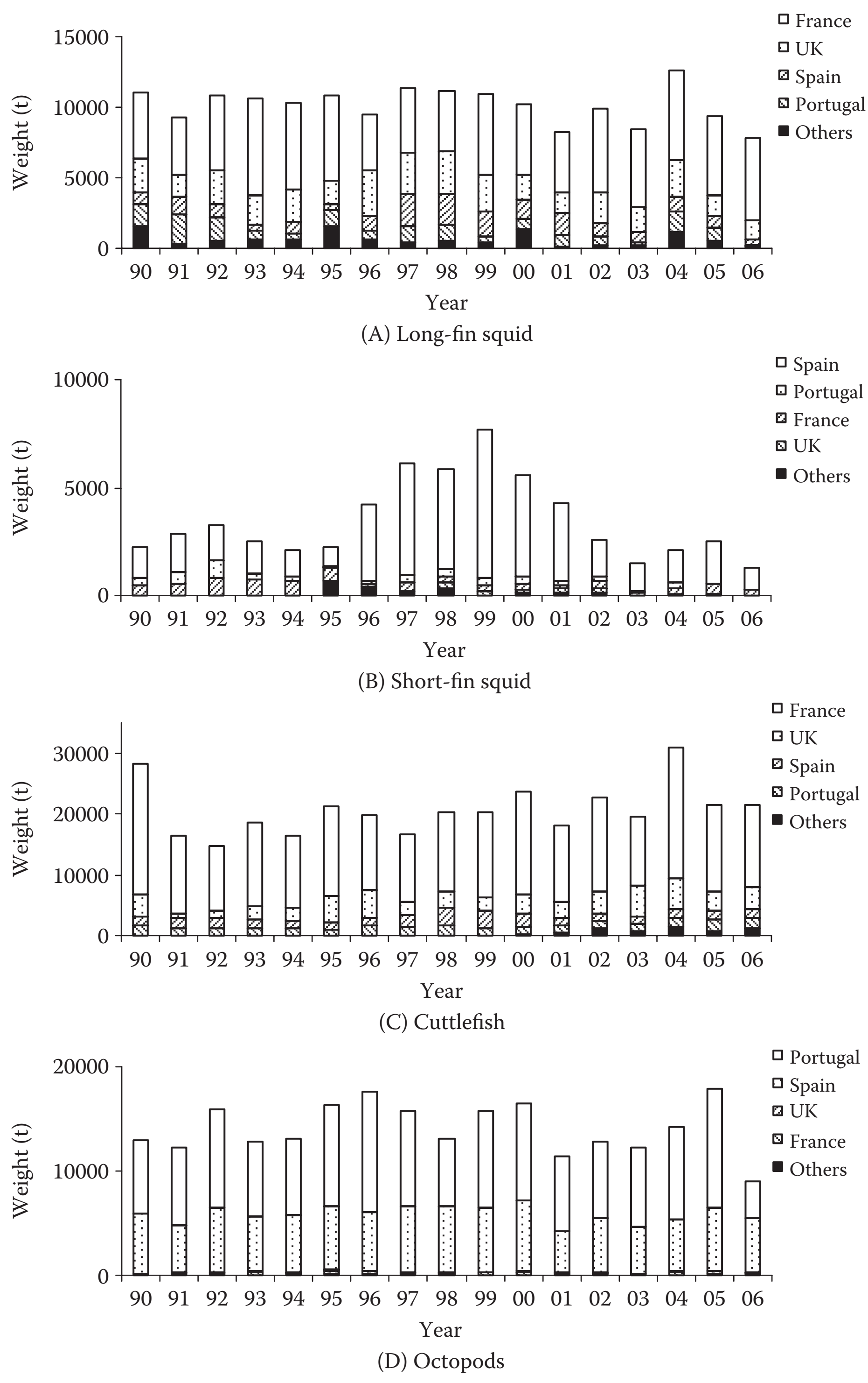


Figure 1 Total landings of cephalopods caught in the north-eastern Atlantic (International Council for the Exploration of the Sea [ICES] Area) by nation (1990–2006): (A) long-fin (loliginid) squid, (B) short-fin (ommastrephid) squid, (C) cuttlefish (including sepiolid) and (D) (incirrate) octopods (Anon. 2005, 2008).

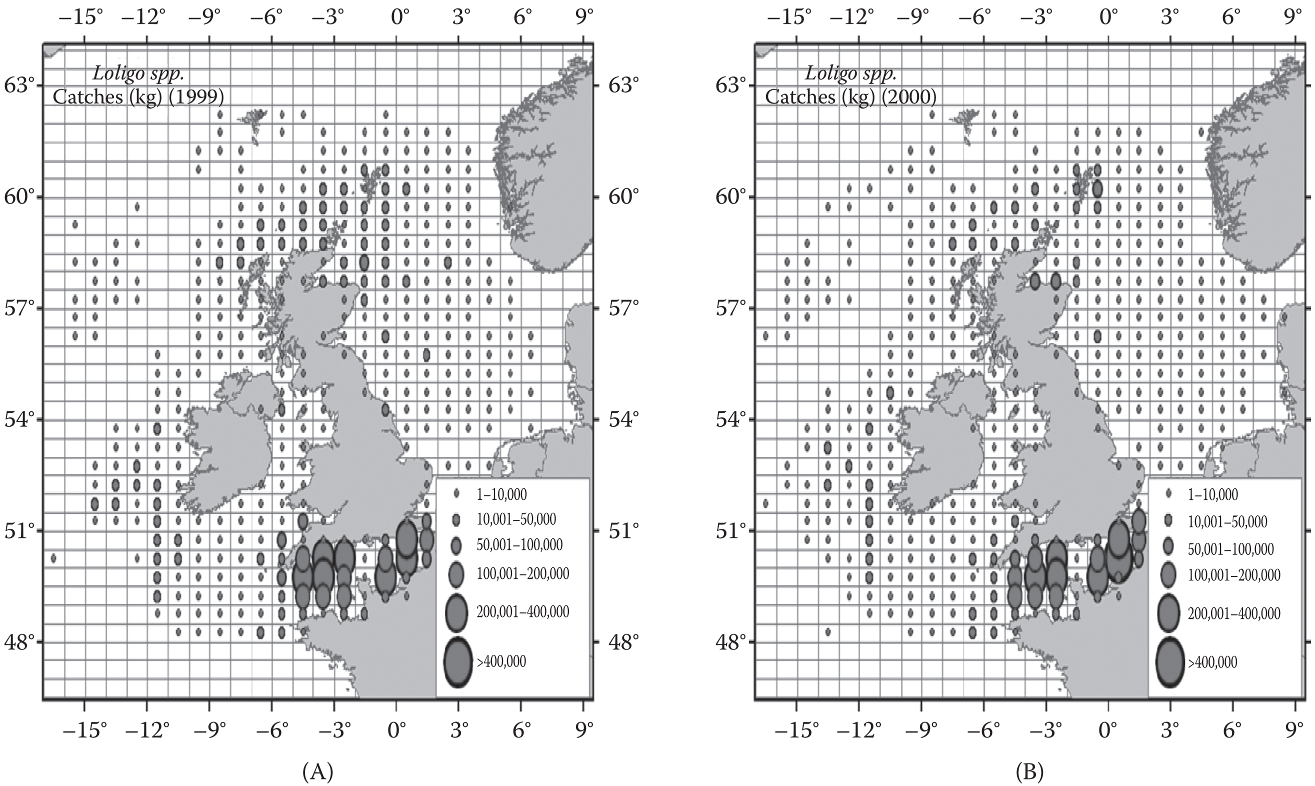


Figure 2 Maps showing distributions of annual long-fin (loliginid) squid catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005, 2008): (A) 1999, (B) 2000, (C) 2001, (D) 2002.

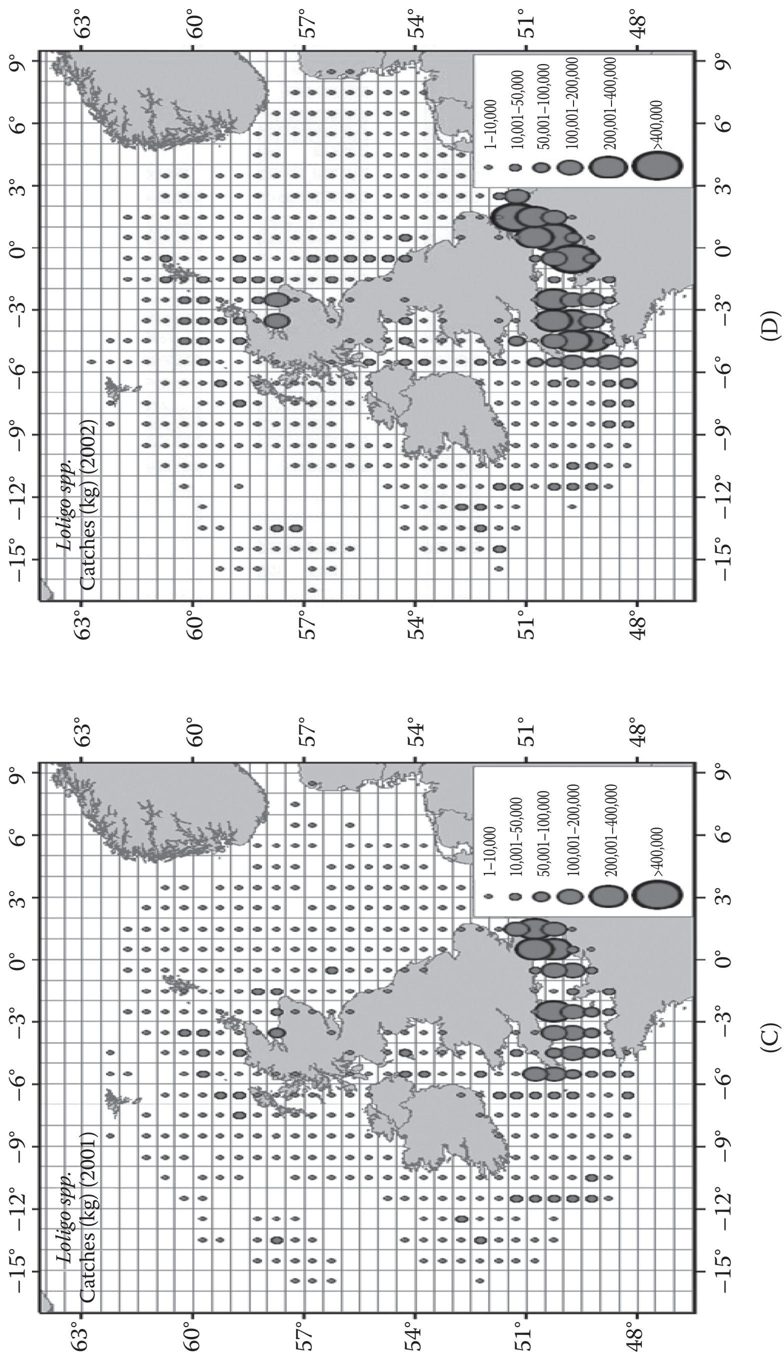


Figure 2 (continued).

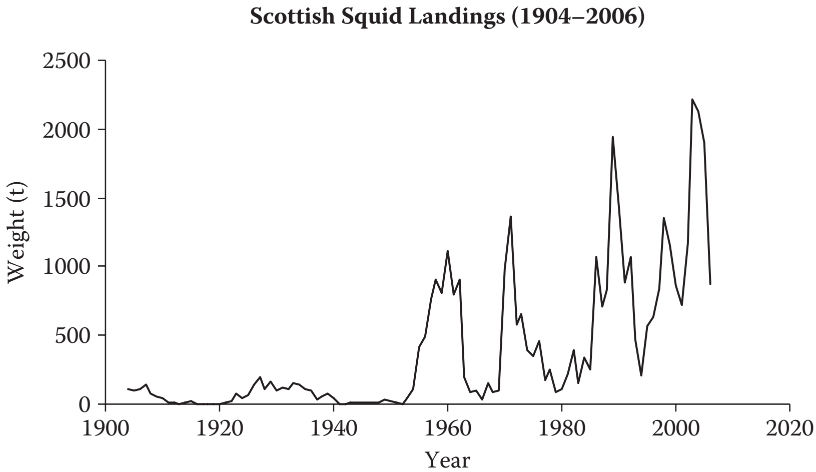


Figure 3 Scottish squid (*Loligo forbesi*) landings during period 1904–2006 (Scottish Sea Fisheries Database, Edinburgh).

Loligo forbesi is the most frequently caught squid species in U.K. waters where it forms the basis of a significant by-catch fishery (Pierce et al. 1994b), with annual landings as high as 3500 t (Collins et al. 1997a). Based on historical fishery data (Figure 3), this species appears to exhibit cyclical population trends on an appropriately decadal scale. At certain times *L. forbesi* is targeted, notably on Rockall Bank in summer (during the 1980s) Pierce et al. 1994a) and in the Moray Firth in autumn (Young et al. 2006). There is also some directed squid fishing, including jig fishing (as described by Hamabe et al. 1982), off the south coast of England, although it is not clear which species of *Loligo* is targeted. On the Spanish and Portuguese Atlantic coasts, inshore jigging catches mainly *Loligo vulgaris*, which is thought to generally occur closer inshore than *L. forbesi*, although it is also the case that *L. forbesi* is increasingly rare to the south (see Chen et al. 2006). Recently, squid fishing has attracted considerable attention in Scotland, and in 2005, small-scale directed squid fisheries were reported in several localities, including the Firth of Forth, off Aberdeen, off the islands of Skye and Lewis.

The main Scottish fishery for *L. forbesi* occurs in coastal waters and usually exhibits a marked seasonal peak around October and November, corresponding to the occurrence of pre-breeding squid (Howard 1979, Pierce et al. 1994c, Young et al. 2006).

Analysis of fishery data collected between 1980 and 1990 indicated that *L. forbesi* was widely distributed on the continental shelf and also occurred on offshore banks, notably Rockall (Pierce et al. 1994a,c). Data from trawling surveys confirm the wide distribution while also highlighting its patchy nature. Research trawling surveys record squid in U.K. waters in all seasons. Pierce et al. (1998) presented data from demersal trawl surveys along the west coast of Scotland during November (1990–1994), which showed that highest catches of *L. forbesi* occurred north of Ireland near the Stanton Bank area (~3200/h in one haul). Good catches occurred north and west of the Hebrides and in Donegal Bay, whereas catches south and west of Ireland were relatively poor. Data collected from research cruises carried out in 2004 showed highest catch numbers from waters to the west of the Isle of Man. Recent analysis of long-term trends in abundance points to the possible influence of oceanographic conditions on abundance of *L. forbesi* in Scottish waters (Pierce & Boyle 2003) and suggests that the relative importance of summer and winter breeding populations may show marked shifts on a decadal timescale (Zuur & Pierce 2004, Pierce et al. 2005).

Loligo vulgaris is also landed mainly as a by-catch of multispecies demersal and pelagic trawl fisheries in the north-eastern Atlantic and Mediterranean (Figure 4a). In U.K. waters, the English

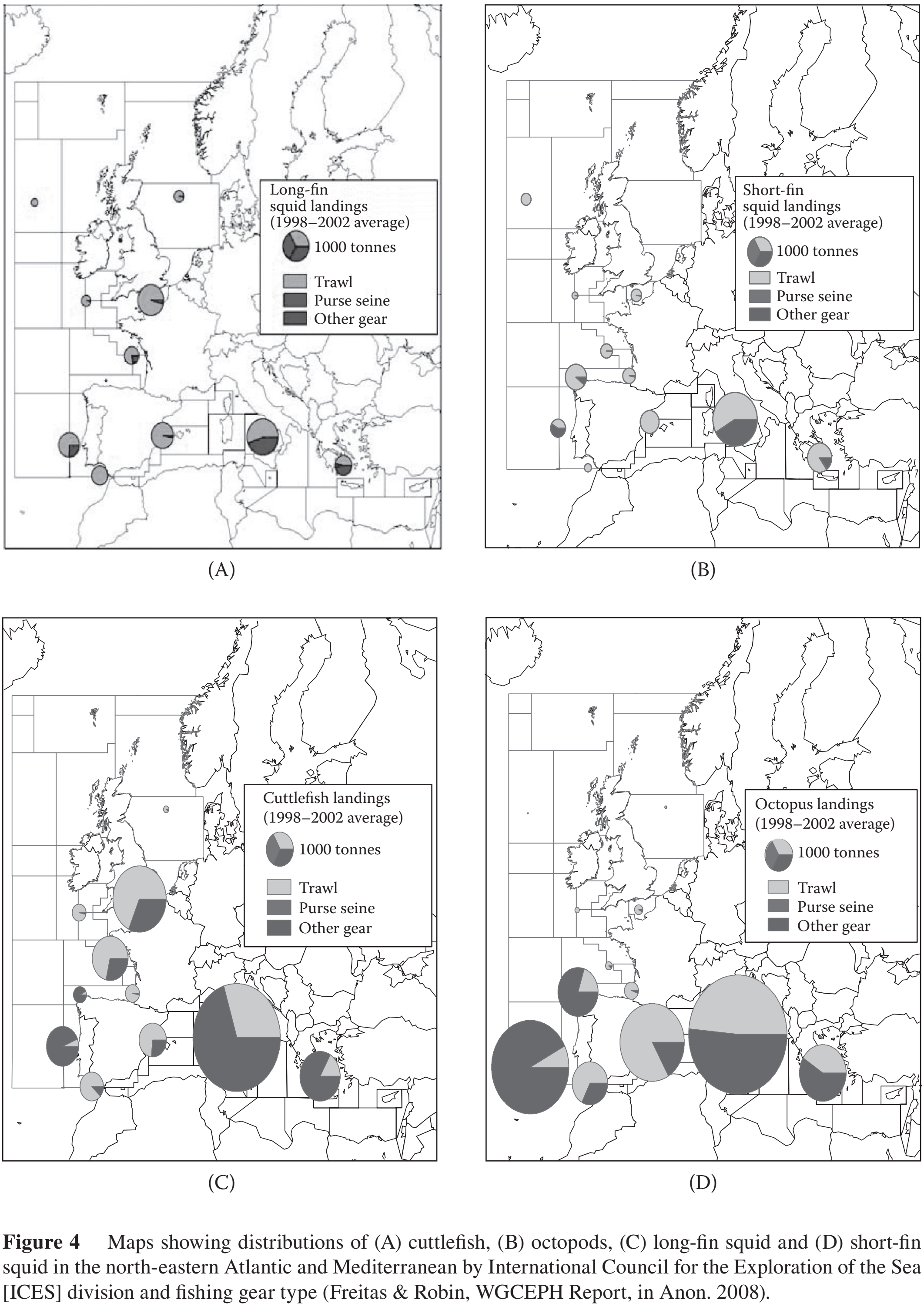


Figure 4 Maps showing distributions of (A) cuttlefish, (B) octopods, (C) long-fin squid and (D) short-fin squid in the north-eastern Atlantic and Mediterranean by International Council for the Exploration of the Sea [ICES] division and fishing gear type (Freitas & Robin, WGCEPH Report, in Anon. 2008).

Channel and off the north-western coast of Spain, it is usually landed in mixed catches with *L. forbesi*. In these areas where the two species overlap, the landing statistics refer to *Loligo* spp. (Robin & Boucaud-Camou 1993). Therefore, the overall catch of *L. vulgaris* in U.K. waters is currently unknown, although it is believed to be significant. Further south, *L. vulgaris* is an important secondary target species in the Saharan Bank trawl fishery (Raya et al. 1999) and it is also targeted by a number of small, inshore, directed hand-jig fisheries operating from the coasts of Spain and Portugal (Guerra et al. 1994). Landings from the small-scale fisheries are poorly reported but in north-western Spain they may be of a similar order of magnitude to the trawl by-catch landings (Pierce 1999). In Greek and Portuguese waters, spawning aggregations of *L. vulgaris* are also targeted using beach seines, gill nets and trammel nets.

Substantial catches of *Alloteuthis* spp. are also landed in southern Spain, although they are often mixed with *Loligo* spp. and there are no separate, quantitative records currently available (Anonymous 2008).

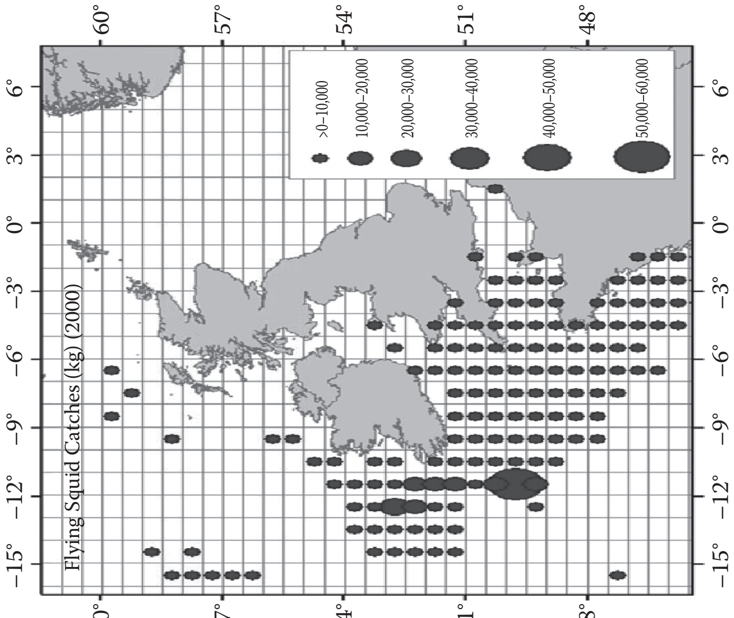
Exploitation of short-fin squid

Total landings of short-fin squid (Family Ommastrephidae) from the north-eastern Atlantic ranged from about 3000 to 10,000 t per annum during the past decade (Table 11). Landings have generally been sporadic, although landings from Spain and Portugal have been fairly consistent, at more than 1000 t per annum (Figure 1b). However, very large catches (>4000 t) were landed by the Danish and Norwegian fleets in 2004. French and U.K. landings of short-fin squid (1999–2002) are provided in Figure 5.

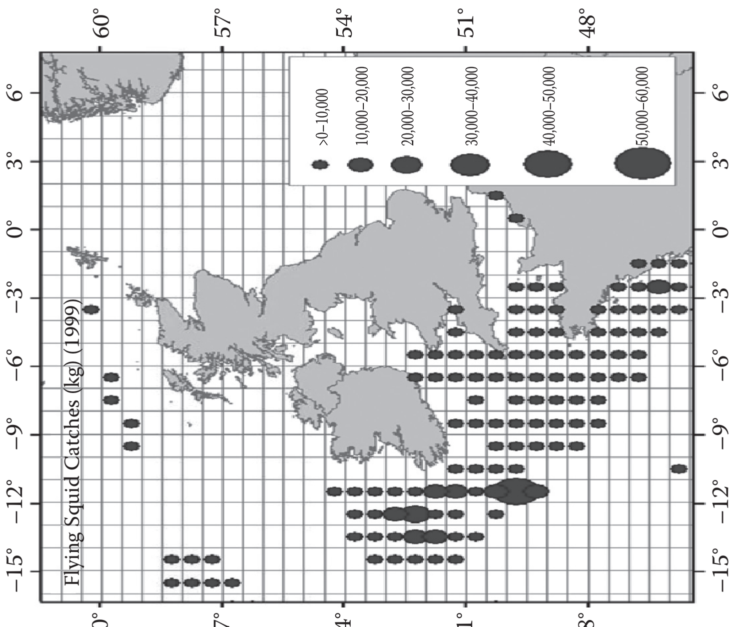
Ommastrephid squid stocks from the north-eastern Atlantic are harvested throughout the year by Spanish and other European fleets. Figure 4b shows the distribution of ommastrephid catches in the north-eastern Atlantic and Mediterranean. They are usually taken as by-catch during demersal and pelagic trawling operations and in gill and trammel nets, in depths of 100–400 m (Mangold & von Boletzky 1987, Jereb & Ragonese 1991a, González et al. 1994, González et al. 1996a). Different species (predominantly *Illex coindetii* and *Todaropsis eblanae*, occasionally *Ommastrephes bartramii* and *Todarodes sagittatus*) are often landed together as mixed 'short-fin' squid. Consequently, landings data for individual ommastrephid species are often unavailable. Nevertheless, ommastrephid

Table 11 Total annual short-fin squid (f. Ommastrephidae) landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Illex coindetii*, *Todarodes sagittatus*, *Todaropsis eblanae* and *Ommastrephes bartramii*) (Anonymous 2008)

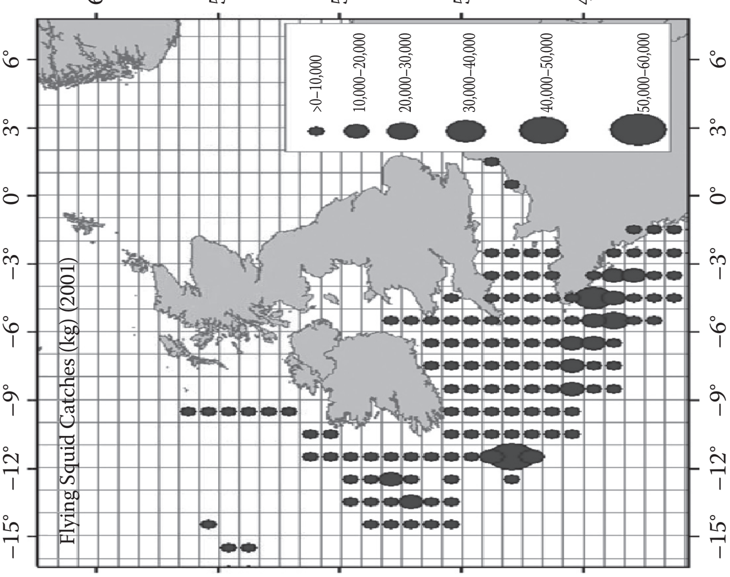
	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Denmark	0	0	0	0	0	0	16	4360	0	0
France	375	216	289	266	128	358	94	235	456	230
Iceland	5	4	3	1	0	0	0	1	0	0
Ireland	0	347	9	112	135	154	0	77	36	24
Norway	190	2	+	+	0	0	0	4642	0	0
Portugal	364	388	314	323	232	205	119	321	0	0
Spain	5185	4591	6874	4719	3573	1685	1253	1471	2023	1018
United Kingdom	26	293	204	186	193	169	1	27	20	10
Total (ICES)	6145	5841	7693	5607	4260	2571	1348	2114	2536	1282


Flying Squid Catches (kg) (2000)
>0–10,000
10,000–20,000
20,000–30,000
30,000–40,000
40,000–50,000
50,000–60,000
−15°
−12°
−9°
−6°
−3°
0°
3°
6°
60°
57°
54°
51°
48°

(B)


Flying Squid Catches (kg) (1999)
>0–10,000
10,000–20,000
20,000–30,000
30,000–40,000
40,000–50,000
50,000–60,000
−15°
−12°
−9°
−6°
−3°
0°
3°
6°
60°
57°
54°
51°
48°

(A)



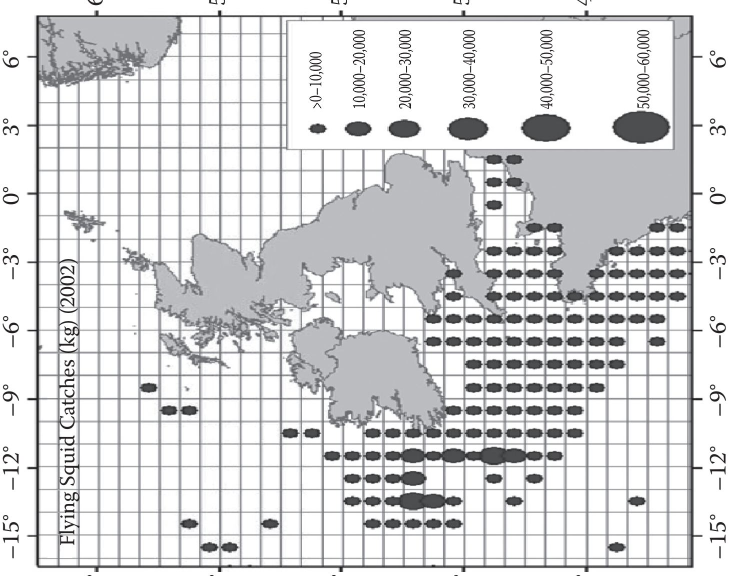


Figure 5 Maps showing distributions of annual short-fin (ommastrephid) squid catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005): (A) 1999, (B) 2000, (C) 2001, (D) 2002.

squid stocks are now regarded to be a high-value fishery resource (Jereb & Ragonese 1995). During the past decade, the total ommastrephid catch in European waters has ranged from 3000 to 7000 t annually, with U.K. fleets accounting for up to 300 t per annum (Anonymous 2005).

A significant, directed fishery for *T. sagittatus* has previously been operated by north European countries, notably Norway, during 1980–1987. During this period, *T. sagittatus* invaded coastal waters of the Faroe Islands, south-western Iceland and north-western Norway in late summer and autumn, with some squids migrating into the North Sea (Sundet 1985). Large numbers of *T. sagittatus* were also taken as by-catch by demersal trawlers around Shetland at this time (Joy 1990). Very large numbers of *T. sagittatus* can be caught in U.K. waters on occasion, particularly around Shetland and off the west coast of Scotland. However, since there is no current market for this species in Scotland, it is usually discarded by Scottish fishing vessels (Joy 1989). The directed fishery in Norwegian waters has not operated since 1990 due to a decline in seasonal invasions, although catches of 352 and 190 t of short-fin squid, presumed to be *T. sagittatus*, were reported in 1995 and 1997, respectively (Anonymous 2005).

At present, *Illex coindetii*, *Ommastrephes bartramii* and *Todaropsis eblanae* are not exploited commercially by U.K. fleets and consequently there is little information available on their abundance in U.K. waters. However, reports from adjacent waters indicate that they can at times be widespread and abundant in the north-eastern Atlantic and may represent a significant potential fishery resource. The North Atlantic stock of *Ommastrephes bartramii* is estimated to be about 2.5 million t (Nigmatullin et al. 1991); this species is already exploited commercially in the Pacific (Bower & Ichii 2005). The occurrence of *Todaropsis eblanae* in the Irish Sea was reported by Collins et al. (1995a). This species was occasionally caught during research cruises carried out in the spring, summer and autumn of 1992 and 1993. Lordan et al. (2001) studied the distribution and abundance of cephalopod species caught during demersal trawls surveys west of Ireland and in the Celtic Sea. The most numerous species in catches was *Loligo forbesi* followed by *Todaropsis eblanae,* which was concentrated close to the shelf break in most years. However, in 1994 there were also large catches off the south coast of Ireland. It is also reported to be superabundant in the North Sea in some years, a phenomenon possibly linked to hydrographical anomalies such as influxes of warm high-salinity Atlantic seawater (Hastie et al. 1994).

Exploitation of other squid species

Aside from loliginids and ommastrephids, there are a number of other squid species in U.K. waters that may have some fishery potential. *Gonatus fabricii*, for example, is considered to be the most abundant squid of Arctic and subarctic waters (Nesis 1965, Kristensen 1984). Spawning concentrations of *G. fabricii* may be a valuable, exploitable resource, based on the large catches of subadults frequently taken by midwater trawlers operating in the Norwegian Sea (Wiborg et al. 1984, Bjørke & Gjøsæter 2004). Using a fishery production model, Bjørke & Gjøsæter (1998) estimated the spawning stock biomass of *G. fabricii* in the Norwegian Sea to be about 5 million t. Bjørke (2001) estimated the annual consumption of *G. fabricii* by sperm whales alone to be about 385,000 t. Santos et al. (1999) estimated the annual consumption of *Gonatus* spp. in Norwegian waters by sperm whale to be 400,000–520,000 t. In Greenland, Inuit fishermen use *G. fabricii* as bait in local cod and shellfish fisheries. It is also frequently taken as by-catch in shrimp trawls. The high lipid content of the digestive gland (>60%) makes this species potentially suitable for industrial use (Kristensen 1984). Although there are no British records of large spawning aggregations of *G. fabricii* or *G. steenstrupi*, juvenile gonatids are relatively common in U.K. waters based on the numbers found in plankton samples (Collins et al. 2001).

Table 12 Total annual cuttlefish (sepiids and sepiolids) landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Sepia officinalis*, *Sepia* spp. and sepiolid spp.) (Anonymous 2008)

	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Belgium	17	26	24	59	261	742	569	819	599	729
Denmark	0	0	0	0	3	16	42	60	49	90
France	11,046	13,015	13,926	16,974	12,395	15,434	11,305	21,511	14,142	13,475
Netherlands	+	+	+	101	163	382	250	388	174	310
Portugal	1,423	1,734	1,161	1,365	1,348	1,368	1,208	1,727	1,857	1,859
Spain	1,956	2,720	2,819	2,154	1,154	125	1,287	1,418	1,531	1,456
United Kingdom	2,210	2,780	2,280	3,101	2,710	3,547	5,008	5,514	3,015	3,593
Total (ICES)	16,652	20,275	20,210	23,754	18,034	22,614	19,659	30,988	21,371	21,513

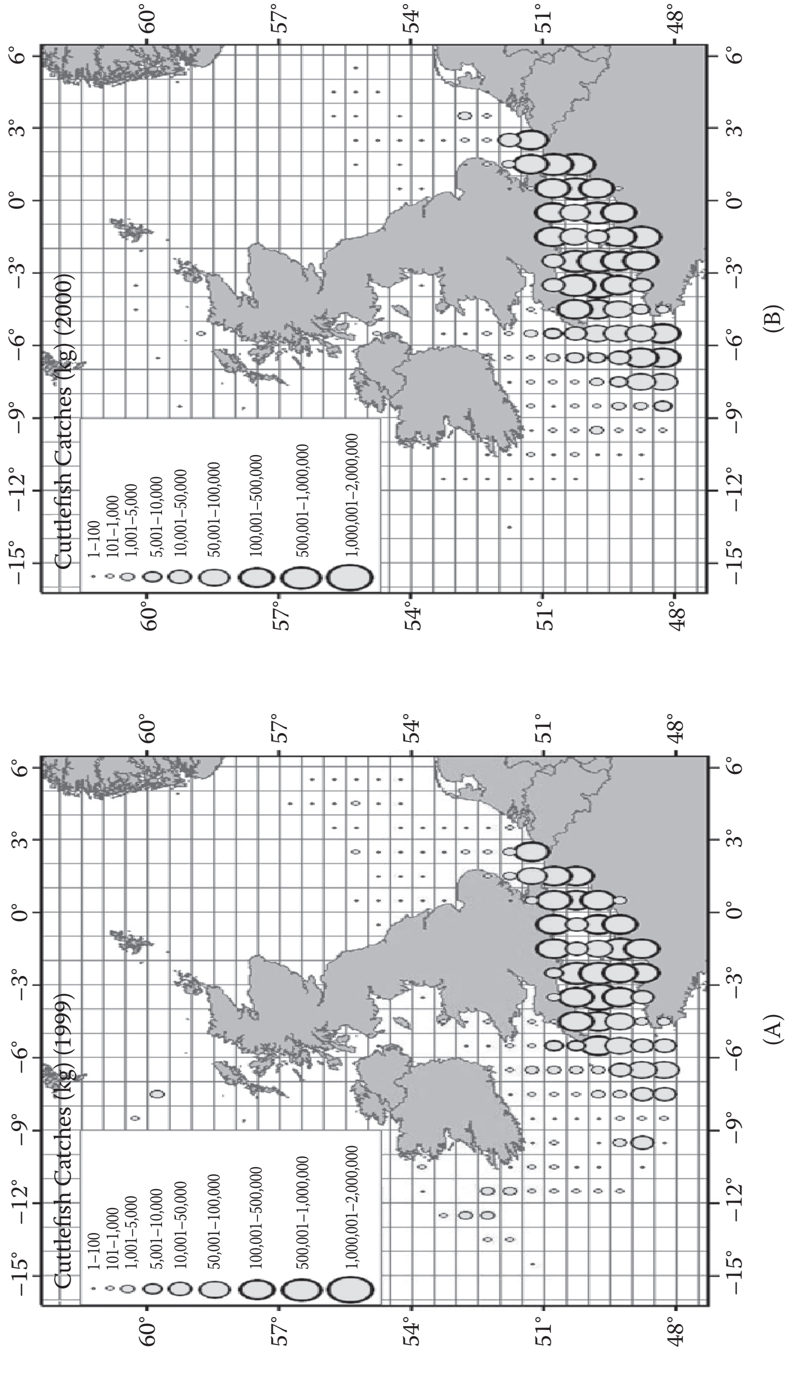
Exploitation of sepiolids

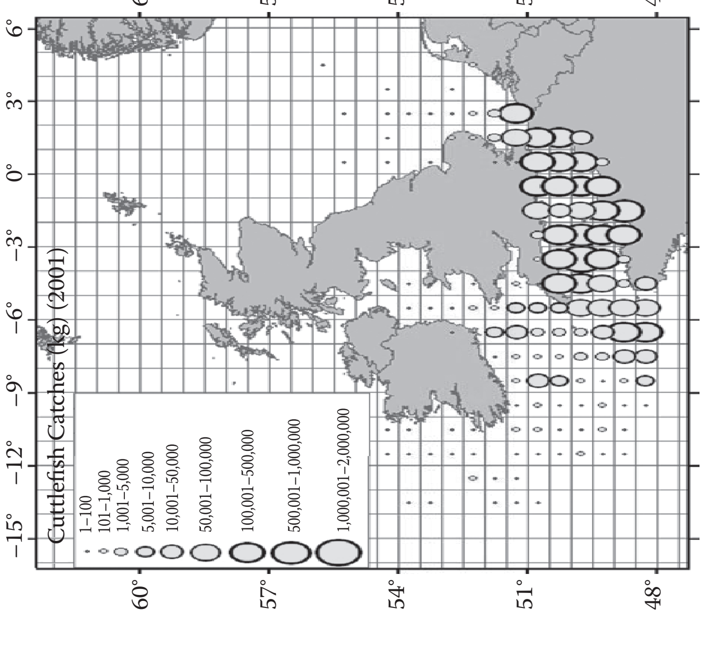
Small, bottom-living sepiolids are not presently considered to be of commercial value by U.K. fishermen and are usually discarded from catches. However, they may be very abundant in U.K. waters. Stephen (1944) reported a record of 256 specimens of *Sepiola atlantica* taken in a single haul, indicating fishery potential. In southern European waters of the Atlantic and Mediterranean, significant numbers of *Sepietta* spp., *Sepiola* spp. and *Rossia macrosoma* are often landed and marketed. No fisheries data for specific sepiolid catches are available, however, since these are currently recorded for fishery statistical purposes (together with commercial *Sepia* spp.) as ‘cuttlefish’ (Table 12).

Exploitation of cuttlefishes

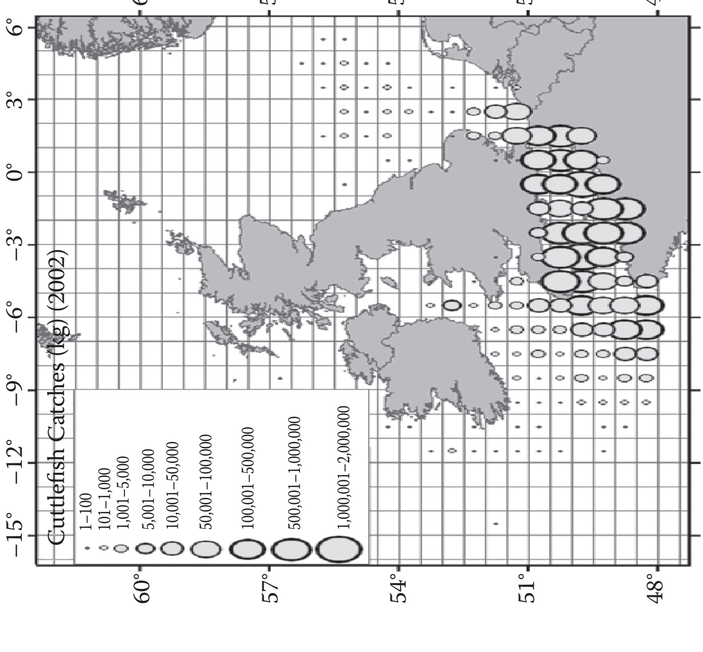
Total landings of cuttlefish (including sepiolids) from the north-eastern Atlantic (ICES Area) ranged from about 16,000 to 24,000 t per annum during the past decade (Table 12). The four main fishing fleets involved, based in France, Portugal, Spain and the United Kingdom, currently account for 95–99% of total landings (Figure 1c). The bulk of the total catch (60–65%) was in fact landed by the French fleet alone.

Sepia officinalis is an important commercial species that is exploited by a number of fisheries in Europe. The mean annual catch of this species (1993–2003) was about 41,000 t, taken more or less equally from the Atlantic and Mediterranean (Anonymous 2005). Figure 4c shows the distribution of cuttlefish catches in the north-eastern Atlantic and Mediterranean. The main fisheries for *S. officinalis* are currently based in France (Atlantic) and Italy (Mediterranean). U.K. fleets account for 2200–5100 t per annum, mostly from the English Channel (Anonymous 2005). In the United Kingdom and France, cuttlefish are landed by otter and beam trawlers, both as target species and as a by-catch of demersal fin fisheries. The main northern cuttlefish grounds are located in the English Channel and adjacent waters, the French Atlantic coast and the Bay of Biscay (Denis & Robin 2001; Figure 6). Further south, they are caught by a variety of artisanal gears, including gill nets, trammel nets, traps and jigs. Different cuttlefish species are grouped together in official catch statistics. Although the bulk of reported cuttlefish catches in European waters are *Sepia officinalis*, significant numbers of *S. elegans*, *S. orybignyana* and some sepiolid species (e.g., *Sepietta* spp. *Sepiola* spp., *Rossia macrosoma*) are also taken on occasion and marketed as ‘cuttlefish’ (Dunn 1999, Denis & Robin 2001, Reid & Jereb 2005).


Cuttlefish Catches (kg) (1999)
Cuttlefish Catches (kg) (2000)
1–100
101–1,000
1,001–5,000
5,001–10,000
10,001–50,000
50,001–100,000
100,001–500,000
500,001–1,000,000
1,000,001–2,000,000
−15°
−12°
−9°
−6°
−3°
0°
3°
6°
60°
57°
54°
51°
48°
(A)
(B)



(C)



(D)

Figure 6 Maps showing distributions of annual cuttlefish (including sepiolid) catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005): (A) 1999, (B) 2000, (C) 2001, (D) 2002.

Table 13 Total annual octopod landings (tonnes) (1997–2006) in the north-eastern Atlantic by country (includes *Octopus vulgaris and Eledone* spp.) (Anonymous 2008)

	Year									
Country	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Belgium	45	47	41	44	29	70	0	51	22	27
France	93	90	216	205	98	81	33	221	154	132
Ireland	7	3	10	12	14	13	0	13	30	3
Netherlands	0	0	0	0	5	0	0	0	1	0
Portugal	9,217	6,446	9,266	9,280	7,284	7,369	7,550	8,840	11,484	3,441
Spain	6,291	6,347	6,133	6,824	3,867	5,119	4,471	4,882	6,031	5,238
United Kingdom	148	110	52	135	164	180	137	188	184	148
Total (ICES)	15,801	13,043	15,718	16,500	11,461	12,831	12,191	14,195	17,906	8,999

Exploitation of incirrate octopods

Total landings of octopods from the north-eastern Atlantic (ICES Area) ranged from 12,000 to 16,000 t per annum during the past decade (Table 13). Three main fishing fleets, based in France, Portugal and Spain, accounted for more than 90% of annual landings (Figure 1d), although relatively big landings (>100 t) were occasionally reported in Ireland and the United Kingdom.

Eledone cirrhosa is one of the most important commercial cephalopod species in southern Europe and is of high value, especially in the western Mediterranean (Mangold & von Boletzky 1987, Relini et al. 1998, Sartor et al. 1998). Figure 4d shows the distribution of octopod catches in the north-eastern Atlantic and Mediterranean. It is usually caught by bottom trawling and more than 90% of the catches in the western Mediterranean are landed (Sartor et al. 1998). Mediterranean catches of *E. cirrhosa* are often separated into two categories for marketing (Belcari et al. 1990, Belcari & Sartor 1999). Small specimens (<5 cm ML) are highly valued and a number of targeted fisheries for these operate in certain areas during spring and summer, coinciding with the annual peak in recruitment (Relini & Orsi Relini 1984, Belcari et al. 1990, Sánchez, et al. 2004). Juvenile *E. cirrhosa*, known as 'popets' in Catalonia and 'moscardini" in Tuscany, are an important component of multispecies trawl fisheries in the Mediterranean (Belcari & Sartor 1999). At present, U.K. fleets account for only 50–230 t per annum (Anonymous 2005), probably reflecting the absence of local markets more than low abundance (Figure 7).

Octopus vulgaris is currently exploited as a target species in both the north-eastern Atlantic and Mediterranean, in depths of 20–200 m, by demersal trawl fleets and numerous small coastal fisheries (utilising hand jigs, pots, traps and trammel nets) operating in southern Europe and north-western Africa.

Conservation issues for cephalopods in the north-eastern Atlantic

Fishing pressure

There are particular problems for the fishery assessment and sustainable management of cephalopod stocks, largely associated with their general biology, short life histories and lack of knowledge for most species (Caddy 1983, Rosenberg et al. 1990, Pierce & Guerra 1994). The typical short life cycle of cephalopods provides little opportunity to adjust fishing effort on individual cohorts (Bravo de Laguna 1989) and renders them vulnerable to overfishing (Bravo de Laguna 1989). In U.K.

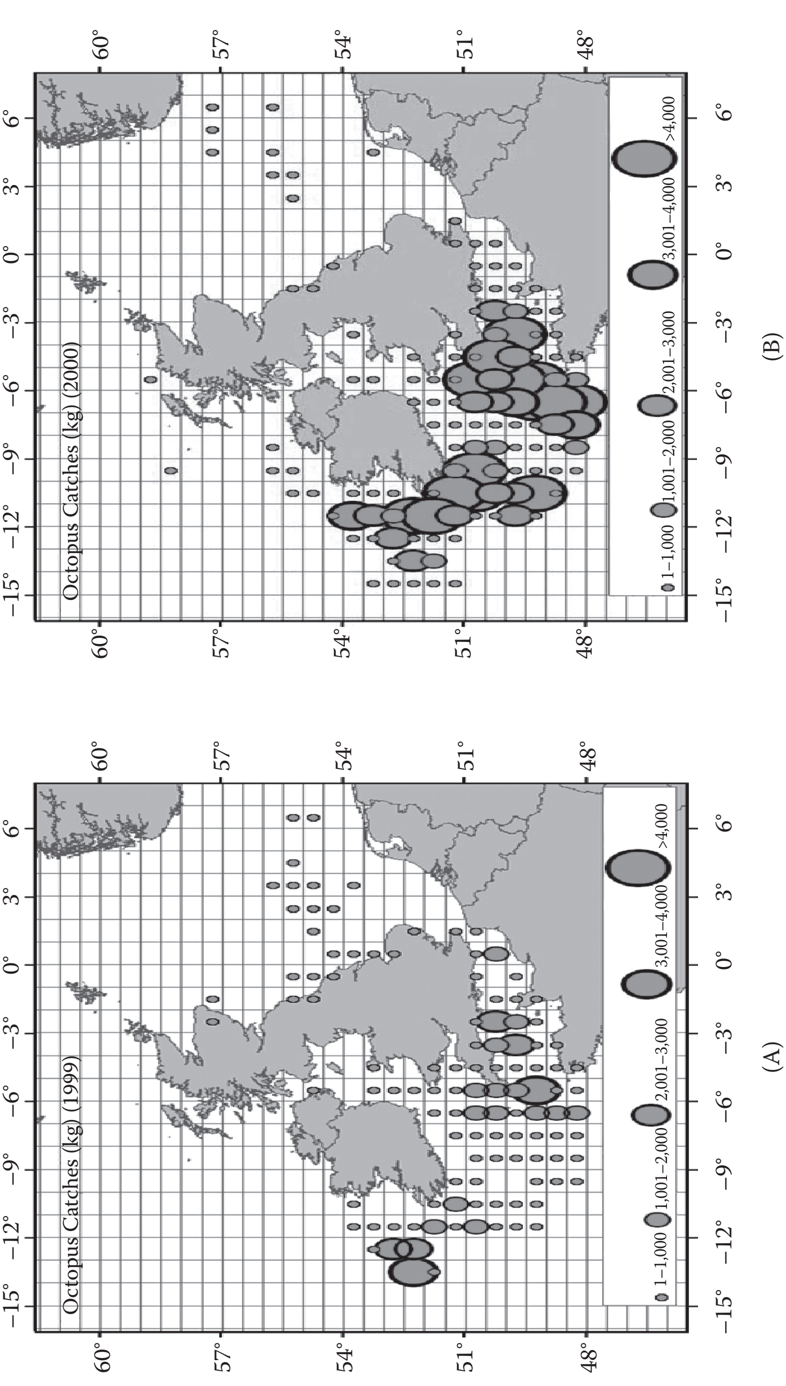


Figure 7 Maps showing distributions of annual (incirrate) octopod catches by International Council for the Exploration of the Sea [ICES] rectangles, reported by U.K. and French fishing fleets (1999–2002) (Anon. 2005): (A) 1999, (B) 2000, (C) 2001, (D) 2002.

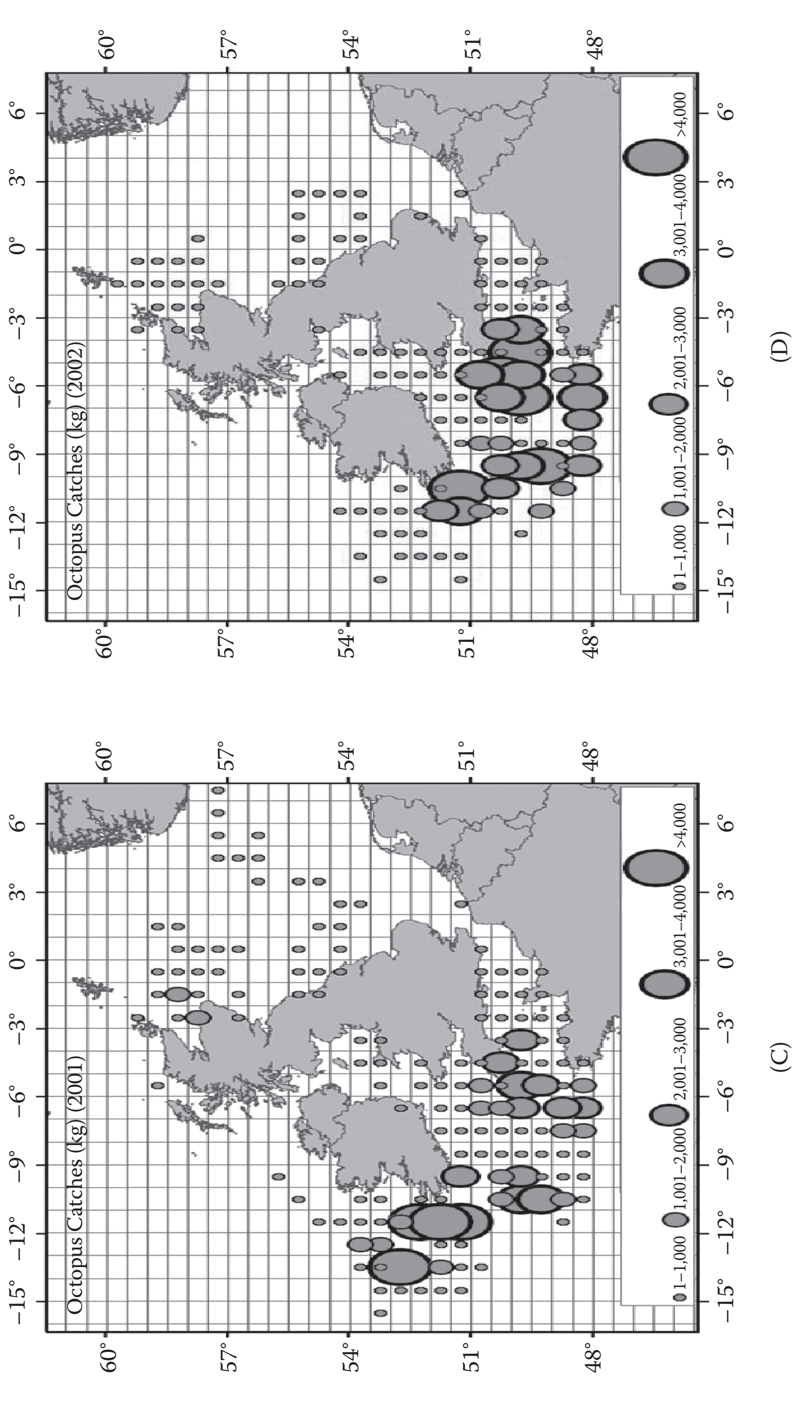


Figure 7 (continued).

waters, the by-catch fisheries take *Loligo forbesi* of a wide range of body sizes. Pierce et al. (1994a) observed that in Scottish catches of *L. forbesi*, mean ML at recruitment is no more than half that of fully mature animals. Thus growth overfishing may already be a problem in U.K. waters (Pierce & Guerra 1994). In the short term, recruitment overfishing may have more serious consequences for cephalopod stocks than for finfish stocks. In the long term, however, cephalopod stocks may be able to recover more quickly from overexploitation (Caddy 1983).

At present, there is very little or no management of cephalopod fisheries in European waters. In Galicia, north-western Spain, the Department of Fishing and Maritime Affairs of the Galician Autonomous Community (Xunta de Galicia) establish an annual ban on *Octopus vulgaris* fishing (from 9 May to 7 July for 2008) and there are seasonal weight restrictions on total catches landed in Spanish ports. Moreover, regional minimum size/weight restrictions are enforced on four species: *Loligo vulgaris* 10 cm, *Sepia officinalis* 8 cm, *Sepia elegans* 4 cm, *Octopus vulgaris* 1 kg (Xunta de Galicia 2007). In Portugal, minimum size/weight restrictions are also enforced for *Loligo vulgaris*, *Sepia officinalis* and *Octopus vulgaris*. A minimum weight restriction of 1 kg is also applied nationally to *Octopus vulgaris*. Squid (mainly *Loligo forbesi*) are largely by-caught by multispecies fisheries and represent a very small proportion of total U.K. fish landings (Pierce & Guerra 1994).

For most cephalopod species, abundance and geographic distribution vary widely from year to year and management options are currently constrained by procedures used to regulate target (whitefish) fisheries (Pierce & Guerra 1994). To date, there have been relatively few attempts to assess cephalopod stocks in the north-eastern Atlantic, and none are subject to routine assessment (Payne et al. 2006). A number of approaches have been employed with some success, including depletion models (Pierce et al. 1996, Young et al. 2004), modified cohort analysis (Royer et al. 2002, 2006), environmental predictors of recruitment (Robin & Denis 1999, Sims et al. 2001, Pierce & Boyle 2003, Zuur & Pierce 2004, Challier et al. 2005) and production models (FAO 1986, Payne et al. 2006). A considerable amount of fisheries-related research has been carried out on a few European stocks, including those of *Loligo forbesi* and *L. vulgaris* (Robin & Denis 1999, Pierce & Boyle 2003). However, most stocks have never been properly assessed (Pierce & Guerra 1994, Payne et al. 2006). Assessments of cephalopod stocks (utilising traditional techniques developed for fish stocks) have been difficult to implement for a number of reasons, including complex (within-year) recruitment patterns, insufficient (targeted) survey data and the susceptibility of distribution, abundance and life history of many species to environmental factors (Boyle & Pierce 1994, Payne et al. 2006, Pierce et al. 2008b).

Heavy metal contamination

Heavy metals, including arsenic, barium, cadmium, chromium, copper, iron, mercury, nickel, lead and zinc, reach the marine environment via rivers and certain marine operations, such as the exploitation of offshore resources and disposal of dredged materials. Highest concentrations of trace metals are found near freshwater outlets, with much lower levels in the open sea. Metallic contaminants are incorporated in the body of top marine predators via the food chain (Bustamante et al. 1998, Lahaye et al. 2005, Stowasser et al. 2005). Consequently, diet is the first factor controlling metal intake (Aguilar et al. 1999). Transfer of trace elements from prey to predator greatly depends on the bioavailability of the metal, which is determined by the detoxification processes in prey species. Metals located in the cytosolic fraction are readily available to higher trophic levels, whereas those bound to the insoluble subcellular fraction have a lower potential for transfer (Wallace & Lopez 1997). Consequently, the physicochemical forms of metals in different prey species appear to be a key factor that might control metal bioaccumulation in top marine predators. The most recent surveys of mercury levels in cephalopods from the north-eastern Atlantic indicated higher levels of mercury in demersal cephalopods than in pelagic species (Bustamante et al. 2006, Pierce et al.

2008b). Concentrations of cadmium were on average much higher in ommastrephid squid than loliginid squid (Pierce et al. 2008b).

As trace elements, certain metals (e.g., copper, selenium, zinc) are essential for the metabolism of organisms, but toxic in high doses. Other metals such as cadmium and mercury play no biological role. Cadmium, for example, derives its toxicological effect from the fact that it closely resembles zinc in its chemical properties and therefore is readily taken up by the body. The main danger of heavy metals to an organism lies in their tendency to be stored in the tissue faster than they can be broken down or excreted, that is, they bioaccumulate to harmful levels in the tissue.

Cephalopods represent an important link in marine food webs, being consumed by many top predators such as marine mammals, birds and fish (e.g., Clarke 1966, Croxall & Prince 1996, Smale 1996, Santos et al. 2001a, Stowasser et al. 2005). Studies of trace metal contents in cephalopod tissues indicated significant bioaccumulation in the digestive gland (hepatopancreas) (Martin & Flegal 1975, Schipp & Hevert 1978, Miramand & Bentley 1992, Caurant & Amiard-Triquet 1995, Bustamante et al. 1998, 2006, Stowasser et al. 2005). The availability of trace metals in cephalopods indicates their importance as vectors of contaminant transfer in the food chain.

Like many other molluscs, cephalopods rapidly accumulate high levels of cadmium, copper, mercury and zinc and other trace metals (Martin & Flegal 1975, Finger & Smith 1987, Stowasser et al. 2005). High levels of copper were found in the digestive gland of several cephalopod species (*Octopus vulgaris, Eledone moschata* and *Sepia officinalis*). Although copper is essential to marine molluscs, these studies revealed digestive gland copper levels 100 times higher than those of vertebrate liver and 105 times that of seawater (Rocca 1969). *Loligo opalescens* from Monterey Bay, California showed copper levels three orders of magnitude higher than concentrations found in other molluscs (Martin & Flegal 1975). Bustamante et al. (1998) found relatively low levels of copper but highly elevated levels of cadmium in the digestive gland of two octopod species in waters off the Kerguelen Islands. Since in molluscs in general copper and cadmium bind on the same metalloproteins in the digestive gland, some competition between the two metals may occur.

Cadmium, mercury and zinc have been shown to accumulate largely in the digestive gland of cephalopod species. High concentrations of cadmium have been found in the digestive glands of *Todarodes pacificus, Illex coindetii*, *Loligo opalescens*, *L. forbesi*, *Ommastrephes bartramii*, *Symplectoteuthis oualaniensis*, *Octopus salutii*, *Graneledone* sp., *Benthoctopus thielei* (Tanaka et al. 1983, Bustamante et al. 1998, Storelli & Marcotrigiano 1999, Craig & Overnell 2003, Stowasser et al. 2005, Pierce et al. 2008b). Even in areas like the Faroe and Kerguelen islands, which are relatively isolated from human activity, high cadmium concentrations were found in both cephalopods and their marine mammal predators (Caurant & Amiard-Triquet 1995, Bustamante et al. 1998). A study of *Sepioteuthis lessoniana* concluded that cadmium was accumulated from food rather than from surrounding seawater and that the digestive gland was the main retention organ in the body (Koyama et al. 2000). Cadmium and mercury levels in squid are highly variable between and within species (Table 14, see Stowasser et al. 2005, Pierce et al. 2008b). Spatial and temporal variations of

Table 14 Concentrations of cadmium (Cd) and mercury (Hg) recorded in four squid species caught in U.K. waters

Species	Sample size (*n*)	Cd concentration[a] (mean, $\mu g.g^{-1}$ dwt ± SD)	Hg concentration[a] (mean, $\mu g.g^{-1}$ dwt ± SD)
Alloteuthis subulata	20	9.48 ± 2.30	0.07 ± 0.01
Loligo forbesi	105	12.20 ± 9.92	0.22 ± 0.18
Todaropsis eblanae	23	25.10 ± 25.9	0.13 ± 0.10
Todarodes sagittatus	11	65.3 ± 61.1	0.28 ± 0.11

[a] Levels recorded in digestive gland tissues.

Source: From Pierce et al. 2008b.

Table 15 Monthly concentrations of cadmium (Cd) and mercury (Hg) recorded in *Loligo forbesi* in three geographic areas around the United Kingdom and Ireland

Area	Cd concentration[a] (mean $\mu g.g^{-1}$ dwt ± SD)		Hg concentration[a] (mean $\mu g.g^{-1}$ dwt ± SD)	
	Jan	Aug	Jan	Aug
Moray Firth	9.14 ± 3.57	14.9 ± 3.70	0.19 ± 0.06	0.08 ± 0.01
	Mar	Nov	Mar	Nov
Scottish west coast	28.8 ± 19.00	11.9 ± 10.30	0.31 ± 0.05	0.13 ± 0.08
	Apr	Nov	Apr	Nov
Irish west coast	18.10 ± 2.94	30.2 ± 8.18	0.36 ± 0.27	0.08 ± 0.01

Source: From Pierce et al. 2008b.

Table 16 Mean concentrations of trace metals in squid and whiting and median values recorded in piscivorous (porpoise, minke whale) and teuthophagous (Risso's dolphin, sperm whale) marine mammals in Scottish waters (mg/kg wet weight) (FRS, 1998)

	Cadmium	Copper	Lead	Zinc	Mercury	Arsenic
Squid	0.030	7.12	0.02	11.0	0.03	7.91
Whiting	0.001	0.14	<0.01	3.75	0.04	4.27
Risso's dolphin	5.00–8.73	4.18–9.09	0.10–0.89	26.7–46.2	1.47–5.22	—
Sperm whale	17.0	5.00	0.73	48.3	22.7	—
Porpoise	0.016	11.5	0.11	48.5	1.02	—
Minke whale	0.13	3.93	<0.07	87.4	1.84	—
FSC	0.02	20	2	50	0.5	—

Note: Limits set by the Food Standard Committee (FSC) are shown for comparison.

the concentrations of these metals in the tissues of *Loligo forbesi* were also observed, with the highest levels recorded west of Scotland during March (Table 15) although these may be confounded by seasonal migrations (Stowasser et al. 2005).

The potential for bioaccumulation and biomagnification of metals in the food chain is illustrated by results from a survey conducted by the U.K. Fisheries Research Services (FRS 1998). The mean concentrations of trace metals in squid (presumably *L. forbesi*), a fish (whiting) and various marine mammals are presented in Table 16. The Food Standards Committee's maximum recommended limits are also given for comparisons. In squid, levels of cadmium were 30 times those in whiting (*Merlangus merlangius*) and exceeded recommended safe limits for food. The presence of biomagnification could clearly be seen from highly elevated levels in cadmium in the marine mammals and the teuthophagous species compared to the piscivorous species.

Cephalopods are potentially an important (seafood) source of increased burdens of cadmium and mercury in human tissues (Pierce et al. 2008b). The viscera, containing elevated levels of these metals, are normally removed prior to consumption (thereby reducing exposure to contamination). However, in a number of countries, including Italy and Spain, small *Loligo* spp. and *Alloteuthis* spp. are often eaten whole (Shaw 1994). In Japan, the digestive gland is in fact considered to be a delicacy. Consideration of these 'high-risk' consumer groups is required, therefore, when evaluating the implications of heavy metal contamination of cephalopod tissue for public health (Pierce et al. 2008b).

Oil and gas production

At present, offshore oil and gas production is a major environmental issue in European waters, with important sedimentary basins in the North Sea, Irish Sea and north-eastern Atlantic (Pierce et al. 2002, Stowasser et al. 2004, Sacau et al. 2005). The main risks of oil pollution are currently from accidental spills, bunkering operations, fishing vessel casualties and tanker source spillages (Advisory Committee on Protection of the Sea [ACOPS] 1999). A wide variety of wastes is produced during oil and gas production. Some regulated discharge of wastes into the sea is permitted. These wastes include machinery cooling water, deck drainage, domestic sewage, drill cuttings, drilling fluids and produced waters. In addition, submerged structures and equipment may be protected against corrosion and fouling with sacrificial anodes and antifouling coatings that leach toxic metals (aluminium, copper, mercury, tin, zinc) into the water column (Sacau et al. 2005). Major discharges associated with drilling operations are drill cuttings and drilling fluids (Menzie 1983). Drill cuttings are particles of crushed, relatively inert sedimentary rock contaminated with drilling fluid residue and thus a potential source of several trace metal pollutants, including arsenic, barium, chromium, cadmium, copper, iron, lead, mercury, nickel and zinc (Neff et al. 1987). However, as noted in the previous section, the uptake of these elements by cephalopods is probably more of an issue for consumers of cephalopods than for the animals themselves.

There may also be problems for cephalopods associated with oil and gas exploration activities. Nine stranded giant squid (*Architeuthis* sp.) were recovered from Spanish waters during 2001–2003. On examination, no surface damage was observed but all specimens had massive internal injuries. These may have been caused by offshore seismic surveys for oil and gas that were being conducted in the vicinity during this time (Guerra et al. 2004b). Oil and gas production and exploration will continue in the north-eastern Atlantic for a considerable period.

Radionuclide contamination

Radionuclides discharged by the nuclear industry may also have a contaminating effect on marine biota. The main contribution to anthropogenic marine radioactivity is from global fallout from nuclear testing performed in the atmosphere. Due to global atmospheric transports and precipitation patterns the fallout is maximal at mid-latitudes between 30° and 60° and minimal at the equator and poles. Fewer nuclear tests in the Southern Hemisphere and the limited stratospheric exchange between hemispheres cause 76% of fallout to occur in the Northern Hemisphere (Aarkrog 2003).

In U.K. waters, the concentrations of anthropogenic radionuclides in the marine environment have also been significantly influenced by waterborne discharges from European nuclear reprocessing plants, notably Sellafield in the United Kingdom and Cap de la Hague in France (Livingston & Povinec 2000). Many radionuclides exhibit low solubility in seawater and high particle reactivity. This means in coastal regions they are rapidly removed from the water column and absorbed in sediments (Livingston & Povinec 2000). For example most of the plutonium discharged by Sellafield remains in a relatively narrow coastal zone incorporated into sediments. However initial discharges from Sellafield in the late 1970s were so large that suspended particles of plutonium could be measured in seawater at distances of hundreds of kilometres in the North Atlantic. Although recent years have seen the improvement of waste treatments, Sellafield is still a major source of potentially harmful radionuclides such as iodine and technetium. These are highly soluble in seawater, have very long half-lives, are transported over long distances from the source and readily accumulate in seafood (STOA 2001, Aarkrog 2003).

The danger of radionuclides lies in their accumulation in living tissues and the consequent transport and further concentration to toxic levels along the food chain. Studies of radionuclides in U.K. waters found that concentrations declined over the last decade and reflected decreasing emissions from the Sellafield plant in the same period (STOA 2001 and Table 7). Watson et al. (1999) found activity concentration of both plutonium and caesium in seals and porpoises to decrease with increasing distance from the source (Sellafield) and found elevated concentrations in animals of higher trophic levels and higher weights within the same species. Concentrations of plutonium and americium were found to be high and mainly unchanged over the course of 10 yr in shellfish (molluscs) from the Irish Sea. In contrast concentrations in fish were hardly detectable and low in crustaceans. Levels declined over the course of 10 yr for both taxa in concordance with decreasing emissions from the Sellafield reprocessing plant (Ryan et al. 1999).

A food web study from the Norwegian and Barents Sea found radiocaesium concentrations to be low for this area (Heldal et al. 2002). However, concentrations were found to multiply from lowest levels in krill and squid (*Gonatus fabricii*) by a factor of 10 to highest values found in harbour porpoise (*Phocoena phocoena*). Studies of naturally occurring radionuclides in marine organisms found polonium concentrations to be dependent of the diet of the organism (Cherry et al. 1989, Carvalho & Fowler 1994). High concentrations were found in benthic molluscs and marine mammals through bioaccumulation from lower trophic levels. Both fish and squid (*Loligo vulgaris*) showed lower levels than either other shellfish species or marine mammals (Cherry et al. 1989, Heyraud et al. 1994, Dahlgaard 1996, Betti et al. 2004). Contamination levels in molluscs seemed to be related to reproductive cycles in *Mytilus galloprovincialis* (Charmasson et al. 1994) and ontogenetic changes in feeding in the case of *L. vulgaris* (Heyraud et al. 1994).

Climate change

Cephalopods are highly sensitive to environmental conditions and change at a range of spatial and temporal scales (Pierce et al. 2008a). Two main types of relationship between cephalopod population dynamics and environmental conditions are recognised. These concern effects on the geographic distribution of species abundance and on critical biological processes such as egg survival, growth, recruitment and migration. Species-environment interactions are influenced by both large-scale atmospheric and oceanic processes and local environmental variations (Pierce et al. 2008a). Mobile pelagic species, such as ommastrephid squids, are directly affected by oceanographic conditions, whilst shallow-water, neritic species such as cuttlefish may be impacted by coastal variations in water quality and salinity that are influenced by rainfall and run-off. Climate change, therefore, is expected to have a significant effect on many cephaliopod species in the north-eastern Atlantic and elsewhere.

The embryonic development and hatching, growth and maturation, timing of reproduction and migration and biogeographic distribution of many cephalopod species are influenced by temperature (Boyle 1983). Observed changes in abundance of the squid *Loligo forbesi* in Scottish waters appeared to be related to climatic variation. Pierce & Boyle (2003) reported significant correlations between abundance of *L. forbesi* in coastal waters of the North Sea and a number of annual environmental indices, including winter NAO Index, average SST and sea-surface salinity. SST in particular appeared to influence recruitment strength.

North Atlantic climatic variation also appears to affect the timing of migration of *Loligo forbesi* in the English Channel. Analyses of historical research survey data by Sims et al. (2001) indicated that the eastwards migration of this species was earlier when water temperatures in the preceding months were higher, corresponding with warm (positive) phase of the NAO. The difference in timing of peak squid abundance between the warmest and coolest years was 120–150 days. Sea bottom temperature appeared to determine the extent of squid movement. It was also noted that these effects of water temperature and climatic fluctuations on the timing and extent of squid movements occurred irrespective of season (Sims et al. 2001). Since the early 1990s, marked declines in catches of *L. forbesi* in Iberian waters indicated a disappearance of this species from much of the southern part of its range, possibly linked to a rise in SST observed during this period (Chen et al. 2006).

Other loliginid species from different parts of the world also appear to be affected by climatic variations. On the Falkland Shelf, for example, seasonal changes in migratory patterns of Patagonian long-fin squid (*Loligo gahi*) have been associated with changes in water mass characteristics. A 5.5°C isotherm appeared to limit the distribution of *L. gahi* to deeper waters, irrespective of season, whilst the distribution of squid on the feeding grounds was associated with the warmest possible water layers (Arkhipkin et al. 2004). The extent of frontal waters and SST are affected by climate in the South Atlantic and these appear to directly influence annual recruitment success of an ommastrephid species, the Argentinian short-fin squid *Illex argentinus* (Waluda et al. 2001). As Robinson et al. (2005) pointed out, any significant long-term changes in these associated with climate change could therefore affect the distribution and abundance of *I. argentinus*.

Therefore, as mentioned, important changes in cephalopod biodiversity in the north-eastern Atlantic may occur within the next few decades. Global warming (sea temperature rise), for example, may result in the continued advance of a number of warm-water species into the north-eastern Atlantic and the simultaneous retreat of certain cold-water species to higher latitudes.

Another process associated with climate change that may affect cephalopods is the general rise in oceanic CO_2 concentration that has been observed in recent years. For example, ommastrephid squid such as *I. argentinus* are characterised by high metabolic rates and extremely pH-sensitive blood oxygen transport systems, and elevated CO_2 may affect their growth and reproduction (Pörtner et al. 2004).

Disturbance of spawning grounds

Another serious potential impact on cephalopod species in U.K. waters would be the physical disturbance of spawning grounds due to displacement of bottom sediments. Models of the distributions of mature adult *Loligo forbesi* in relation to habitat characteristics suggest that extensive areas of seabed within U.K. waters are potentially suitable spawning habitat for this species, although it remains unclear how many of these areas are actually used by squid (Stowasser et al. 2005). However, at present it is unclear how many of these areas are actually used by squid. Since *L. forbesi* is an annual species (Boyle et al. 1995), serious failure to reproduce and recruit in one year may endanger the survival of the population. In U.K. waters, spawning could occur over an extended area and the *L. forbesi* population is probably less dependent on specific spawning sites so that localised disturbance would not affect breeding success of the whole population. However, seasonal targeted fishing for squid, particularly in restricted areas where high concentrations of spawning activity occur, may have some impact on spawning success.

It is possible that drilling activities, dredging operations (gravel extractions) and extensive fisheries could have an impact on spawning grounds of *Loligo forbesi*. High turbidity is known to disrupt spawning behaviour in *L. vulgaris* in South African waters while low oxygen levels can limit distribution (Augustyn 1991). However cephalopod diversity is unlikely to be significantly affected by such disturbance since drilling operations are localised. Quantifying the effects of human activity on the marine ecosystem is problematic since no pristine 'baseline' marine habitats exist and historical data are sparse—and may still be impacted by historical activities (Frid et al. 2000).

Acknowledgements

This review was produced as part of the U.K. DTI's offshore energy SEA programme. The SEA programme is funded and managed by the DTI and coordinated on their behalf by Geotek Limited and Hartley Anderson Limited. The Spanish cephalopod landing data were collected by the 'Instituto Español de Oceanografía' (IEO) Sampling and Information Network, under the Project 'Monitoring and Analysis of the Fishing Activity in the ICES Area' (SAP-2).

References

Aarkrog, A. 2003. Radio-caesium fixation dynamics: measurement in six Cumbrian sediments. *Environmental Pollution* **129**, 31–37.

Adam, W. 1952. Résultats scientifiques des expéditions océanographiques belges dans les eaux cotieres africaines de l'Atlantique Sud (1948–1949), Céphalopodes. *Bulletin du Musée Royal d'Histoire naturelle de Belgique* **3**, 1–142.

Advisory Committee on Protection of the Sea (ACOPS). 1999. *Annual Survey of Reported Discharges Attributed to Vessels and Offshore Oil and Gas Installations Operating in the United Kingdom Pollution Control Zone, 1998.* London: Maritime and Coastguard Agency.

Aguado, F. & García, B. 2002. Growth and food intake models in *Octopus vulgaris* Cuvier (1797): influence of body weight, temperature, sex and diet. *Aquaculture International* **10**, 361–377.

Aguilar, A., Borrell, A. & Pastor, T. 1999. Biological factors affecting variability of persistent pollutant levels in cetaceans. *Journal of Cetacean Research and Management (Special Issue)* **1**, 82–116.

Aleksandronetz, Yu.A., Magaras, Yu.I. & Nigmatullin, C.M. 1983. Distributional patterns and range structure in nektonic squid family Ommastrephidae in open waters of the world ocean in connection with macroscale circulation [in Russian]. In *Taxonomy and Ecology of Cephalopods*, Ya.I. Starobogatov & K.N. Nesis (eds). Leningrad: Leningrad Zoological Institute of the USSR Academy of Sciences, 99–102.

Alford, R.A. & Jackson, G.D. 1993. Do cephalopods and larvae of other taxa grow asymptotically? *American Naturalist* **141**, 717–728.

Amaratunga, T. 1983. The role of cephalopods in the marine ecosystem. In *Advances in Assessment of World Cephalopod Resources*, I.F. Caddy (ed.). FAO Fisheries Technical Papers **231**, 379–415.

Anderson, F., Pilsits, A., Clutts, S., Laptikhovsky, V., Bello, G., Balguerias, E., Lipinski, M., Nigmatullin, C., Pereira, J.M.F., Piatkowski, U., Robin, J.P., Salman, A. & Tasende, M.G. 2008. Systematics of *Alloteuthis* (Cephalopoda: Loliginidae) based on molecular and morphometric data. *Journal of Experimental Marine Biology and Ecology* **364**, 99–109.

Anonymous. 2005. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH). *International Council for the Exploration of the Sea*, ICES CM 2005/G:02. ICES: Copenhagen.

Anonymous. 2008. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH). *International Council for the Exploration of the Sea*, ICES CM 2008/G:02. ICES: Copenhagen.

Arkhipkin, A.I. 1996. Geographic variation in growth and maturation of the squid *Illex coindetii* (Oegopsida, Ommastrephidae) off the north-west African coast. *Journal of the Marine Biological Association of the United Kingdom* **76**, 1091–1106.

Arkhipkin, A.I. & Bjørke, H. 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. *Polar Biology* **22**, 357–365.

Arkhipkin, A.I., Campana, S.E., Fitzgerald, J. & Thorrold, S.R. 2004. Spatial and temporal variation in elemental signatures of statoliths from the Patagonian longfin squid (*Loligo gahi*). *Canadian Journal of Fisheries and Aquatic Science*s **61**, 1212–1224.

Arkhipkin, A.I. & Laptikhovsky, V.V. 2000. Age and growth of the squid *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) on the north-west African shelf. *Journal of the Marine Biological Association of the United Kingdom* **80**, 747–748.

Arkhipkin, A.I., Laptikhovsky, V.V. & Golub, A. 1999. Population structure and growth of the squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) in north-west African waters. *Journal of the Marine Biological Association of the United Kingdom* **79**, 467–477.

Arkhipkin, A.I. & Nigmatullin, C.M. 1997. Ecology of the oceanic squid *Onychoteuthis banksi* and the relationship between the genera *Onychoteuthis* and *Chaunoteuthis* (Cephalopoda: Onychoteuthidae). *Journal of the Marine Biological Association of the United Kingdom* **77**, 839–869.

Arvanitidis, C., Koutsoubas, D., Robin, J.P., Pereira, J., Moreno, A., Cunha, M.M., Valavanis, V. & Eleftheriou, A. 2002. A comparison of the fishery biology of three *Illex coindetii* Verany, 1839 (Cephalopoda: Ommastrephidae) populations from the European Atlantic and Mediterranean waters. *Bulletin of Marine Science* **71**, 129–146.

Augustyn, C.J. 1991. The biomass and ecology of chokka squid, *Loligo vulgaris reynaudi*, off the west coast of South Africa. *South African Tydskr DierkJournal of Zoology* **26**, 164–181.

Auteri, R., Mannini, P. & Volpi, C. 1988. Regime alimentare di *Eledone cirrhosa* (Lamarck, 1798) e *Sepia orbignyana* (Férrussac in Orbigny, 1826) (Mollusca, Cephalopoda) nel Tirreno Settentrionale. *Quaderni del Museo di Storia Naturale di Livorno* **9**, 67–73.

Baddyr, M., 1988. *The biology of the squid* Loligo vulgaris *in relation to the artisanal fishing site of Tifnit, Morocco.* Unpublished Ph.D. thesis, Institut Agronomique et Vètèrinaire Hassan II, Rabat, Morocco.

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

Belcari, P. 1999. *Sepia elegans* Blainville, 1827. In *Sintesi delle conoscenze sulle risorse dap esc dei fondi del Mediterraneo centrale (Italia e Corsica)*, G. Relini et al. (eds). *Biologia Marina Mediterranea* **6**, 675–679.

Belcari, P., Biagi, F. & Fedi, F. 1990. Relazione taglia peso in *Eledone cirrhosa* (Lam, 1798). *Obelia* **16**, 591–594.

Belcari, P. & Sartor, P. 1993. Bottom trawling teuthofauna of the northern Tyrrhenian Sea. *Scientia Marina* **57**, 145–152.

Belcari, P. & Sartor, P. 1999. *Eledone cirrhosa* (Lamarck, 1798). In *Sintesi delle conoscenze sulle risorse dap esc dei fondi del Mediterraneo centrale (Italia e Corsica)*, G. Relini et al. (eds). *Biologia Marina Mediterranea* **6**, 737–746.

Belcari, P., Sartor, P., Nannini, N. & de Ranieri, S. 1999. Length-weight relationship of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) of the northern Tyrrhenian Sea in relation to sexual maturation. *Biologia Marina Mediterranea* **6**, 524–528.

Bello, G. 1991. Relationship between tentacle club length and body size in *Sepia elegans*. In *First International Symposium on the Cuttlefish Sepia*, E. Boucaud-Camou (ed.). Caen: Centre de Publications de l'Université de Caen, 93–98.

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

Bello, G. & Deickert, A. 2003. Multiple spawning and spawning batch size in *Sepietta oweniana* (Cephalopoda: Sepiolidae). *Cahiers de Biologie Marine* **44**, 307–314.

Berdar, A. & Cavallaro, G. 1975. Ulteriore contributo alla conosczenza dei cephalopodi spiaggiati lungo la costa siciliana dell Stretto di Messina. *Memorie di Biologia Marina e di Oceanografia* **5**, 121–138.

Bergström, B. & Summers, W.W. 1983. *Sepietta oweniana*. In *Cephalopod Life Cycles. Volume 1. Species Accounts*, P.R. Boyle (ed.). London: Academic Press, 75–91.

Bergström, B.I. 1985. Aspects of natural foraging by *Sepia oweniana*. *Ophelia* **24**, 65–74.

Bettencourt, V., Coelho, M.L., Andrade, J.P. & Guerra, A. 1996. Age and growth of the squid *Loligo vulgaris* off the south coast of Portugal, using statolith analysis. *Journal of Molluscan Studies* **62**, 359–366.

Betti, M., Aldave de las Heras, L., Janssens, A., Henrich, E., Hunter, G., Gerchikov, M., Dutton, M., van Weers, A.W., Nielsen, S., Simmonds, J., Bexon, A. & Sazykina, T. 2004. Results of the European Commission Marina II Study Part II—effects of discharges of naturally occurring radioactive material. *Journal of Environmental Radiation* **74**, 243–254.

Bjørke, H. 2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. *Fisheries Research* **52**, 113–120.

Bjørke, H. & Gjøsæter, H. 1998. Who eats the larger *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea? *International Council for the Exploration of the Sea*, ICES CM/M:10. ICES: Copenhagen.

Bjørke, H. & Gjøsæter, H. 2004. Cephalopods in the Norwegian Sea. In *The Norwegian Sea Ecosystem*, H.R. Skoldal (ed.). Trondheim, Norway: Tapur Academic Press, 371–394.

Bjørke, H., Hansen, K. & Sundt, R.C. 1997. Egg masses of the squid *Gonatus fabricii* (Cephalopoda, Gonatidae) caught with pelagic trawl off northern Norway. *Sarsia* **82**, 149–152.

Blanco, C., Salomon, O. & Raga, J.A. 2001. Diet of the bottlenose dolphin (*Tursiops truncatus*) in the western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **81**, 1053–1058.

Borges, T.C. & Wallace, J.C. 1993. Some aspects of the fishery biology of the ommastrephid squid *Todarodes sagittatus* (Lamarck, 1798) from the northeast Atlantic. In *Recent Advances in Cephalopod Fisheries Biology*, T. Okutani et al. (eds). Tokyo: Tokai University Press, 25–36.

Boucaud, O. & Daguzan, J. 1990. Étude expérimentale de l'influence de la temperature sur le déroulement embryonaire de la seiche *Sepia officinalis* L. (Céphalopode, Sepioidae). *Cahiers de Biologie Marine* **31**, 131–145.

Boucaud-Camou, E., Koueta, N., Boismery, J. & Medhioub, A. 1991. The sexual cycle of *Sepia officinalis* L. from the Bay of Seine. In *Acta 1st International Symposium on the Cuttlefish, Sepia, Caen 1989*, E. Boucaud-Camou (ed.). Caen: 141–151.

Bower, J.R. & Ichii, T. 2005. The red flying squid (*Ommastrephes bartramii*): a review of recent research and the fishery in Japan. *Fisheries Research* **76**, 39–55.

Boyle, P.R. 1983. *Eledone cirrhosa*. In *Cephalopod Life Cycles. Vol. 1. Species Accounts*, P.R. Boyle (ed.). London: Academic Press, 365–386.

Boyle, P.R. 1986. Report on a specimen of *Architeuthis* stranded near Aberdeen, Scotland. *Journal of Molluscan Studies* **52**, 81–82.

Boyle, P.R. 2002. Cephalopod biomass and production: an introduction to the symposium. *Bulletin of Marine Science* **71**, 13–16.

Boyle, P.R., Collins, M.A. & Williamson, G.R. 1998. The cephalopod by-catch of deep-water trawling on the Hebrides slope. *Journal of the Marine Biological Association of the United Kingdom* **78**, 1023–1026.

Boyle, P.R. & Daly, H.I. 2000. Fecundity and spawning in a deep-water cirromorph octopus. *Marine Biology* **137**, 317–324.

Boyle, P.R. & Knobloch, D. 1983. The female reproductive cycle of the octopus, *Eledone cirrhosa*. *Journal of the Marine Biological Association of the United Kingdom* **63**, 71–83.

Boyle, P.R. & Ngoile, M.A.K. 1993. Population variation and growth in *Loligo forbesi* (Cephalopoda: Loliginidae) from Scottish waters. In *Recent Advances in Cephalopod Fisheries Biology*, T. Okutani et al. (eds). Tokyo: Tokai University Press, 48–59.

Boyle, P.R., Mangold, K. & Ngoile, M.A.K. 1988. Biological variation in *Eledone cirrhosa* (Cephalopoda: Octopoda): simultaneous comparison of North Sea and Mediterranean populations. *Malacologia* **29**, 77–87.

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

Boyle, P.R., Pierce, G.J. & Hastie, L.C. 1995. Flexible reproductive strategies in the squid *Loligo forbesi*. *Marine Biology* **121**, 501–508.

Boyle, P.R. & von Boletzky, S. 1996. Cephalopod populations: definition and dynamics. *Philisophical Transactions of the Royal Society of London B* **215**, 985–1002.

Bravo de Laguna, J. 1989. Managing and international multispecies fishery: the Saharan trawl fishery for cephalopods. In *Marine Invertebrate Fisheries: Their Assessment and Management*, J.F. Caddy (ed.). New York: Wiley, 591–612.

Brieby, A. & Jobling, B. 1985. Predatory role of the flying squid (*Todarodes sagittatus*) in north Norwegian waters. *NAFO Scientific Council Studies* **9**, 125–132.

Brierley, A.S., Thorpe, R.S., Pierce, G.J., Clarke, M.R. & Boyle, P.R. 1995. Genetic variation in the neritic squid *Loligo forbesi* (Myopsida: Loliginidae) in the northeast Atlantic Ocean. *Marine Biology* **12**, 79–86.

Brown, E.G. & Pierce, G.J. 1998. Monthly variation in the diet of harbour seals in inshore waters along the southeast Shetland (UK) coastline. *Marine Ecology Progress Series* **167**, 275–289.

Brown, E.G., Pierce, G.J., Hislop, J.R.G. & Santos, M.B. 2001. Interannual variation in the summer diets of harbour seals *Phoca vitulina* at Mousa, Shetland (UK). *Journal of the Marine Biological Association of the United Kingdom* **81**, 325–337.

Brunetti, N.E., Ivanovic, M.L. & Sakai, M. 1999. Calamares de Importancia Comercial en Argentina. Biología, Distribución, Pesquerías y Muestreo Biológico. Instituto Nacional de Investigacíon y Desarrollo Pesquero (INIDEP) **4**. Publicaciones Especiales de INIDEP. Mar del Plata, Argentina, 45 pp.

Bustamante, P., Caurant, F., Fowler, S.W. & Miramand, P. 1998. Cephalopods as a vector for the transfer of cadmium to top marine predators in the north-east Atlantic Ocean. *Science of the Total Environment* **220**, 71–80.

Bustamante, P., Garrigue, C., Breau, L., Caurant, F., Dabin, W., Greaves, J. & Dodemont, R. 2003. Trace elements in two odontocete species (*Kogia breviceps* and *Globicephala macrorhynchus*) stranded in New Caledonia (South Pacific). *Environmental Pollution* **124**, 263–271.

Bustamante, P., Grigioni, S., Boucher-Rodoni, S., Caurant, F. & Miramand, P. 2000. Bioaccumulation of 12 trace elements in the tissue of the nautilus *Nautilus macromphalus* from New Caledonia. *Marine Pollution Bulletin* **40**, 688–696.

Bustamante, P., Lahaye, V., Durnez, C., Churlaud, C. & Caurant, F. 2006. Total and organic Hg concentrations in cephalopods from the North East Atlantic waters: influence of geographical origin and feeding ecology. *Science of the Total Environment* **368**, 585–596.

Caddy, J.F. 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. In *Advances in Assessment of World Cephalopod Resources*, J.F. Caddy (ed.). Rome: FAO. Fisheries Technical Paper (FAO) **231**, 416–449.

Caddy, J.F. 1995. Cephalopods and demersal finfish stocks: some statistical trends and biological interactions. In *Proceedings of the Third International Cephalopoda Trade Conference*. London: Agra Europe, 1–14.

Caddy, J.F. & Rodhouse, P.J. 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Reviews in Fish Biology and Fisheries* **8**, 431–444.

Carlini, R., Pulcini, M. & Wurtz, M. 1992. Cephalopods from the stomach contents of Cuvier's beaked whale *Ziphius cavirostris* (Cuvier, 1823) stranded at Fiumino, central Tyrrhenian Sea. In *Proceedings of the Sixth Annual Conference of the European Cetacean Society*. San Remo, Italy, 190–191.

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

Carvalho, F.P. & Fowler, S.W. 1994. A double-tracer technique to determine the relative importance of water and food as sources of polonium-210 to marine prawns and fish. *Marine Ecology Progress Series* **103**, 251–264.

Casali, G., Piccinetti, M. & Soro, S. 1998. Distribuzione di cefalopodi in Alto e Medio Adriatico. *Biologia Marina Mediterranea* **5**, 307–318.

Castley, J.G., Cockroft, V.G., Kerley, G.H. 1991. A note on the stomach contents of fur seals *Arctocephalus pusillus pusillus* beached on the south-east coast of South Africa. *South African Journal of Marine Science* **11**, 573–577.

Castro, J.J. & Guerra, A. 1990. The diet of *Sepia officinalis* Linnaeus 1758 and *Sepia elegans* D'Orbigny 1835 (Cephalopoda Sepioidea) from the Ria de Vigo, northwest Spain. *Scientia Marina* **54**, 375–388.

Castro, J.J. & Hernández-García, V. 1995. Ontogenetic changes in mouth structures, foraging behaviour and habitat use of *Scomber japonicus* and *Illex coindetii*. *Scientia Marina* **59**, 347–355.

Caurant, F. & Amiard-Triquet, C. 1995. Cadmium contamination in pilot whales *Globicephala melas*: source and potential hazard to the species. *Marine Pollution Bulletin* **30**, 207–210.

Challier, L., Royer, J., Pierce, G.J., Bailey, N., Roel, B.A., Robin, J.P. 2005. Environmental and stock effects on recruitment variability in the English Channel squid *Loligo forbesi*. *Aquatic Living Resources* **18**, 353–360.

Charmasson, S., Arnaud, M., Piermattei, S. & Romero, L. 1994. Sources of radioactivity in the Mediterranean Sea, report of working group 1. In *The Radiological Exposure of the Population of the European Community from Radioactivity in the Mediterranean Sea: MARINA-MED Project* (Cigna, A., Delfanti, R. & Serro, R., eds). Proceedings of the Seminar at Rome, 17–19 May 1994; EUR-15564, pp. 11–70.

Chen, C.S., Pierce, G.J., Wang, J., Robin, J.P., Poulard, J.C., Pereira, J., Zuur, A.F., Boyle, P.R., Bailey, N., Beare, D.J., Jereb, P. Ragonese, S. Mannini, A & Orsi Relini, L. 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: trends in *Loligo* spp. abundance in the northeast Atlantic and possible environmental influences. *Fisheries Research* **78**, 44–54.

Cherel, Y. & Duhamel, G. 2004. Antarctic jaws: cephalopod prey of sharks in Kerguelen waters. *Deep-Sea Research* Part 1 **51**, 17–31.

Cherry, R. D., Heyraud, M. & James, A. G. 1989. Diet prediction in common clupeoid fish using polonium-210 data. *Journal of Environmental Radioactivity* **10**, 47–65.

Chesalin, M.V. 1987. On the nutrition of *Sthenoteuthis pteropus* (Steenstrup 1855) with Myctophidae (Pisces). *Ekologya Moria* **25**, 75–80.

Clarke, M.R. 1966. Review of the systematics and ecology of oceanic squids. *Advances in Marine Biology* **4**, 91–300.

Clarke, M.R. 1996. Cephalopods as prey III. Cetaceans. *Philosophical Transactions of the Royal Society of London B* **351**, 1053–1065.

Clarke, M.R. & Goodall, N. 1994. Cephalopods in the diets of three odontocete cetacean species stranded at Tierra del Fuego, *Globicephala melaena* (Traill, 1809), *Hyperoodon planifrons* Flower, 1882 and *Cephalorhynchus commersonii* (Lacepede, 1804). *Antarctic Science* **6**,149–154.

Clarke, M.R. & Lu, C.C. 1995. Cephalopoda of Maderian waters. *Boletin do Museu Municipal do Funchal* **4**, 181–200.

Clarke, M.R., Martins, H.R. & Pascoe, P. 1993. The diet of sperm whales (*Physeter macrocephalus* Linnaeus) off the Azores. *Philosophical Transactions of the Royal Society of London B* **339**, 67–82.

Clarke, M.R. & Pascoe, P.L. 1985. The stomach contents of a Risso's dolphin (*Grampus griseus*) stranded at Thurlestone, South Devon. *Journal of the Marine Biological Association of the United Kingdom* **65**, 663–665.

Clarke, M.R. & Pascoe, P.L. 1997. Cephalopod species in the diet of a sperm whale (*Physeter catodon*) stranded at Penzance, Cornwall. *Journal of the Marine Biological Association of the United Kingdom* **77**, 1255–1258.

Clarke, M.R. & Roper, C.F.E. 1998. Cephalopods represented by beaks in the stomach of a sperm whale stranded at Paekakariki, North Island, New Zealand. *South African Journal of Marine Science* **20**, 129–133.

Clarke, M.R. & Stevens, J.D. 1974. Cephalopods, blue sharks and migration. *Journal of the Marine Biological Association of the United Kingdom* **54**, 949–957.

Coelho, M.L., Quintela, J., Bettencourt, V., Olavo, G. & Villa, H. 1994. Population structure, maturation and fecundity of the squid *Loligo vulgaris* from southern Portugal. *Fisheries Research* **21**, 87–102.

Collins, M.A. 1998. A female giant squid (*Architeuthis*) stranded on the Aberdeenshire coast. *Journal of Molluscan Studies* **64**, 489–492.

Collins, M.A., Boyle, P.R., Pierce, G.J., Key, L.N., Hughes, S.E. & Murphy, J. 1999. Resolution of multiple cohorts in the *Loligo forbesi* population from the west of Scotland. *ICES Journal of Marine Science* **56**, 500–509.

Collins, M.A., Brown, E.G. & Pierce, G.J. 1995b. Note on a specimen of the gelatinous octopus *Haliphron atlanticus* Steenstrup caught in Shetland Islands waters. *The Shetland Naturalist* **1**, 123–124.

Collins, M.A., Burnell, G.M. & Rodhouse, P.G. 1995a. Recruitment, maturation and spawning of *Loligo forbesi* (Cephalopoda: Loliginidae) in Irish waters. *ICES Journal of Marine Science* **52**, 127–137.

Collins, M.A., De Grave, S., Lordan, C., Burnell, G.M. & Rodhouse, P.G. 1994. Diet of the squid *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Irish waters. *ICES Journal of Marine Science* **51**, 337–344.

Collins, M.A., Lordan, C., Flannery, K., Quigley, D.T.G. & Howard, F.G. 1997b. New records of cephalopods caught in Irish and Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* **77**, 561–564.

Collins, M.A. & Pierce, G.J. 1996. Size selectivity in the diet of *Loligo forbesi* (Cephalopoda: Loliginidae). *Journal of the Marine Biological Association of the United Kingdom* **76**, 1081–1090.

Collins, M.A., Pierce, G.J. & Boyle, P.R. 1997a. Population indices of reproduction and recruitment in *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish and Irish waters. *Journal of Applied Ecology* **34**, 778–786.

Collins, M.A. & Villanueva, R. 2006. Taxonomy, ecology and behaviour of the cirrate octopods. *Oceanography and Marine Biology: An Annual Review* **44**, 277–322.

Collins, M.A., Yau, C., Allcock, L. & Thurston, M.H. 2001. Distribution of deep-water benthic and bentho-pelagic cephalopods from the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **81**, 105–117.

Collins, M.A., Yau, C., Boyle, P.R., Friese, D. & Piatkowski, U. 2002. Distribution of cephalopods from plankton surveys around the British Isles. *Bulletin of Marine Science* **71**, 239–254.

Cordes, S. 2002. *Age determination of the squid* Loligo forbesi *(Cephalopoda) based on statoliths.* Unpublished M.Sc. thesis, University of Bremen.

Craig, S. 1996. *Total mercury concentration in the cephalopods,* Loligo forbesi *(Steenstrup),* Todaropsis eblanae *(Ball) and* Todarodes sagittatus *(Lamark)*. Unpublished Hons. thesis, University of Aberdeen.

Craig, S. 2001. *Environmental conditions and yolk biochemistry: factors influencing embryonic development in the squid* Loligo forbesi *(Cephalopoda: Loliginidae) Steenstrup 1856*. Unpublished Ph.D. thesis, University of Aberdeen.

Craig, S. & Overnell, J. 2003. Metals in squid, *Loligo forbesi*, adults, eggs and hatchlings. No evidence for a role for Cu- or Zn-metallothionein. *Comparative Biochemistry and Physiology C* **134**, 311–317.

Croxall, J.P. & Prince, P.A. 1996. Cephalopods as prey. I. Seabirds. *Philosophical Transactions of the Royal Society of London Series B* **351**, 1023–1043.

Cuccu, D., Damele, F., Follesca, M.C., Mureni, M. & Cau, A. 2003. Aspetti biologici di *Eledone cirrhosa* (Cephalopoda Octopoda) nei mari circostanti las Sardegna. *Biologia Marina Mediterranea* **10**, 119–126.

Cuccu, D., Jereb, P., Addis, P., Pendugiu, A.A., Sabatini, A. & Cau, A. 2005. Eccezionali catture di *Todarodes saggitatus* (Cephalopoda: Ommastrophidae) nei mari sardi. *Biologia Marina Mediterranea* **12**, 500–503.

Cunha, M.M., Moreno, A. & Pereira, J.M.F. 1995. Spatial and temporal occurrences of *Loligo* spp. in Portuguese waters. *International Council for the Exploration of the Sea*, ICES CM 1995/K:33. ICES: Copenhagen.

Dahlgaard, H. 1996. Polonium-210 in mussels and fish from the Baltic-North Sea Estuary. *Journal of Environmental Radioactivity* **32**, 91–96.

Daly, H.I., Boyle, P.R. & Collins, M.A. 1998. Reproductive status of *Opisthoteuthis* sp. over an annual cycle. *South African Journal of Marine Science* **20**, 187–192.

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

Dawe, E.G. 1988. Length-weight relationships for short-finned squid in Newfoundland and the effect of diet on condition and growth. *Transactions of the American Fisheries Society* **117**, 591–599.

Dawe, E.G. & Brodziak, J.K.T. 1998. Trophic relationship, ecosystem variability and recruitment. In *Squid Recruitment Dynamics. The Genus* Illex *as a model. The Commercial* Illex *Species. Influences on Variability,* P.G. Rodhouse et al. (eds). FAO Fisheries Technical Paper **376**, 125–156.

Degner, E. 1925. Cephalopoda. *Report on the Danish Oceanographical Expeditions 1908–10 to the Mediterranean and Adjacent Seas* **2**, 1–94.

den Hartog, J.C. & Clarke, M.R. 1996. A study of stomach contents of Cory's Shearwater, *Calonectris diomedea borealis* (Cory, 1881) (Aves: Procellariidae), from the Macaronesian Islands. *Zoologische Medeldelingen (Leiden)* **70**, 117–133.

Denis, V. & Robin, J.P. 2001. Present status of French Atlantic fishery for cuttlefish (*Sepia officinalis*). *Fisheries Research* **182**, 1–12.

De Pierrepont, J.F., Dubois, B., Desormonts, S., Santos, M.B. & Robin, J.P. 2005. Stomach contents of English Channel cetaceans stranded on the coast of Normandy. *Journal of the Marine Biological Association of the United Kingdom* **85**, 1539–1546.

Dexter, R.W. 1969. Studies on the food habits of whiting, redfish, and pollock in the Gulf of Maine. *Journal of the Marine Biological Association of India* **11**, 288–294

Domain, F., Jouffre, D. & Caverivière, A. 2000. Growth of *Octopus vulgaris* from tagging in Senegalese waters. *Journal of the Marine Biological Association of the United Kingdom* **80**, 699–705.

Dunn, M.R. 1999. Aspects of the stock dynamics and exploitation of cuttlefish, *Sepia officinalis* (Linnaeus, 1758), in the English Channel. *Fisheries Research* **40**, 277–293.

Durward, R.D., Vessey, E., O'Dor, R.K. & Amaratunga, T. 1980. Reproduction in the squid, *Illex illecebrosus*: first observations in captivity and implications for the life cycle. *International Commission Northwest Atlantic Fisheries Selected Paper* **6**, 7–13.

Falcon, L.I., Vecchione, M. & Roper, C.F.E. 2000. Paralarval gonatid squids (Cephalopoda: Oegopsida) from the mid-north Atlantic Ocean. *Proceedings of the Biological Society of Washington* **113**, 532–541.

Falk, K., Jensen, J.K. & Kampp, K. 1992. Winter diet of Atlantic puffins (*Fratercula arctica*) in the northeast Atlantic. *Colonial Waterbirds* **15**, 230–235.

Finger, J.M. & Smith, J.D. 1987. Molecular association of Cu, Zn, Cd and Po-210 in the digestive gland of the squid *Nototodarus gouldi*. *Marine Biology* **95**, 87–91.

Fiscus, C.H. 1993. Catalogue of cephalopods at the National Marine Mammal Laboratory. NOAA Technical Memo NMFS-AFSC-16, 183 pp.

Flamigni, C. & Giovanardi, O. 1984. Biological data, collected during the Pipeta expeditions on the squid *Loligo vulgaris* Lam in the Adriatic. *FAO Fisheries Report* **290**, 143–146.

Food and Agricultural Organization (FAO). 1986. *Report from the Third ad hoc Working Party on the Evaluation of the Cephalopod Stocks in the Northern Area of the COPACE,* Dakar, CECAF project. CECAF/TECH/86/41, Rome.

Forsythe, J.W. & Hanlon, R.T. 1989. Growth of the eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). *Aquaculture and Fisheries Management* **20**, 1–14.

Forsythe, J.W. & van Heukelem, W.F., 1987. Growth. In *Cephalopod Life Cycles Vol. 2: Comparative Reviews*, P.R. Boyle (ed.). London: Academic Press, 135–156.

Frid, C.L.J., Harwood, K.G., Hall, S.J. & Hall, J.A. 2000. Long-term changes in the benthic communities on North Sea fishing grounds. *ICES Journal of Marine Science* **57**, 1303–1309.

Frodello, J.P, Romeo, M. & Viale, D. 2000. Distribution of mercury in the organs and tissues of five toothed whale species of the Mediterranean. *Evironmental Pollution* **108**, 447–452.

FRS. 1998. Environmental monitoring of the seas around Scotland 1994–1997. Fisheries Research Services Report, Marine Laboratory, Aberdeen.

Furness, R.W. 1994. An estimate of the quantity of squid consumed by seabirds in the eastern North Atlantic and adjoining seas. *Fisheries Research* **21**, 165–177.

Gaard, E. 1987. An investigation of the squid *Loligo forbesi* Steenstrup on Faroe Bank. *International Council for the Exploration of the Sea*, ICES CM1987/K:18. ICES: Copenhagen.

Gage, J.D. & Tyler, P.A. 1991. *Deep Sea Biology: A Natural History of Organisms at the Deep-sea Floor.* Cambridge, U.K.: Cambridge University Press.

Garthe, S., Montevecchi, W.A., Ojowski, U. & Stenhouse, I.J. 2004. Diets of northern fulmar (*Fulmaris glacialis*) chicks in the northwest Atlantic Ocean. *Polar Biology* **27**, 277–280.

Georgakarakos, S., Haralabous, J., Valavanis, V. Arvanitidis, C., Koutsoubas, D. & Kapantagakis, A. 2002. Loliginid and ommastrephid stock prediction in Greek waters using time series analysis techniques. *Bulletin of Marine Science* **71**, 269–287.

Gi Leon, I.G. 1982. *Etude de populations de seiches (*Sepia officinalis *Linné) du Golfe de Gascogne*. Unpublished Ph.D. thesis, Université de Nantes.

González, A.F., Castro, B.G. & Guerra, A., 1996b. Age and growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis. *ICES Journal of Marine Science* **53**, 802–810.

González, A.F., Otero, J., Guerra, A., Prego, R., Rocha, F.J. & Dale, A.W. 2005. Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain). *Journal of Plankton Research* **27**, 271–277.

González, A.F., Rasero, M. & Guerra, A. 1994. Preliminary study of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in northern Spanish Atlantic waters. *Fisheries Research* **21**, 115–126.

González, A.F., Rasero, M. & Guerra, A., 1996a. La explotación de *Illex coindetii* y *Todaropsis eblanae* (Mollusca: Cephalopoda) en aguas de Galicia. *Nova Acta Cientifica Compostelana* **6**, 3–21.

González, A.F. & Sánchez, P. 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. *Scientia Marina* **66**, 199–208.

Goodman-Lowe, G.D. 1998. Diet of the Hawaiian monk seal (*Monachus schauinslandi*) from the northwestern Hawaiian Islands during 1991 and 1994. *Marine Biology* **132**, 535–546.

Gowland, F.C., Boyle, P.R. & Noble, L.R. 2002. Morphological variation provides a method of estimating thermal niche in hatchlings of the squid *Loligo forbesi* (Mollusca: Cephalopoda). *Journal of Zoology* **258**, 505–513.

Grieg J.A. 1930. The Cephalopod Fauna of Svalbard. *Tromsó Museums Ǻrshefter Naturhistorisk* **53**, 1–19.

Grimpe, G. 1925. Zur Kenntnis der Cephalopodenfauna der Nordsee. *Wissenschaftliche Meeresuntersuchungen Helgoland* **16**, 1–124.

Guerra, A. 1978. Sobre la alimentación y el comportamiento alimentario de *Octopus vulgaris*. *Investigación Pesquera* **42**, 351–364.

Guerra, A. 1982. Cephalopods collected in the Gulfo de Cadiz 81 cruise to Southwest Spain. *Resultados Cientificos* **10**, 17–50.

Guerra, A. 1985. Food of the cuttlefish *Sepia officinalis* and *S. elegans* in the Ria de Vigo (NW Spain) (Mollusca: Cephalopoda). *Journal of Zoology* **207**, 511–519.

Guerra, A. 1992. Mollusca, Cephalopoda. In *Fauna Iberica. Museo Nacional de Ciencias Naturales*, M.A. Ramos (ed.). Madrid: CSIC.

Guerra, A. & Castro, B.G. 1989. Some aspects of the biology of *Sepia elegans* (Cephalopoda, Sepioidea) from the Ria de Vigo, northwest Spain. *Vie et Milieu* **39**, 213–218.

Guerra, A., Gonzalez, A.E., Dawe, E.G. & Rocha, F. 2004a. Records of giant squid in the NE Atlantic, and two records of male *Architeuthis* sp. off the Iberian peninsula. *Journal of the Marine Biological Association of the United Kingdom* **84**, 427–431.

Guerra, A., González, A.F., Rocha, F., Gracía, J. & Vecchione, M. 2004b. Calamares gigantes varados: víctimas de exploraciones acústicas. *Investigación y Ciencia* **334**, 35–37.

Guerra, A. & Rocha, F. 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). *Fisheries Research* **21**, 43–70.

Guerra, A., Sánchez, P. & Rocha, F. 1994. The Spanish fishery for *Loligo*: recent trends. *Fisheries Research* **21**, 217–230.

Hamabe, M., Hamuro, C. & Ogura, M. 1982. *Squid Jigging from Small Boats.* Farnham, U.K.: Fishing News Books.

Hanlon, R.T. & Messenger, J. 1998. *Cephalopod Behaviour.* Cambridge, U.K.: Cambridge University Press.

Hanlon, R.T., Yang, W.T., Turk, P.E., Lee, P.G. & Hixon, R.F. 1989. Laboratory culture and estimated life span of eastern Atlantic squid, *Loligo forbesi* Steenstrup, 1856 (Mollusca: Cephalopoda). *Aquaculture and Fisheries Management* **20**, 15–33.

Hastie, L.C., Joy, J.B., Pierce, G.J. & Yau, C. 1994. Reproductive biology of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* **74**, 367–382.

Heldal, H.E., Varskog, P. & Føyn, L. 2002. Distribution of selected anthropogenic radionuclides (^{137}Cs, ^{238}Pu, $^{239,\ 240}$PU and ^{241}Am) in marine sediments with emphasis on the Spitsbergen-Bear Island area. *Science of the Total Environment* **293**, 233–245.

Hernández-Garcia, V. 1995. The diet of the swordfish *Xiphias gladius* Linnaeus, 1758, in the central east Atlantic, with emphasis on the role of cephalopods. *Fishery Bulletin* **93**, 403–411.

Hernández-Garcia, V. 2002. Reproductive biology of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) off northwest Africa (4°N, 35°N). *Bulletin of Marine Science* **71**, 347–366.

Herrmann, M., Gonschior, H. & Piatkowski, U. 2001. Hydrographic changes push European common squid *Alloteuthis subulata* into Kiel Bay, western Baltic Sea. *International Council for the Exploration of the Sea*, ICES CM 2001/K:13. ICES: Copenhagen.

Heyraud, M., Cherry, R.D., Oschadleus, H.D., Augustyn, C.J., Cherry, M.I. & Sealy, J.C. 1994. Polonium-210 and lead-210 in edible molluscs from near the Cape of Good Hope: sources of variability in polonium-210 concentrations. *Journal of Environmental Radioactivity* **24**, 253–272.

Hislop, J.R.G., Robb, A.P., Bell, M.A. & 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.

Hjelset, A.M., Andersen, M., Gjertz, I., Lydersen, C. & Gulliksen, B. 1999. Feeding habits of bearded seals (*Erignathus barbatus*) from the Svalbard area, Norway. *Polar Biology* **21**, 186–193.

Hjort, J.& Ruud, J.T. 1929. Whaling and fishing in the North Atlantic. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **56**, 1–123.

Holme, N.A. 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom* **54**, 481–503.

Hornborg, S. 2005. *The Swedish cephalopod fauna. Species composition and patterns of abundance.* Unpublished M.Sc. thesis, University Göteborg.

Howard, F.G. 1979. Recent trends in the Scottish fishery for *Loligo forbesi*, together with some notes on the biology of the species. *International Council for the Exploration of the Sea*, ICES CM 1979/K:36. ICES: Copenhagen.

Hughes, S. 1998. *Growth history patterns in squid as assessed by gladius structure*. Unpublished Ph.D. thesis, University of Aberdeen.

Iglesias, J., Fuentes, L., Sánchez, F.J., Otero, J.J., Moxica, C. & Lago, M.J. 2006. First feeding of *Octopus vulgaris* Cuvier, 1797 paralarvae using *Artemia*: effect of prey size, prey density and feeding frequency. *Aquaculture* **261**, 817–822.

Iglesias, J., Otero, J.J., Moxica, C., Fuentes, L. & Sánchez, F.J. 2004. The completed life cycle of the octopus (*Octopus vulgaris* Cuvier) under culture conditions: paralarval rearing using *Artemia* and zoeae, and first data on juvenile growth up to eight months of age. *Aquaculture International* **12**, 481–487.

Iglesias, J., Sánchez, F.J., Bersano, J.G.F., Carrasco, J.F., Dhont, J., Fuentes, L., Linares, F., Muñoz, J.L., Okumura, S., Roo, J., Van der Meeren, T., Vidal, E.A.G. & Villanueva, R. 2007. Rearing of *Octopus vulgaris* paralarvae: present status, bottlenecks and trends. *Aquaculture* **226**, 1–15.

Imamura, S. 1990. Larval rearing of octopus (*Octopus vulgaris* Cuvier). The progress of technological development and some problems remaining. *Collecting and Breeding* **52**, 339–343.

Imber, M.J., Jolly, J.N. & Brooke, M.L. 1995. Food of three sympatric gadfly petrels (*Pterodroma* spp.) breeding on the Pitcairn Islands. *Biological Journal of the Linnean Society* **56**, 233–240.

Itami, K., Izawa, Y. Maeda, S. & Nakai, K. 1963. Notes on the laboratory culture of the octopus larvae. *Nippon Suissan Gakkaishi* **29**, 514–520.

Jaekel, S., 1937. Tintenfische in der westlichen Ostsee. *Archives Mulluskenkunde* **69**, 129–136.

Jereb, P., Massi, D., Norrito, G. & Fiorentino, F. 2001. Preliminary observation of environmental effects on spatial distribution and abundance of *Eledone cirrhosa* and *Illex coindetii* in the Strait of Sicily (Central Mediterranean Sea). *International Council for the Exploration of the Sea,* ICES CM 2001/K:34.

Jereb, P. & Ragonese, S. 1991a. The association of the squid *Illex coindetii* (Cephalopoda) with target species trawled in the Sicilian Channel. *Bulletin of Marine Science* **49**, 664.

Jereb, P., & Ragonese S. 1991b. The role played by *Sepia officinalis* L. 1758, in the Southern Sicilian fisheries [Il ruolo della seppia comune, *S. officinalis*, nella pesca siciliana.] In *The Cuttlefish,* E. Boucaud-Camou (ed.). *Acta 1st International Symposium on the Cuttlefish Sepia*. Caen: Publications Université de Caen, 349.

Jereb, P. & Ragonese, S. 1995. An outline of the biology of the squid *Illex coindetii* in the Sicilian Channel (Central Mediterranean). *Journal of the Marine Biological Association of the United Kingdom* **75**, 373–390.

Jereb, P. & Roper, C.F.E. 2005. *Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Vol. 1. Chambered Nautiluses and Sepiods (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae).* FAO Species Catalogue for Fishery Purposes No. 4, Vol. 1. Rome: FAO.

Joy, J.B. 1989. *The fishery biology of ommastrephid squids in Shetland waters*. Unpublished M.Sc. thesis, University of Aberdeen.

Joy, J.B. 1990. The fishery biology of *Todarodes sagittatus* in Shetland waters. *Journal of Cephalopod Biology* **1**: 1–19.

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

Korzun, Y.V., Nesis K.N., Nigmatullin Ch.M., Ostapenko A.A. & Pinchukov M.A. 1979. New data on the distribution of squids, Family Ommastrephidae in the world ocean. *Oceanology* **19**, 472–475.

Koyama, J., Nanamori, N. & Segawa, S. 2000. Bioaccumulation of waterborne and dietary cadmium by oval squid, *Sepioteuthis lessioniana* and its distribution among organs. *Marine Pollution Bulletin* **40**, 961–967.

Kristensen, T.K. 1983. *Gonatus fabricii*. In *Cephalopod Life Cycles. Vol 1. Species Accounts*, P.R. Boyle (ed.). London: Academic Press, 159–173.

Kristensen, T.K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. *Meddelelser om Grønland, Bioscience* **13**, 1–20.

Kunisaki, N. 2000. Nutritional properties of squid and cuttlefish. In *Nutritional and Functional Properties of Squid and Cuttlefish,* M. Okozumi & T. Fujii (eds). Tokyo, Japan: National Co-operative Association of Squid Producers, 22–59.

Laptikhovsky, V. 2000. Fecundity of the squid *Loligo vulgaris* Lamarck, 1798 (Myopsida, Loliginidae) off northwest Africa. *Scientia Marina* **64**, 275–278.

Laptikhovsky, V., Salman, A., Önsoy, B. & Katagan, T. 2002. Systematic position and reproduction of squid of the genus *Alloteuthis* (Cephalopoda: Loliginidae) in the eastern Mediterranean. *Journal of the Marine Biological Association of the United Kingdom* **82**, 983–985.

Laptikhovsky, V.V. & Nigmatullin, C.M. 1999. Egg size and fecundity in females of the subfamilies Todaropsinae and Todarodinae (Cephalopoda: Ommastrephidae). *Journal of the Marine Biological Association of the United Kingdom* **79**, 569–570.

Lahaye, V., Bustamante, P., Spitz, J., Das, K., Meynier, L., Magnin, V., Dabin, W. & Caurant, F. 2005. Long-term dietary preferences of common dolphins in the Bay of Biscay using a metalic tracer. *Marine Ecology Progess Series* **305**, 275–285.

Leftkaditou, E., Maiorano, P. & Mytilineou, Ch. 2001. Cephalopod Species Captured by Deep-Water Exploratory Trawling in the Eastern Ionian Sea. *NAFO Special Symposium on Deep-Sea Fisheries*, Varadero, Cuba, September 2001, NAFO SCR Doc. 01/131.

Lefkatidou, E. & Papaconstantinou, C. 1995. Distribution, growth and maturity of *E. cirrhosa* (Cephalopoda Octopoda) in the Thracian Sea (eastern Mediterranean). *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee* **34**, 247.

Lefkatidou, E., Souplet, A., Peristeraki, N., Gonzalez, M., Kavadas, S. Vidoris, P., Cuccu, D. & Papaconstantinou, C. 2000. Preliminary investigation of factors affecting the spatial distribution and abundance of *Eledone cirrhosa* (Cephalopoda Octopoda) in the Mediterranean Sea. In *Demersal Resources in the Mediterranean*, J.A. Bertrand & G. Relini (eds). Ifremer, *Actes de Colloques* **26**, 53–63.

Le Goff, R. & Daguzan, J. 1991. Growth and life cycles of the cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) in south Brittany (France). *Bulletin of Marine Science* **49**, 341–348.

Lelli, S., Belluscio, A., Carpentieri, P. & Colloca, F. 2005. Ecologia trofica di *Illex coindetii* e *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) nel Mar Tirreno centrale. *Biologia Marina Mediterranea* **12**, 531–534.

Livingston, H.D. & Povinec, P.P. 2000. Anthropogenic marine radioactivity. *Ocean and Coastal Management* **43**, 689–712.

lo Bianco, S. 1909. Notizie biologiche reguardanti sepcialmente il periodo di maturá sessuale degli animali del Golfo di Napoli. *Mitteilungen Zoologischen Station zu Neapel* **19**, 51–761.

López, A. 2002. *Estatus dos pequenos cetáceos da plataforma de Galicia.* Unpublished Ph.D. thesis, Universidad de Santiago de Compostela.

Lordan, C., Burnell, G.M. & Cross, T.F. 1998. The diet and ecological importance of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Irish waters. *South African Journal of Marine Science* **20**, 153–164.

Lordan, C. & Casey, J. 1999. The first evidence of offshore spawning in the squid species *Loligo forbesi*. *Journal of the Marine Biological Association of the United Kingdom* **79**, 379–381.

Lordan, C., Collins, M.A., Key, L.N. & Browne, E.D. 2001. The biology of the ommastrephid squid, *Todarodes sagittatus*, in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **81**, 299–306.

Lu, C.C. 1973. *Systematics and zoogeography of the squid genus* Illex *(Oegopsida: Cephalopoda)*. Unpublished Ph.D. thesis, Memorial University of Newfoundland.

Lu, C.C. 1982. First record of *Todaropsis eblanae* (Ball, 1841) (Cephalopoda: Oegopsidae) in the Pacific Ocean. *Venus (Japanese Journal of Malacology)* **41**, 67–70.

Lum-Kong, A., Pierce, G.J. & Yau, C. 1992. Timing of spawning and recruitment in *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* **72**, 301–311.

Lydersen, C., Gjertz, I. & Weslawski, J.M. 1989. Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. *Polar Research* **25**, 107–114.

Macalaster, E. 1976. *The natural history and biology of a deep-water octopus,* Bathypolypus arcticus *(Prosch)*. Unpublished M.Sc. thesis, Dalhousie University.

MacNaughton, R., Rogan, E., Hernández-García, V. & Lordan, C. 1998. The importance of cephalopods in the diet of blue shark (*Prionace glauca*) south and west of Ireland. *International Council for the Exploration of the Sea*, ICES CM/M:07. ICES: Copenhagen.

Mangold, K. 1987. Reproduction. In *Cephalopod Life Cycles. Vol. 2. Comparative Reviews*, P.R. Boyle (ed.). London: Academic Press, 157–200.

Mangold, K. & Froesch, D. 1977. A reconsideration of factors associated with sexual maturation. *Symposia of the Zoological Society of London* **38**, 541–555.

Mangold, K. & von Boletzky, S. 1987. Cephalopodes. In *Fiches FAO d'Identification des Espèces pour les Besoins de la Pèche (Rev. 1) Méditeranée et mer Noire. Zone de Peche 37*, W. Fischer et al. (eds). Rome: FAO, 633–714.

Mangold, K., von Boletzky, S. & Froesch, D. 1971. Reproductive biology and embryonic development of *Eledone cirrhosa* (Cephalopoda: Octopoda). *Marine Biology* **8**, 109–117.

Mangold-Wirz, K. 1963. Biologie des cephalopods benthiques et nectoniques de la Mer Catalane. *Vie Milieu* **13**, 1–285.

Martin, B. & Christiansen, B. 1997. Diets and standing stocks of benthopelagic fishes at two bathymetrically different midoceanic localities in the northeast Atlantic. *Deep-Sea Research Part 1* **44**, 541–558.

Martin, J.H. & Flegal, A.R. 1975. High copper concentrations in squid livers in association with elevated levels of silver, cadmium and zinc. *Marine Biology* **30**, 51–55.

Martins, H.R. 1982. Biological studies of the exploited stock of *Loligo forbesi* (Mollusca: Cephalopoda) in the Azores. *Journal of the Marine Biological Association of the United Kingdom* **62**, 799–808.

Martins, M.C. 1997. *Biology of pre- and post-hatching stages of* Loligo vulgaris *Lamarck, 1798 and* Loligo forbesi *Steenstrup, 1856 (Mollusca, Cephalopoda).* Unpublished Ph.D. thesis, University of Aberdeen.

Massy, A.L. 1909. The Cephalopoda Dibranchia of the coasts of Ireland. *Scientific Investigations of the Fisheries Branch, Department of Agriculture for Ireland, 1907,* **1**, 1–39.

Matallanas, J., Casadevall, M., Carrasson, M., Boix, J. & Fernandez, V. 1995. The food of *Seriola dumerili* (Pisces: Carangidae) in the Catalan Sea (western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom* **75**, 257–260.

Menzie, C.A. 1983. Environmental concerns related to offshore oil and gas activities: muddy issues. *Oceanus* **26**, 32–38.

Meynier, L. 2004. *Food and feeding ecology of the common dolphin,* Delphinus delphis *in the Bay of Biscay: intraspecific dietary variation and food transfer modelling.* Unpublished M.Sc. thesis, University of Aberdeen.

Miramand, P. & Bentley, D. 1992. Concentration and distribution of heavy metals in tissues of two cephalopods, *Eledone cirrhosa* and *Sepia officinalis*, from the French coast of the English Channel. *Marine Biology* **114**, 407–414.

Moiseev, S.I. 1987. Underwater observations of North Atlantic squids from the manned submersible 'Sever 2'. In *Underwater Fishery Investigations. Collection of Scientific Papers.* Murmansk, Russia: PINRO, 71–78.

Moiseev, S.I. 1991. Observation of the vertical distribution and behaviour of nektonic squids using manned submersibles. *Bulletin of Marine Science* **49**, 446–456.

Moiseev, S.I. 2001. *Vertical Distribution and Behaviour of Nektonic Squid (Family Ommastrephidae) and Some Other Groups of Cephalopods*. Moscow: P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences.

Moreno, A. 1990. Alloteuthis *spp. (Cephalopoda: Loliginidae), um recurso natural subexplorado. Aspectos da sua biologia.* Unpublished Diplom. thesis, Universidade de Lisboa.

Moreno, A. 1995. Aspectos da biologia de *Alloteuthis subulata* e distribuição de *Alloteuthis* spp. (Cephalopoda: Loliginidae) nas águas portuguesas. *Relatorios Cientificos e Tecnicos Instituto Portugues de Investigacao Maritima* Lisbon, Portugal, **8**.

Moreno, A., Cunha, M. & Pereira, J.M.F. 1994. Population biology of veined squid (*Loligo forbesi*) and European squid (*Loligo vulgaris*) from the Portuguese coast. *Fisheries Research* **21**, 71–86.

Moreno, A., dos Santos, A., Piatkowski, U., Santos, A.M.P., & Cabral, H. 2009. Distribution of cephalopod paralarvae in relation to the regional oceanography of western Iberia. *Journal of Plankton Research* **31**, 73–91.

Moreno, A. & Pereira, J.M.F. 1998. Cephalopod paralarval distribution in Iberian Atlantic waters. *International Council for the Exploration of the Sea*, ICES CM 1998/M: 42.

Moreno, A., Pereira, J., Arvanitidis, C., Robin, J.P., Koutsoubas, D., Perales-Raya, C., Cunha, M.M., Balguerías, E. & Denis, V. 2002. Biological variation of *Loligo vulgaris* (Cephalopoda: Loliginidae) in the eastern Atlantic and Mediterranean. *Bulletin of Marine Science* **71**, 515–534.

Moreno, A. & Sousa Reis, C. 1995. Seasonal distribution of loliginid early young stages in the Portuguese continental shelf. *International Council for the Exploration of the Sea,* ICES CM 1995/K:32.

Moriyasu, M. 1981. *Biologie des pêches de céphalopodes benthiques. Application aux éledones, Eledone cirrhosa (Lam., 1798) du Golfe du Lion.* Thesis, Université des Sciences et Techniques du Langue du Languedoc, Montpellier, 225 pp.

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

Muus, B.J. 1959. Skallus, Søtænder, Blæksprutter. *Danmarks Fauna* **65**, 293 pp. København: Dansk Naturhistorisk Forening.

Najai, S. 1983. *Contribution à l'étude de la biologie des pêches des Céphalopodes de Tunisie. Application à l'espèce Sepia officinalis Linné, 1758.* Unpublished Ph.D. thesis, Faculté des Sciences de Tunis.

Neff, J.M., Rabalais, N.N. & Boesch, D.F. 1987. Offshore oil and gas development activities potentially causing long-term environmental effects. In *Long-term Environmental Effects of Offshore Oil and Gas Development,* D.F. Boesch & N.N. Rabalais (eds). London: Elsevier Applied Science, 149–173.

Nesis, K. 1979. Squids of the family Ommastrephidae in the Australian-New Zealand region [in Russian]. *Nekton and Ichthyoplankton of the Australian-New Zealand region. Transactions of the P.P. Shirshov Institute of Oceanology* **106**, 140–146.

Nesis, K. 1987. *Cephalopods of the World.* New York: TNP.

Nesis, K.N. 1965. Distribution and feeding of young squids *Gonatus fabricii* in the Labrador Sea and the Norwegian Sea. *Oceanology* **5**, 102–108.

Ngoile, M.A.K. 1987. *Fishery biology of the squid* Loligo forbesi *(Cephalopoda: Lolignindae) in Scottish waters.* Unpublished Ph.D. thesis, University of Aberdeen.

Nigmatullin Ch.M. 1975. Feeding of common species of cephalopoda mollusca from Spanish Sahara and Mauritania shelf [in Russian]. *Trudy AtlantNIRO* **58**, 177–186.

Nigmatullin, Ch.M. 1987. Ecological niche of oceanic squid family Ommastrephidae: ontogenic and evolutionary aspects. In *Molluscs. Results and Perspectives of Investigation. 8th Meeting on the Investigation of Molluscs*, Y.I. Starobogatov et al. (eds). Leningrad: Zoological Leningrad, Institute, USSR Academy of Sciences, 452–454.

Nigmatullin, Ch.M. & Ostapenko, A.A. 1976. Feeding of *Octopus vulgaris* Lam. from the Northwest African coast. *International Council for the Exploration of the Sea*, ICES CM 1976 K:6. ICES: Copenhagen.

Nigmatullin, Ch.M., Parfenyuk, A.V. & Nikolsky, V.N. 1991. Ecology and resources of epipelagic nektonic squids of the Atlantic Ocean and southeastern Pacific Ocean. In *State of Biological Resources of Fishery Industry in the Central and South Atlantic and Eastern Pacific*. Kaliningrad, Russia: AtlantNIRO, 142–177.

Nixon, M. 1983. *Teuthowenia megalops*. In *Cephalopod Life Cycles Vol. 1*, P.R. Boyle (ed.). London: Academic Press, 233–247.

Norman, M.D. 2000. *Cephalopods: A World Guide.* Frankfurt: IKAN.

Nyegaard, M. 2001. *An Analysis of Reproductive Behaviour, Demography, Diet and Spatial Distribution of the European Common Squid (*Alloteuthis subulata*) in the Irish Sea*. Unpublished M.Sc. thesis, University of Tromsø.

O'Dor, R.K. & Balch, N. 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. *NAFO Scientific Council Studies* **9**, 69–76.

O'Dor, R.K., Balch, N., Foy, E.A., Hirtle, R.W.M., Johnston, D.A. & Amaratunga, T. 1982. Embryonic development of the squid *Illex illecebrosus*, and the effect of temperature on development rates. *Journal of Northwest Atlantic Fishery Science* **3**, 41–45.

Orsi Relini, L., Mannini, A., Fiorentino, F., Palandri, G. & Relini, G. 2006. Biology and fishery of *Eledone cirrhosa* in the Ligurian Sea. *Fisheries Research* **78**, 72–78.

Otero, J., Rocha, F., González, A.F., Gracia, J. & Guerra, A. 2005. Modelling artisanal coastal fisheries of Galacia (NW Spain) based on data obtained from fishers: the case of *Octopus vulgaris*. *Scientia Marina* **69**, 577–585.

Ovcharov, O.P., Greze, E.V. & Nikolsky, V.N. 1985. Features of the quantitative distributions of lanternfishes (Mychtophidae) near the surface. *Voprosy Ikhtiologii* **4**, 682–685.

Paulij, W.P., Herman, P.M.J., Van Hannen, E.J. & Denuce, J.M., 1990. The impact of photoperiodicity on hatching of *Loligo vulgaris* and *Loligo forbesi*. *Journal of the Marine Biological Association of the United Kingdom* **70**, 597–610.

Pawson, M.G. 1995. Biogeographical identification of English Channel fish and shellfish stocks. MAFF Fisheries Research Techical Report 99, CEFAS, Lowestoft.

Payne, A.G., Agnew, D.J. & Pierce, G.J. (eds) 2006. Trends and assessment of cephalopod fisheries. *Fisheries Research (Special Issue)* **78**.

Pedersen, J. 1999. Diet comparison between pelagic and demersal whiting in the North Sea. *Journal of Fish Biology* **55**, 1096–1113.

Pereira, J.M.F. 1996. First record of *Sepietta obscura* Naef, 1916 in Atlantic waters. *Biologia Instituto Portugues de Investigacao Maritima* **2**, 97–99.

Pereira, J.M.F., Moreno, A. & Cunha, M.M. 1998. Western European squid distribution: a review. *International Council for the Exploration of the Sea*, ICES CM 1998/M:29. ICES: Copenhagen.

Piatkowski, U. 1998. Modern target sampling techniques provide new insights into the biology of early life stages of pelagic cephalopods. *Biologia Marina Mediterranea* **5**, 260–272.

Pierce, G.J. (ed.) 1999. Data collection for assessment of cephalopod fished stocks. *Report to the Commission of European Communities*, Directorate General for Fisheries Study 96/081, University of Aberdeen.

Pierce, G.J., Bailey, N. & Robin, J.P. 1996. Stock assessment for *Loligo* spp. in the Northeast Atlantic. *International Council for the Exploration of the Sea*, ICES CM 1996/K:23. ICES: Copenhagen.

Pierce, G.J., Bailey, N., Stratoudakis, Y. & Newton, A. 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. *ICES Journal of Marine Science* **55**, 14–33.

Pierce, G.J. & Boyle, P.R. 2003. Empirical modelling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. *Fisheries Research* **59**, 305–326.

Pierce, G.J., Boyle, P.R., Hastie, L.C. & Key, L. 1994a. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fisheries Research* **21**, 17–41.

Pierce, G.J., Boyle, P.R., Hastie, L.C. & Santos, M.B. 1994c. Diets of squid *Loligo forbesi* in the northeast Atlantic. *Fisheries Research* **21**, 149–163.

Pierce, G.J., Boyle, P.R., Hastie, L.C. & Shanks, A.M. 1994b. Distribution and abundance of the fished population of *Loligo forbesi* in UK waters: analysis of fishery data. *Fisheries Research* **21**, 193–216.

Pierce, G.J. & Guerra, A. 1994. Stock assessment methods used for cephalopod fisheries. *Fisheries Research* **21**, 255–285.

Pierce, G.J., Miller, A., Thompson, P.M. & Hislop, J.R.G. 1991. Prey remains in grey seal (*Halichoerus grypus*) faeces from the Moray Firth, north-east Scotland. *Journal of Zoology* **224**, 337–341.

Pierce, G.J. & Santos, M.B. 1996. Trophic interactions of squid *Loligo forbesi* in Scottish waters. In *Aquatic Predators and Their Prey*, S.P.R. Greenstreet & M.L. Tasker (eds). London: Fishing News Books, 58–64.

Pierce, G.J., Santos, M.B., Ross, H.M., Reid, R.J., Patterson, A.I.P., López, A. & Cedeira J., 2007. Diets of teuthophagous small cetaceans from the Scottish and Galician coasts. Poster, European Cetacean Society, San Sebastian, Spain, April 2007.

Pierce, G.J., Stowasser, G., Hastie, L.C. & Bustamante, P. 2008b. Geographic, seasonal and ontogenetic variation in cadmium and mercury concentrations in squid (Cephalopoda: Teuthoidea) from UK waters. *Ecotoxicology and Environmental Safety* **70**, 422–432.

Pierce, G.J., Thorpe, R.S., Hastie, L.C., Brierly, A.S., Guerra, A., Boyle, P.R., Jamieson, R. & Avila, P. 1994d. Geographic variation in *Loligo forbesi* in the northeast Atlantic Ocean: Analysis of morphometric data and tests of causal hypotheses. *Marine Biology* **119**, 541–547.

Pierce, G.J., Valavanis, V.D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J.M., Katara, I., Piatkowski, U., Pereira, J., Balguerias, E., Sobrino, I., Lefkaditou, E., Wang, J., Santurtun, M., Boyle, P.R., Hastie, L.C., MacLeod, C.D., Smith, J.M., Viana, M., Gonzalez, A.F. & Zuur, A.F. 2008a. A review of cephalopod–environment interactions in European Seas. *Hydrobiologia* **612**, 49–70.

Pierce, G.J., Wang, J., Zheng, X., Bellido, J.M., Boyle, P.R., Denis, V. & Robin, J-P. 2001. A cephalopod fishery GIS for the Northeast Atlantic: development and application. *International Journal of Geographical Information Science* **15**, 763–784.

Pierce, G.J., Young, I.A.G. and Wang, J., 2002. An overview of cephalopods relevant to the SEA 2 and SEA 3 Areas. Report No TR_009_Rev1. Department of Trade and Industry. Available HTTP: http://www.offshore-sea.org.uk/consultations/SEA_3/TR_SEA3_Cephalopods.pdf. Accessed September 2008.

Pierce, G.J., Zuur, A.F., Smith, J.M., Santos, M.B., Bailey, N., Chen, C. & Boyle, P.R. 2005. Interannual variation in life-cycle characteristics of the veined squid (*Loligo forbesi*) in Scottish (UK) waters. *Aquatic Living Resources* **18**, 327–340.

Pinchukov, M.A. 1975. *Distribution, biology and intraspecies structure of the Atlantic flying squid* Ommastrephes bartrami *Lesueur, 1821* [in Russian]. Unpublished M.A. thesis (in Russian), Kazan University, 68.

Pörtner, H.O., Langenbuch, M. & Reipschläger, A. 2004. Biological impact of elevated ocean CO_2 concentrations: lessons from animal physiology and earth history. *Journal of Oceanography* **60**, 705–718.

Potelov, V., Nilssen, K.T., Svetochev, V. & Haug, T. 1997. Feeding habits of harp *Phoca groenlandica* and hooded seals *Cystophora cristata* during moult (April to June) in the Greenland Sea. *NAMMCO Scientific Publications* **2**, 40–49.

Quetglas, A., Alemany, F., Carbonell, A., Merella, P., & Sánchez, P. 1998a. Some aspects of the biology of *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) from the Balearic Sea (Western Mediterranean). *Scientia Marina* **62**, 73–82.

Quetglas, A., Alemany, F., Carbonell, A., Merella, P., & Sánchez, P. 1998b. Biology and fishery of *Octopus vulgaris* Cuvier, 1797, caught by trawlers in Mallorca (Balearic Sea, Western Mediterranean). *Fisheries Research* **36**, 237–249.

Quetglas, A., Carbonell, A. & Sánchez, P. 2000. Demersal continental shelf and upper slope cephalopods assemblages from the Balearic Sea (north-western Mediterranean): biological aspects of some deep-sea species. *Estuarine and Coastal Shelf Science* **50**, 739–749.

Rae, B.B. & Lamont, J.M. 1963. Rare marine invertebrates found in the Scottish area. *Scottish Naturalist* **71**, 23–28.

Ragonese, S. & Bianchini, M. L. 1990. Sulla fattilità della pesca dei totani tramite 'jigging' nel Canale di Sicilia (Cephalopoda: Oegopsida). *Quaderni dell' Istituto di Idrobiologia e Acquacoltura 'G. Brunelli'* **10**, 65–79.

Rasero, M., Gonzalez, A.F., Castro, B.G. & Guerra, A. 1996. Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Illex coindetii* (Cephalopoda: Ommastrephidae) in Galician waters. *Journal of the Marine Biological Association of the United Kingdom* **76**, 73–87.

Raya, C.P., Balguerias, E., Fernández-Núñez, M.M. & Pierce, G.J. 1999. On the reproduction and age of the squid *Loligo vulgaris* from the Saharan Bank (north-west African coast). *Journal of the Marine Biological Association of the United Kingdom* **79**, 111–120.

Reid, A. & Jereb, P. 2005. Family Sepiolidae. In *Cephalopods of the World. An Annotated and Illustrated Catalogue of Species Known to Date. Vol. 1. Chambered Nautiluses and Sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae),* P. Jereb & C.F.E. Roper (eds). FAO Species Catalogue for Fisheries Purposes No. 4(1), Food and Agriculture Organization of the United Nations, Rome, 153–203.

Relini, G. & Orsi Relini, L. 1984. The role of cephalopods in the inshore trawl fishing of the Ligurian Sea. *Oebalia* **10**, 37–58.

Relini, G., Zamboni, A., Masse, D. & Fiorentino, Em. 1998. Behaviour of the exploited demersal resources of the Ligurian Sea through twelve year series of biomass indices. *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranée* **35**, 480–481.

Ridgway, J., Breward, N., Langston, W. J., Lister, R., Rees, J. G. & Rowlatt, S. M. 2003. Distinguishing between natural and anthropogenic sources of metals entering the Irish Sea. *Applied Geochemistry* **18**, 283–309.

Ritchie, J. 1918. Occurrence of a giant squid (*Architeuthis*) on the Scottish coast. *Scottish Naturalist* **1918**, 133–139.

Ritchie, J. 1920. Giant squid cast ashore on N. Uist, Outer Hebrides. *Scottish Naturalist* **71**, 57.

Ritchie, J. 1922. Giant squids on the Scottish coast. *Report of the British Association for the Advancement of Science* **1922**, 423.

Robertson, K.M. & Chivers, S.J. 1997. Prey occurrence in pantropical spotted dolphins, *Stenella attenuata*, from the eastern tropical pacific. *Fishery Bulletin* **95**, 334–348.

Robin, J.P. & Boucaud-Camou, E. 1993. Proportion of squid *Loligo forbesi* and *Loligo vulgaris* in French landings of the Channel bottom trawl fishery: sampling scheme of the Port-en-Bessin landings and preliminary results. *International Council for the Exploration of the Sea*, ICES CM 1993/K:20. ICES: Copenhagen.

Robin, J.P. & Denis, V. 1999. Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. *Journal of Applied Ecology* **36**, 101–110.

Robin, J.P., Denis, V., Royer, J. & Challier, L. 2002. Recruitment, growth and reproduction in *Todaropsis eblanae* (Ball, 1841) in the area fished by French Atlantic trawlers. *Bulletin of Marine Science* **71**, 711–724.

Robinson, R.A., Learmonth, J.A., Hutson, A.M., MacLeod, C.D., Sparks, T.H., Leech, D.I. & Pierce, G.J. 2005. Climate change and migratory species: a report for DEFRA on research contract CR0302. *BTO Research Report 414*, British Trust for Ornithology.

Robson, G.C. 1932. *A Monograph of the Recent Cephalopoda Based on the Collections in the British Museum (Natural History). Part II. The Octopoda (Excluding the Octopodinae), Vol. 2.* London: British Museum (Natural History).

Rocca, E. 1969. Copper distribution in *Octopus vulgaris* Lam. Hepatopancreas. *Comparative Biochemistry and Physiology* **28**, 67–82.

Rocha, F. 1994. *Aspectos biológicos y ecológicos de* Loligo vulgaris *y* Loligo forbesi *(Cephalopoda: Loliginidae) en las costas de Galicia*. Unpublished Ph.D. thesis, Universidad de Oviedo.

Rocha, F., Castro, B.G., Gil, M.S. & Guerra, A. 1994. The diets of *Loligo vulgaris* and *L. forbesi* (Cephalopoda: Loliginidae) in northwestern Spanish Atlantic waters. *Sarsia* **79**, 119–126.

Rocha, F. & Guerra, A. 1999. Age and growth of two sympatric squid *Loligo vulgaris* and *Loligo forbesi*, in Galician waters (north-west Spain). *Journal of the Marine Biological Association of the United Kingdom* **79**, 697–707.

Rocha, F., Guerra, A. & Gonzale, A.F. 2001. A review of reproductive strategies in cephalopods. *Biological Reviews* **76**, 291–304.

Rodhouse, P.G., Clarke, M.R. & Murray, A.W.A. 1987. Cephalopod prey of the wandering albatross *Diomedea exulans*. *Marine Biology* **96**, 1–10.

Rodhouse, P.G., Swinfen, R.C. & Murray, A.W.A. 1988. Life cycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata*. *Marine Ecology Progress Series* **45**, 245–253.

Roeleveld, M.A. 1989. The occurrence of two species of squid *Todarodes* in the Benguela system. *South African Journal of Science* **85**, 659–663.

Roper, C.F.E. & Mangold, K.M. 1998. Systematic and distributional relationships of *Illex coindetii* to the genus *Illex* (Cephalopoda: Ommastrephidae). In *Squid Recruitment Dynamics—The Genus* Illex *as a Model, the Commercial* Illex *Species and Influences on Variability*, P.G. Rodhouse et al. (eds). FAO Fisheries Technical Paper **376**, 13–26. Rome: Food and Agriculture Organization of the United Nations.

Roper, C.F.E., Sweeney, M.J. & Nauen, C.E. 1984. *FAO Species Catalogue Vol. 3. Cephalopods of the World. An Annotated and Illustrated Catalogue of Species of Interest to Fisheries.* FAO Fisheries Synopsis No. 125, **3**. Rome: Food and Agriculture Organization of the United Nations.

Roper, C.F.E. & Young, R.E. 1972. First record of juvenile giant squid, *Architeuthis* (Cephalopoda: Oegopsida). *Proceedings of the Biological Society of Washington* **85**, 205–222.

Rosenberg, A.A., Kirkwood, G.P., Crombie, J.A. & Beddington, J.R. 1990. The assessment of stocks of annual squid species. *Fisheries Research* **8**, 335–350.

Royer, J., Périès, P., Robin, J.P. 2002. Stock assessments of English Channel loliginid squids: updated depletion method and new analytical methods. *ICES Journal of Marine Science* **59**, 445–457.

Royer, J., Pierce, G.J., Foucher, E. & Robin, J.P. 2006. The English Channel stock of *Sepia officinalis*: modelling variability in abundance and impact of the fishery. *Fisheries Research* **78**, 96–106.

Ruby, G. & Knudsen, J. 1972. Cephalopods from the Eastern Mediterranean. *Israeli Journal of Zoology* **21**, 83–97.

Russell, E.S. 1909. Preliminary notices of the Cephalopoda collected by the fishery cruiser *Goldseeker* 1903–1908. *Annals and Magazine of Natural History* **8**, 446–455.

Russell, E.S. 1922. Report on the Cephalopoda collected by the research steamer *Goldseeker* during the years 1903–1908. *Scientific Investigations of the Fishery Board for Scotland, 1921* (3) 1–45.

Ryan, P., Dowdall, A.M., Long, S., Smith, V., Pollard, D. & Cunningham, J.D. 1999. Plutonium and americium in fish, shellfish and seaweed in the Irish environment and their contribution to dose. *Journal of Environmental Radioactivity* **44**, 349–369.

Sacau, M., Pierce, G.J., Stowasser, G., Wang, J. & Santos, M.B. 2005. An overview of cephalopods relevant to the SEA 6 Area. Department of Trade and Industry Report. Available HTTP: http://www.offshore-sea.org.uk/consultations/SEA_6/SEA6_Cephalopods_UOA.pdf. Accessed September 2008.

Sakurai, Y., Young, R.E., Hirota, J., Mangold, K., Vecchione, M., Clarke, M.R. & Bower, J. 1995. Artificial fertilization and development through hatching in the oceanic squids *Ommastrephes bartramii* and *Sthenoteuthis* oualaniensis (Cephalopoda: Ommastrephidae). *Veliger* **38**, 185–191.

Salat, J., Font, J. & Cruzado, A. 1978. Datos oceanogràficos frente a Barcelona (1975–1976). *Datos Informativos Instuto Investigacion Pesquera* 5.

Salman, A. 1998. Reproductive biology of *Sepietta oweniana* (Pfeffer, 1908) (Sepiolidae: Cephalopoda) in the Aegean Sea. *Scientia Marina* **62**, 379–383.

Salman, A., Katagan, T. & Benli, H.A. 1997. Bottom trawl teuthofauna of the Aegean Sea. *Archives of Fisheries and Marine Research* **45**, 183–196.

Salman, A., Katagan, T. & Benli, H.A. 2002. Cephalopod fauna of the eastern Mediterranean. *Turkish Journal of Zoology* **26**, 47–52.

Salman, A. & Laptikhovsky, V. 2002. First occurrence of egg masses of *Loligo forbesi* (Cephalopoda: Loliginidae) in deep waters of the Aegean Sea. *Journal of the Marine Biological Association of the United Kingdom* **82**, 925–926.

Sánchez, P. 1981. Regime alimentaire d' *E. cirrhosa* (Lamarck, 1798) (Mollusca, Cephalopoda) dans la Mer Catalane. *Rapport de la Commission Internationale pour l'Exploration Scientific de la Mer Méditerránea* **27**, 209–212.

Sánchez, P. 1982. Regimen alimentario de *Illex coindetii* (Verany, 1837) en el mar Catalan. *Investigacion Pesquera* **46**, 443–449.

Sánchez, P., Belcari, P. & Sartor, P. 1998. Composition and spatial distribution of cephalopods in two north-western Mediterranean areas. In *Cephalopod Biodiversity, Ecology and Evolution*, A.I.L. Payne et al. (eds). *South African Journal of Marine Science* **20**, 17–24.

Sánchez, P. & Martin, P. 1993. Population dynamics of the exploited cephalopod species of the Catalan Sea (NW Mediterranean). *Scientia Marina* **57**, 153–159.

Sánchez, P., Maynou, F. & Demestre, M. 2004. Modelling catch, effort and price in a juvenile *E. cirrhosa* fishery over a 10-year period. *Fisheries Research* **68**, 319–327.

Sánchez, P. & Obarti, R. 1993. The biology and fishery of *Octopus vulgaris* caught with clay pots on the Spanish Mediterranean coast. In *Recent Advances in Fisheries Biology*, T. Okutani et al. (eds). Tokyo: Tokai University Press, 477–487.

Santos, M.B., Berrow, S. & Pierce, G.J. 2006b. Stomach contents of a sperm whale calf *Physeter macrocephalus* found dead in Co. Clare (Ireland). *Irish Naturalists' Journal* **28**, 272–275.

Santos, M.B., Pierce, G.J., Boyle, P.R., Reid, R.J., Ross, H.M., Patterson, I.A.P., Kinze, C.C., Tougaard, S., Lick, R., Piatkowski, U. & Hernandez-Garcia, V. 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. *Marine Ecology Progress Series* **183**, 281–294.

Santos, M.B., Pierce, G.J., Fernández, R., López, A., Martínez, J.A. & Ieno, E.N. 2005a. Variability in the diet of bottlenose dolphins (*Tursiops truncatus*) in Galician waters and relationship with prey abundance. *International Council for the Exploration of the Sea*, ICES CM 2005/R:29. ICES: Copenhagen.

Santos, M.B., Pierce, G.J., Garcia Hartmann, M., Smeenk, C., Addink, M.J., Kuiken, T., Reid, R.J., Patterson, I.A.P., Lordan, C., Rogan, E. & Mente, E. 2002. Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **82**, 501–507.

Santos, M.B., Pierce, G.J., González, A.F., Santos, F., Vázquez, M.A., Santos, M.A. & Collins, M.A. 2001c. First records of *Taningia danae* (Cephalopoda, Octopoteuthidae) in Galician waters (NW Spain) and in Scottish waters (UK). *Journal of the Marine Biological Association of the United Kingdom* **81**, 143–150.

Santos, M.B., Pierce, G.J., Ieno, E.N., Addink, M., Smeenk, C. & Kinze, C.C. 2005b. Harbour porpoise (*Phocoena phocoena*) feeding ecology in the eastern North Sea. *International Council for the Exploration of the Sea*, ICES CM 2005/R:15. ICES: Copenhagen.

Santos, M.B., Pierce, G.J., López, A., Martínez, J.A., Fernández, M.T., Ieno, E., Porteiro, C., Carrera, P. & Meixide, M. 2004. Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991–2003 and relationship with prey abundance. *International Council for the Exploration of the Sea*, ICES CM 2004/Q:09. ICES: Copenhagen.

Santos, M.B., Pierce, G.J., Lopez, A., Reid, R.J., Ridoux, V. & Mente, E. 2006a. Pygmy sperm whales *Kogia breviceps* in the northeast Atlantic: new information on stomach contents and strandings. *Marine Mammal Science* **22**, 600–616.

Santos, M.B., Pierce, G.J., Reid, R.J., Patterson, I.A.P., Ross, H.M. & Mente, E. 2001b. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Journal of the Marine Biological Association of the United Kingdom* **81**, 873–878.

Santos, M.B., Pierce, G.J., Smeenk, C., Addink, M.J., Kinze, C.C., Tougaard, S. & Herman, J. 2001a. Stomach contents of northern bottlenose whales *Hyperoodon ampullatus* stranded in the North Sea. *Journal of the Marine Biological Association of the United Kingdom* **81**, 143–150.

Sartor, P., Belcari, P., Carbonell, A., González, M., Quetglas, A. & Sánchez, P. 1998. On the interest of cephalopods to trawl fisheries in the western Mediterranean. *South African Journal of Marine Science* **20**, 67–72.

Schipp, R. & Hevert, F. 1978. Distribution of copper and iron in some central organs of *Sepia officinalis* (Cephalopoda). A comparative study by flameless atomic absorption and electron microscopy. *Marine Biology* **47**, 391–399.

Scientific Technological Options Assessment (STOA). 2001. *Possible Toxic Effects from the Nuclear Processing Plants at Sellafield (UK) and Cap de La Hague (France)*. Luxembourg: European Parliament.

Scott, W.B. & Tibbo, S.N. 1968. Food and feeding habits of swordfish, *Xiphias gladius*, in the western North Atlantic. *Journal of the Fisheries Research Board of Canada* **25**, 903–919.

Segawa, S., Yang, W.T., Marthy, H.J. & Hanlon, R.T. 1988. Illustrated embryonic stages of the Eastern Atlantic squid *Loligo forbesi*. *Veliger* **30**, 230–243.

Sen, H. 2004. Effects of periodicity on development and incubation of squid (*Loligo vulgaris* Lamarck, 1798) eggs. *Turkish Journal of Fisheries and Aquatic Sciences* **4**, 1–4.

Shaw, P.W. & Boyle, P.R. 1997. Multiple paternity within the brood of single females of *Loligo forbesi* (Cephalopoda: Loliginidae), demonstrated with microsatellite DNA markers. *Marine Ecology Progress Series* **160**, 279–282, Shaw, P.W., Pierce, G.J. & Boyle, P.R. 1999. Subtle population structuring within a highly vagile marine invertebrate, the veined squid *Loligo forbesi*, demonstrated with microsatellite DNA markers. *Molecular Ecology* **8**, 407–417.

Shaw, R. 1994. An economic description and assessment of the squid catching industry in the UK, Portugal and Spain. *Fisheries Research* **21**, 287–304.

Sheahan, D., Rycroft, R., Allen, Y., Kenny, A., Mason, C. & Irish, R. 2001. Contaminant status of the North Sea. SEA2 Technical Report TR-004. Department of Trade and Industry. Available HTTP: http://www.offshore-sea.org.uk/consultations/SEA_2/TR_SEA2_Contamination.pdf. Accessed September 2008.

Shimko, B. 1989. Biology and peculiarities of the squid *Todarodes sagittatus* (Lamarck) distribution at early life stages. *International Council for the Exploration of the Sea*, ICES CM 1989/K:17.

Sifner, S.K. & Vrgoc, N. 2004. Population structure, maturation and reproduction of the European squid, *Loligo vulgaris* in the central Adriatic Sea. *Fisheries Research* **69**, 239–249.

Silva, L., Sobrino, I. & Ramos, F. 2002. Reproductive biology of the common octopus *Octopus vulgaris* Cuvier 1797, (Cephalopoda, Octopodidae) in the Gulf of Cadiz (SW Spain). *Bulletin of Marine Science* **71**, 837–850.

Sims, D.W., Genner, M.J., Southward, A.J. & Hawkins, S.J. 2001. Timing of squid migration reflects North Atlantic climate variability. *Proceedings of the Royal Society of London* B **268**, 2607–2611.

Smale, M.J. 1996. Cephalopods as prey. IV. Fishes. *Philosophical Transactions of the Royal Society London Series B* **351**, 1067–1081.

Smith, J.M., Pierce, G.J., Zuur, A.F. & Boyle, P.R. 2005. Seasonal patterns of investment in reproductive and somatic tissues in the squid *Loligo forbesi*. *Aquatic Living Resources* **18**, 341–351.

Sousa Reis, C. 1989. Premières observations sur la migration 'trophique' des jeunes cephalopods ('larves') de la côte ouest du Portugal. *Açoreana* **7**, 83–85.

Steimer, S. 1993. *Zur biologie der cephalopodenfauna der südlichen Nordsee*. Unpublished Dipl. thesis, University Kiel.

Stephen, A.C. 1944. The Cephalopoda of Scottish and adjacent waters. *Transactions of the Royal Society of Edinburgh* **61**, 247–270.

Storelli, M.M. & Marcotrigiano, G.O. 1999. Cadmium and total mercury in some cephalopods from the South Adriatic Sea (Italy). *Food Additives and Contaminants* **16**, 261–265.

Stowasser, G., Bustamante, P., MacLeod, C.D., Wang, J. & Pierce, G.J. 2005. Spawning areas and selected metal concentrations in squid (*Loligo forbesi*) in UK waters, with notes on metal concentrations in other squid species. Report to Geotek Ltd and Hartley Anderson Ltd in the context of the.UK Department of Trade and Industry's offshore energy Strategic Environmental Assessment programme. University of Aberdeen, Aberdeen, 24 pp.

Stowasser, G., Pierce G., J., Wang, J., and Santos, M. B. 2004. An overview of cephalopods relevant to the SEA 5 Area. Department of Trade and Industry Report. Available HTTP: http://www.offshore-sea.org.uk/consultations/SEA_5/SEA5_TR_Cephalopods_UOA.pdf. Accessed September 2008.

Sundet, J.H. 1985. A short review on the biology and fishery of the squid *Todarodes sagittatus*. *International Council for the Exploration of the Sea*, 1985/K:44. ICES: Copenhagen.

Tanaka, T., Hayashi, Y. & Ishizawa, M. 1983. Subcellular distribution and binding of heavy metals in the untreated liver of the squid: comparison with data from the livers of cadmium and silver exposed rats. *Experientia* **39**, 746–748.

Tinbergen, L. & Verwey, J. 1945. The biology of *Loligo vulgaris* Lam. *Translations Series of the Fisheries Research Board of Canada* **2733**, 35 pp.

Toll, R.B. & Hess, S.C. 1981. Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the Florida Straits. *Fishery Bulletin* **79**, 765–774.

Tollit, D.J., Black, A.D., Thompson, P.M., Mackay, A., Corpe, H.M., van Parijs, S.M. & Parlane, S. 1998. Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology* **244**, 209–222.

Tursi, A., D'Onghia, G., Lefkatidou, E., Maiorano, P. & Panetta, P. 1995. Population biology of *Elodone cirrhosa* (Mollusca, Cephalopoda) in the north Aegean Sea (eastern Mediterranean Sea). *Vie Milieu* **45**, 139–145.

Unsal, I., Unsal, N., Erk, M.H. & Kabasakal, H. 1999. Demersal cephalopods from the Sea of Mamara, with remarks on some ecological characteristics. *Acta Adriatica* **40**, 105–110.

van Oordt, G.J. 1938. The spermatheca of *Loligo vulgaris* 1. Structure of the spermatheca and function of its unicellular glands. *Quarterly Journal of Microscopical Science* **80**, 593–599.

Vecchione, M. 1987. A multispecies aggregation of cirrate octopods trawled from the north of the Bahamas. *Bulletin of Marine Science* **40**, 78– 84.

Vecchione, M. & Young, R.E. 1997. Aspects of the functional morphology of cirrate octopods: locomotion and feeding. *Vie Milieu* **47**, 101–110.

Velasco, F., Olaso, I., & 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.

Viana, M. 2007. *Migration and distribution of the veined squid* Loligo forbesi *in Scottish (UK) waters*. Unpublished M.Sc. thesis, Universidade do Algarve.

Villa, H., Quintela, J., Coelho, M.L., Icely, J.D. & Andrade, J.P. 1997. Phytoplankton biomass and zooplankton abundance on the south coast of Portugal (Sagres), with special reference to spawning of *Loligo vulgaris*. *Scientia Marina* **61**, 123–129.

Villanueva, R. 1995. Experimental rearing and growth of planktonic *Octopus vulgaris* from hatching to settlement. *Canadian Journal of Fisheries and Aquatic Science*s **52**, 2639–2650.

Villanueva, R. 2000. Observations on the behaviour of the cirrate octopod *Opisthoteuthis grimaldii* (Cephalopoda). *Journal of the Marine Biological Association of the United Kingdom* **80**, 555–556.

Villanueva, R. & Norman, M.D. 2008. Biology of the planktonic stages of benthic octopuses. *Oceanography and Marine Biology: An Annual Review* **46**, 105–202.

Villanueva, R., Segonzac, M. & Guerra, A. 1997. Locomotion modes of deep-sea cirrate octopods (Cephalopoda) based on observations from video recordings on the Mid-Atlantic Ridge. *Marine Biology* **129**, 113–122.

von Boletzky, S. 1979. Observations on early post-embryonic development of *Loligo vulgaris* (Mollusca: Cephalopoda). *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranée* **25/26**:10.

von Boletzky, S. 1983. *Sepia officinalis*. In *Cephalopod Life Cycles. Vol. 1. Species Accounts*, P.R. Boyle (ed.). London: Academic Press, 31–52.

von Boletzky, S. 1987. On egg and capsule dimensions in *Loligo forbesi* (Mollusca: Cephalopoda): a note. *Vie Milieu* **37**, 187–192.

von Boletzky, S. 1988. Preliminary observations on laboratory reared *Sepia orbignyana* (Mollusca Cephalopoda). *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranée* **31**, 256.

von Boletzky, S. & Hanlon, R.T. 1983. A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. In *Proceedings of the Workshop on the Biology and Resource Potential of Cephalopods,* C.F.E. Roper et al. (eds). Melbourne: Memoirs of the National Museum of Victoria, 9–13 March, 1981, **44**, 147–187.

von Boletzky, S., Rowe, L. & Aroles, L. 1973. Spawning and development of the eggs, in the laboratory, of *Illex coindetii*. *Veliger* **15**, 257–258.

von Boletzky, S. & von Boletzky, M. 1973. Observations on the embryonic and post-embryonic development of *Rossia macrosoma* (mollusca: Cephalopoda). *Helgoländer* Wissenschaftliche *Meeresuntersuchungen* **25**, 135–161.

Voss, G.L. & Pearcy, W.G. 1990. Deep-water octopods (Mollusca: Cephalopoda) of the northeastern Pacific. *Proceedings of the Californian Academy of Science* **47**, 47–94.

Voss, N.A. 1969. A monograph of the Cephalopoda of the North Atlantic. The family Histioteuthidae. *Bulletin of Marine Science* **19**, 713–867.

Wallace, W.G. & Lopez, G.R. 1997. Bioavailability of biologically sequestered cadmium and the implications of metal detoxification. *Marine Ecology Progress Series* **147**, 149–157.

Waluda, C.M. & Pierce, G.J., 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in United Kingdom waters. *South African Journal of Marine Science* **20**, 323–336.

Waluda, C.M., Rodhouse, P.G., Podestá, G.P., Trathan, P.N. & Pierce, G.J. 2001. Surface oceanography of the inferred hatchling grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. *Marine Biology* **139**, 671–679.

Wang, J., Pierce, G.J., Boyle, P.R., Denis, V., Robin, J-P. & Bellido, J.M. 2003. Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences—a case study using trawl fishery data in French Atlantic coastal, English Channel and adjacent waters. *ICES Journal of Marine Science* **60**, 1149–1158.

Ward, P. & von Boletzky, S. 1984. Shell implosion depth and implosion morphologies in three species of *Sepia* (Cephalopoda) from the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom* **64**, 955–966.

Watson, W.S., Sumner, D.J., Baker, J.R., Kennedy, S., Reid, R. & Robinson, I. 1999. Radionuclides in seals and porpoises in the coastal waters around the UK. *Science of the Total Environment* **234**, 1–13.

Wiborg, K.F. 1972. The squid *Todarodes sagittatus* (Lamarck). Norwegian investigations in the Norwegian Sea and North Atlantic waters 1970–1972. *International Council for the Exploration of the Sea,* C.M. 1972/K:25. ICES: Copenhagen.

Wiborg, K.F. 1980. *Gonatus fabricii* (Lichtenstein). Investigation in Norwegian Sea and the western Barents Sea, 1982–1983. *International Council for the Exploration of the Sea*, ICES CM 1984/K:19. ICES: Copenhagen.

Wiborg, K.F. & Beck, I.M. 1984. The squid *Todarodes sagittatus* (Lamarck) investigations in the Norwegian coastal and bank waters, July 1983–January 1984, and west of the British Isles, March–April 1984. *International Council for the Exploration of the Sea,* C.M. 1984/K: 20. ICES: Copenhagen.

Wiborg, K.F. & Gjøsæter, J.1981. Squid *Todarodes sagittatus* (Lamarck) distribution and biology in northern waters, April 1980–April 1981. *International Council for the Exploration of the Sea,* C.M. 1981/K:14. ICES: Copenhagen.

Wiborg, K.F., Gjøsæter, J., Beck, I.M. & Fossum, P. 1982. Squid *Todarodes sagittatus* (Lamarck) distribution and biology in northern waters, April 1981–April 1982. *International Council for the Exploration of the Sea,* C.M./K:30. ICES: Copenhagen.

Wiborg, K.F., Beck, I.M. &, Gjøsæter, J. 1984. The squid *Gonatus fabricii*, investigations in the Norwegian Sea and western Barents Sea, 1982–1983. *International Council for the Exploration of the Sea*, ICES CM 1984/K:19. ICES: Copenhagen.

Worms, J. 1983. *Loligo vulgaris*. In *Cephalopod Life Cycles Vol. 1*, P.R. Boyle (ed.). London: Academic Press, 143–158.

Wurtz, M., Matricardi, G. & Rebora, F. 1991. Abundance estimates and distribution of *Sepia elegans* and *Sepia orbignyana* in two fishing areas of the central Mediterranean Trawl-survey 1985–87. In *Acta of the First International Symposium on the cuttlefish Sepia, Caen*, E. Boucaud-Camou (ed.). Caen: Centre de Publications de l'Université de Caen, 301–311.

Xavier, J.C., Croxall, J.P., Trathan, P.N. & Rodhouse, P.G. 2003. Inter-annual variation in the cephalopod component of the diet of the wandering albatross *Diomedea exulans*, breeding at Bird Island, South Georgia. *Marine Biology* **142**, 611–622.

Xunta de Galicia. 2007. *Diario Oficial de Galicia (17.809).* No. 215, Mécores, 7 de Novembro do 2007. http://www.xunta.es.diario-oficial

Yatsu, A. 2000. Age estimation of four oceanic squids, *Ommastrephes bartramii*, *Dosidicus gigas*, *Sthenoteuthis oualaniensis*, and *Illex argentinus* (Cephalopoda, Ommastrephidae) based on statolith microstructure. *Japan Agricultural Research Quarterly* **31**, 75–80.

Yatsu, A., Midorikawa, S., Shimada, T., & Uozumi, Y. 1997. Age and growth of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. *Fisheries Research* **29**, 257–270.

Yau, C. 1994. *The ecology and ontogeny of cephalopod juveniles in Scottish waters*. Unpublished Ph.D. thesis, University of Aberdeen.

Yau, C. & Boyle, P.R. 1996. Ecology of *Sepiola atlantica* (Mollusca: Cephalopoda) in the shallow sub-littoral zone. *Journal of the Marine Biological Association of the United Kingdom* **76**, 733–748.

Young, I.A.G., Pierce, G.J., Daly, H.I., Santos, M.B., Key, L.N., Bailey, N., Robin, J.P., Bishop, A.J., Stowasser, G., Nyegaard, M., Cho, S.K., Rasero, M., & Pereira, J.M.F. 2004. Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). *Fisheries Research* **69**, 211–227.

Young, I.A.G., Pierce, G.J., Stowasser, G., Santos, M.B., Wang, J., Boyle, P.R., Shaw, P.W., Bailey, N., Tuck, I. & Collins, M.A. 2006. The Moray Firth directed squid fishery. *Fisheries Research* **78**, 39–43.

Young, R.E. & Hirota, J. 1990. Descriptions of *Ommastrephes bartramii* paralarvae with evidence of spawning in Hawaiian waters. *Pacific Sci*ence **44**, 71–80.

Young R.E., Harman R.F. & Mangold, K.M. 1985. The eggs and larvae of *Brachioteuthis* sp. (Cephalopoda: Teuthoidea) from Hawaiian waters. *Vie et Milieu* **35**, 203–209.

Zuev, G.V. & Nesis, K.N. 1971. *Squid (Biology and Fishing).* Pishchevaya Promyshlennost, Moscow. (Full English translation, Smithsonian Institution, NMNH, Washington, DC.)

Zuev, G.V., Nesis K.N. & Nigmatullin Ch.M. 1976. The distribution of the genera *Ommastrephes* d'Orbigny, 1835, *Sthenoteuthis* Verill, 1880, *Todarodes* Steenstrup, 1880 (Cephalopoda, Oegopsida) in the Atlantic Ocean [in Russian]. *Bulletin MOIP* **81**, 53–63.

Zuev, G.V. & Nigmatullin Ch.M. 1975. The distribution of a North Atlantic squid *Ommastrephes bastrami* Lesueur, 1821 [in Russian]. *Trudy AtlantNIRO* **58**, 187–192.

Zuur, A.F. & Pierce, G.J. 2004. Common trends in northeast Atlantic squid time series. *Journal of Sea Research* **52**, 57–72.