

A1a.3 Cephalopods

A1a.3.1 UK context

This section describes the biology and ecology of the main cephalopod species found within UK waters. Cephalopods are short-lived, carnivorous invertebrates with rapid growth rates that play an important role in marine food webs. Two superorders of the class Cephalopoda are found within the area: the Decapodiformes (squid and cuttlefish) and the Octopodiformes (octopuses). Most cephalopods lack an external shell and are highly mobile predators. They possess complex eyes, similar to those of vertebrates and are often regarded as the most intelligent of invertebrates. The importance of cephalopod stocks to commercial fisheries is increasing, as fish stocks dwindle and become subject to tighter management (Boyle & Pierce 1994, Lishchenko *et al.* 2021). Information on the life history, distribution and abundance of these species comes from reviews of north-east Atlantic and European cephalopods produced by Hastie *et al.* (2009b), Jereb *et al.* (2015), Lishchenko *et al.* (2021), and references cited within. An overview of important cephalopod species in UK waters is provided, followed by a brief description of features specific to each Regional Sea.

A number of species occur in UK waters, with varying degrees of frequency. Most cephalopods are of one of five groups: the long-finned squids (Loliginids), the short-finned squids (Ommastrephids), bobtails (Sepiolids), cuttlefish and octopuses.

Among the most frequently recorded species are: the long-finned squids, *Alloteuthis subulata* and *Loligo forbesii*; the short finned squid, *Todarodes sagittatus*; other squids, *Gonatus fabricii* and *Onychoteuthis banksii*; the bobtail squids, *Rossia macrosoma*, *Sepiolo atlantica* and *Sepietta oweniana*; the octopus, *Eledone cirrhosa*.

Other species that may be encountered include: *Alloteuthis media*, *Loligo vulgaris*, *Illex coindetii*, *Todaropsis eblanae*, *Rossia glaucopis*, *Sepiolo aurantiaca*, *Sepiolo pfefferi*, *Sepia elegans*, *Sepia officinalis* and *Octopus vulgaris*.

A1a.3.1.1 Long-finned squids

Long-finned squids are neritic, demersal species associated with coastal waters. There are four species present in northern European waters and these are of commercial importance.

The European common squid, *Alloteuthis subulata*, is widespread in the eastern Atlantic. It favours warmer waters and so typically migrates into shallower water in summer and into deeper, relatively warmer waters in winter (de Heij & Baayen 2005, Oesterwind *et al.* 2010). *A. subulata* is very similar to *A. media* and it has been suggested that these may be intra-specific forms rather than true, separate species (Laptikhovsky *et al.* 2002). However, although the distributions of the species overlap significantly, *A. media* is not normally found as far north as *A. subulata* (Jereb *et al.* 2015).

The veined squid, *Loligo forbesii*, is typically found in shallow, coastal waters and continental shelf areas. *L. forbesii* tends to avoid waters cooler than 8.5°C and is the largest (up to around 90cm total length) and most northerly distributed of the long-finned squids (Porteiro & Martins 1994, Oesterwind *et al.* 2010). Maturation takes approximately a year and there is a single extended breeding period from December to May, usually with two pulses of recruitment during this time (Boyle & Pierce 1994). They are terminal spawners, laying their eggs in batches before dying (Rocha *et al.* 2001). Research suggests that individuals migrate inshore from

deep waters in the winter months during the peak of spawning (Stowasser *et al.* 2004). *L. forbesii* is the most commercially important squid species in UK waters. It is often mistaken for the similar European squid, *L. vulgaris*, although the distribution of this slightly smaller species rarely extends into northern UK regions (Jereb *et al.* 2015).

A1a.3.1.2 Short-finned squids

Short-finned squids are powerful swimmers, typically found in open, oceanic waters. The European flying squid, *Todarodes sagittatus*, is an aggressive predator, found in both shallow coastal and deep oceanic environments from surface waters to depths of 4,500m (Collins *et al.* 2001). The species is known to undergo large diurnal migrations, feeding near the surface at night. Spawning has been reported at depths of between 70-800m.

Illex coindetii, the broadtail shortfin squid, is an oceanic, benthic-pelagic species, found in both offshore and coastal waters, down to depths of 800m. The occurrence of the species is frequently correlated with that of prey items such as hake, blue whiting and certain decapod crustaceans (Rasero *et al.* 1996) and appears to be heavily influenced by hydrographic conditions (Jereb *et al.* 2001, cited by Hastie *et al.* 2009b).

A1a.3.1.3 Other squids

Gonatus fabricii, the Boreoatlantic armhook squid, is an oceanic, mesopelagic species, found in deep waters across the north Atlantic. It typically ascends to the surface waters at night to forage. Juveniles are very commonly reported from plankton samples taken all around the UK coast (Collins *et al.* 2001). The species is often confused with the very similar *Gonatus steenstrupi* (Atlantic gonate squid), which is found to the west of the UK, but absent from the North Sea (Roper *et al.* 1984, cited in Hastie *et al.* 2009b).

Onychoteuthis banksii (common clubhook squid) is one of the most abundant oceanic, epipelagic squid in the world (Arkhipkin & Nigmatullin 1997). There is very little published information on the biology and ecology of this species, but it is occasionally caught around the UK.

A1a.3.1.4 Sepioids

The bobtail squids are small, squat decapods that are closely related to cuttlefish. Even the larger species rarely exceed around 65mm in total length. There are seven species present in UK waters which are abundant but too small to exploit commercially. They are typically neritic, benthic species, often found in shallow coastal waters and continental shelf areas over sandy or muddy seabeds (Yau 1994, cited in Hastie *et al.* 2009b).

A1a.3.1.5 Cuttlefish

Cuttlefish are highly developed predatory decapods, which feed on small fish and crustaceans. They control their buoyancy with a unique structure, the cuttlebone, and are commercially important in a number of regions. There are three species of cuttlefish found in UK waters: *Sepia elegans* (elegant cuttlefish), *Sepia officinalis* (common cuttlefish) and *Sepia orbignyana* (pink cuttlefish). Of these *S. officinalis* is both the largest, at up to 400mm mantle length, and the most widespread.

A1a.3.1.6 Octopuses

Most octopuses in UK waters are non-finned (incirrate), although a number of species living in deep waters are finned (cirrate). Very little is known about the biology of these deep water species. Unlike the decapods (squids, sepioids and cuttlefish), octopuses have eight legs

lined with suction cup suckers. A number of species are found in UK waters, although the most common are the curled octopus (*Eledone cirrhosa*) and the common octopus (*Octopus vulgaris*).

The curled (or horned) octopus, *Eledone cirrhosa*, is a small benthic octopus that typically occurs in shallow coastal waters, from the lower shore down to depths of 300m, on a variety of seabed types from soft mud to rocky bottoms (Boyle 1983). The lifecycle of the species varies across its geographic distribution. In the North Sea for example, curled octopuses are thought to display either a one year or a two year cycle, based on individual growth and maturation rates (Boyle *et al.* 1988). Sexual maturation peaks from July to September, followed by spawning (Boyle 1983), with females dying once spent (Guerra 1992, cited in Hastie *et al.* 2009b).

The rather larger common octopus is capable of reaching up to 1.3m in length, but is usually much smaller. It is more or less restricted in UK waters to southern and western coasts, where it inhabits rocky areas (Wilson 2006). Populations fluctuate widely from year to year.

A1a.3.2 Features of Regional Sea 1

Oceanic inflows from the Atlantic, coupled with the numerous shallow inshore habitats, make the northern North Sea a region of greater cephalopod diversity and abundance than the southern North Sea. Among the most frequently recorded species are: the long-finned squids, *A. subulata* and *L. forbesii*; the short finned squid, *T. sagittatus*, *G. fabricii* and *O. banksii*; the bobtail squids, *R. macrosoma*, *S. atlantica* and *S. oweniana*; the octopus, *E. cirrhosa*. Other species that may be encountered in the region include: *I. coindetii*, *T. eblanae*, *R. glaucopsis*, *S. aurantiaca*, *S. pfefferi* and *S. elegans*.

A. subulata is widespread throughout the North Sea (de Heij & Baayen 2005), and is most abundant in central and northern parts in winter (Oesterwind *et al.* 2010). Juveniles (aged approximately 3 months) leave the region in November and return the following spring, while males and females are known to move inshore during summer for the spawning season, which is restricted to June and July in the North Sea (Yau 1994, cited by Hastie *et al.* 2009b). *A. media* is not typically found as far north as the northern North Sea.

The veined squid, *L. forbesii*, is present in greatest numbers along the east coast, around the Shetland Islands and within the Moray Firth between January and March (Oesterwind *et al.* 2010, Stowasser *et al.* 2005). Spawning is thought to begin in winter months in the northern North Sea (Oesterwind *et al.* 2010).

The stout bobtail, *R. macrosoma*, is restricted to the central and northern North Sea as it requires higher salinities than are found in the southern North Sea (de Heij & Baayen 2005). Spawning migrations to inshore areas are known to take place from March to November (Mangold-Wirz 1963, cited in Hastie *et al.* 2009b), with the largest individuals usually arriving earlier in the season (Jereb & Roper 2005, cited in Hastie *et al.* 2009b).

S. atlantica is believed to have an extended spawning season between March and September (Yau & Boyle 1996, cited in Hastie *et al.* 2009b). *S. atlantica* is a very small animal (<2cm) and consequently may be under-reported in surveys; Stephen (1944) cites a record of 256 specimens being taken in a single haul in the North Sea.

The giant squid (*Architeuthis dux*) has been recorded in the northern North Sea, with the occasional stranding, particularly on the Aberdeenshire coast, taking place (Stowasser *et al.* 2004).

A1a.3.3 Features of Regional Sea 2

The southern North Sea is not an ideal habitat for most cephalopods due to its shallow water depths (de Heij & Baayen 2005). The only species that is regularly found in the area in large numbers is *A. subulata*, which typically migrates into the southern North Sea in the summer and is considered the dominant cephalopod species in the region (Oesterwind *et al.* 2010, Jereb *et al.* 2015). Other species recorded in the region are: the long-finned squids, *L. forbesii* and *L. vulgaris*; the short finned squid, *T. eblanae*; the bobtail squids, *S. atlantica*, *S. oweniana* and *R. macrosoma*; the cuttlefish, *S. officinalis*; the octopus, *E. cirrhosa*. These nine species, along with *O. banksii*, are the only cephalopods to have been encountered in the southern North Sea during International Bottom Trawl Surveys and International Beam Trawl Surveys between 1996-2003 (de Heij & Baayen 2005).

L. vulgaris is relatively scarce in the southern North Sea, but is most abundant in the region in late spring to summer (Hornburg 2005, cited in Hastie *et al.* 2009b). It is a benthic spawner, attaching egg masses to hard substrates. The winter spawning period in the North Sea is relatively short (Moreno *et al.* 2002, cited in Hastie *et al.* 2009b).

The common cuttlefish, *S. officinalis*, is a neritic, demersal species, typically found in warm, shallow coastal waters, with a significant number encountered in the southern North Sea. The life-span is approximately two years and the spawning season lasts from early spring to mid summer, with spawning typically taking place in water shallower than 30m (Boucaud *et al.* 1991, cited in Hastie *et al.* 2009b). Mature individuals move inshore to spawn, with larger females migrating earlier in the season than smaller females (Hastie *et al.* 2009b). The black eggs are attached in bunches to substrata on the seabed, with embryo development times increasing at cooler water temperatures, taking approximately 90 days at 15°C and just 40-45 days at 20°C (Hastie *et al.* 2009b).

A1a.3.4 Features of Regional Sea 3

Among the most abundant species in the English Channel are *A. subulata*, *A. media*, *L. forbesii*, *L. vulgaris*, *T. sagittatus* and the cuttlefish *S. officinalis* and *S. elegans*. There are also a number of sepiolids present in the region.

The short-finned squid *A. subulata* and *A. media* are particularly abundant in this region and, unlike in other UK regions, they are present all year round (Rodhouse *et al.* 1988). They display a complex pattern of spawning and recruitment, with 3 separate groups of females spawning in spring, summer and autumn. Males display a more complex and unpredictable pattern (Rodhouse *et al.* 1988).

An important summer breeding population of *L. forbesii* is present in the English Channel. Juveniles hatch in the western English Channel and migrate eastwards through the Channel and as far as the southern North Sea to spawn over the summer months, before returning to the western approaches to spawn and die in December and January (Holme 1974). This migration is driven by sea surface temperature, in common with a number of other cephalopod migrations (Pierce & Boyle 2003). *L. vulgaris* is also more abundant in this region than in more northerly parts of the UK. Data from 1993-1994 shows that *L. vulgaris* is more abundant in catches over winter, while *L. forbesii* dominates hauls in summer (Robin & Boucaud-Camou 1995, cited by Pierce *et al.* 2002). The spawning period of *L. vulgaris* in the English Channel is

relatively short, with activity peaking in February (Moreno *et al.* 2002, cited in Hastie *et al.* 2009b),

S. officinalis represents the most valuable cephalopod fishery resource in southern UK waters and the majority of the catch is taken from the English Channel (Pierce *et al.* 2002). The English Channel population is the northernmost spawning stock for the species, with some reproductive characteristics showing adaptation to cold water (Laptikhovsky *et al.* 2019). Adult cuttlefish accumulate at spawning grounds along the south coast of England in spring, while juveniles migrate westwards to deeper waters in autumn; the relatively deep milder waters of the central axis of the Channel appear to represent the winter hibernation area for this species (Denis & Robin 2001, Jereb *et al.* 2015). *S. elegans* is also present in the region but is less abundant than *S. officinalis*.

A1a.3.5 Features of Regional Sea 4 & 5

Cephalopods commonly found in the western approaches around the south-west of England and the Scilly Isles include: *A. subulata* and *A. media*, *L. forbesii* and *L. vulgaris*, *T. sagittatus* and *T. eblanae*. *I. coindetii* is also common in the region, particularly off the south-west of Cornwall (Arvanitidis *et al.* 2002). The common cuttlefish, *S. officinalis*, and the common octopus, *O. vulgaris* may also be found in these regions. Bobtail squids including *S. atlantica* and *S. oweniana* are also present.

A1a.3.6 Features of Regional Sea 6

Cephalopods frequently recorded in the Irish Sea include *A. subulata* and *L. forbesii*, *T. eblanae* and *T. sagittatus*, *S. officinalis*, *E. cirrhosa* as well as a number of sepiolid species.

A. subulata is the most abundant cephalopod in the region. It is common throughout the Irish Sea, particularly at depths of less than 50m (Collins *et al.* 1995). Distribution of this species is linked to physical factors in spring and autumn with peak abundance observed in the warmest waters in March and October (Nyegaard 2001, cited by Hastie *et al.* 2009b). The demographic structure of the population in the region is seasonal, with mature animals dominating in spring and summer and juveniles dominating in autumn (Nyegaard 2001, cited by Hastie *et al.* 2009b).

The Irish Sea population of *L. forbesii* displays a complex demography with 3 separate cohorts of males (and 2 of females) identified (Collins *et al.* 1995). In research surveys carried out during 2004, particularly high catch numbers were reported in waters to the west of the Isle of Man (Sacau *et al.* 2005).

A1a.3.7 Features of Regional Sea 7

Among the most frequently recorded species are: the long-finned squids, *A. subulata* and *L. forbesii*; the bobtail squids, *R. macrosoma* (which tends to be more abundant off the west coast of Scotland than the east (Yau 1994, cited in Hastie *et al.* 2009b)), *S. atlantica*, *S. aurantiaca* and *S. oweniana*; the octopus, *E. cirrhosa* (which is particularly common in this region). Other species that may be encountered in the region include: *T. sagittatus*, *O. banksii* and the cuttlefish *S. elegans*.

The golden bobtail, *S. aurantiaca*, is typically found at depths of between 0-150m and most commonly at 40m. The high abundance of juveniles in Scottish waters in August and September suggests that the spawning period is similar to that of *S. atlantica*. Otherwise, relatively little is known about the ecology and life history of the species.

S. oweniana is found in shallow coastal waters and continental shelf areas, at depths of between 20-600m, where it favours muddy seabeds. This species is a multiple spawner, with spawning activity taking place between September and February in Scottish waters (Yau 1994, cited in Hastie *et al.* 2009b).

A1a.3.8 Features of Regional Sea 8

Among the most frequently recorded species are: the long-finned squids, *A. subulata* and *L. forbesii*; the short finned squid, *T. sagittatus*; *G. fabricii* and *O. banksii*; the bobtail squids, *R. macrosoma*, *S. atlantica* and *S. oweniana*; the octopus, *E. cirrhosa*. Other species that may occasionally be encountered in the region include: *I. coindetii*, *T. eblanae*, *Galitheuthis armata*, *G. steenstrupi*, *R. glaucopis*, *S. aurantiaca* and *S. pfefferi*.

The European flying squid, *T. sagittatus*, forms huge aggregations around the coasts of Scotland and Shetland in certain years (Joy 1990), although by late December the squid have begun to migrate into deeper continental shelf water to over-winter and spawn – spawning depths of 70-800m have been reported. The similar *T. eblanae* (lesser flying squid), is also known to form large aggregations in the region, although the species rarely ventures into shallow or surface waters.

The sepiolid *R. glaucopis* is generally found in cool, coastal northern waters, typically at depths of approximately 120m. The northern North Sea is the southerly limit of distribution for the species and it is not often recorded in Scottish waters (Yau 1994, cited in Hastie *et al.* 2009b).

A1a.3.9 Features of Regional Sea 9

Among the most frequently recorded species are: the long-finned squid, *L. forbesii*; the short finned squid, *T. sagittatus*; *G. fabricii* and *O. banksii*; the octopuses, *Bathypolypus arcticus* and *Benthoctopus piscatorium*. Other species that may occasionally be encountered in the region include: *T. eblanae*, *G. steenstrupi*, *Brachioteuthis riisei*, *R. glaucopis*, *Graneledone verrucosa* and *E. cirrhosa*.

The deepwater incirrate octopuses *Bathypolypus arcticus* (spoonarm octopus), *Benthoctopus piscatorium* and *Graneledone verrucosa* are widespread throughout the deep, cool waters of the north Atlantic, down to depths of 2,500m and have all been recorded in the Faroe-Shetland Channel (Collins *et al.* 2001). Little is known about the ecology of these predatory species.

A1a.3.10 Features of Regional Sea 10 & 11

Among the most frequently recorded species in these deep-water regions are: *L. forbesii*, *A. subulata*, *T. eblanae*, *T. sagittatus*, *I. coindetii*, the bobtail *S. atlantica* and the octopus *E. cirrhosa*. A large number of deep water octopuses are found in these regions such as the incirrate species *B. arcticus*, *B. piscatorium* and *G. verrucosa*. Species of cirrate octopuses, about which very little is known, are also present in these regions. Examples include *Opisthoteuthis massyae*, *Cirrotheuthis muelleri* and *Staurotheuthis syrtensis* (Hastie *et al.* 2006).

A1a.3.11 Evolution of the baseline

A1a.3.11.1 Climate

Cephalopods have been shown to respond both actively and passively to environmental variations. Typically, oceanographic conditions will particularly affect pelagic species, while benthic species distribution tends to be driven more by the physical habitat (*i.e.* seabed conditions) and coastal species by water quality and salinity (Pierce *et al.* 2009). Due to the

complicated life-histories and reproductive strategies displayed by many species, the response to changing climate is likely to be equally complex.

However, it is known that for many species, temperature has an important influence on a number of life history processes, including recruitment (through maturation rate and the rate of embryonic development), the timing of migration and the distribution range (Boyle 1983). As well as this, food availability and predator abundance and distribution are likely to be affected by changes in the marine environment. Pierce & Boyle (2003) found the abundance of *L. forbesii* in Scottish coastal waters was correlated with a number of environmental indices, including the winter North Atlantic Oscillation index, average sea surface temperature (SST) and sea surface salinity. It was also found that sea surface temperature had an influence on the strength of recruitment in the year. Direct effects of temperature on physiology, life-cycles and life-history of squids were reviewed by Pecl & Jackson (2008) to inform a discussion on the potential impacts at population and ecosystem levels.

The ranges of *L. forbesii* and *L. vulgaris* overlap extensively (Guerra & Rocha 1994), although *L. forbesii* is more abundant in the north of this range and *L. vulgaris* in the south (Pierce *et al.* 1994a). There is a trend of decreasing numbers of *L. forbesii* in the south of its range and increasing numbers in the north, which has been associated with SST (Chen *et al.* 2006). SST has also been linked to the winter abundances of *L. forbesii* in the North Sea (Sims *et al.* 2001), and the distribution of *A. subulata* in the Irish Sea (Nyegaard 2001, cited by Hastie *et al.* 2009b). In the case of *A. subulata*, there is a predominance of small individuals in the Irish Sea during autumn months and more mature individuals during spring and summer, in line with patterns of spawning and hatching in the species. Warmer water may therefore result in an increase in the complexity of the size structure and reproductive cohorts within the population (Hastie *et al.* 2009a).

At the global level, a review of time-series across the last six decades from both fishery dependent and independent sources, has highlighted the expansions of global cephalopod populations across all oceans (Doubleday *et al.* 2017); the increase in abundance across very different species and habitats was interpreted as evidence of link to large-scale processes, with fast, adaptive cephalopod species increasing in abundance over a range of habitats – possibly linked to fishing pressure on finfish and other environmental pressures.

A strong causal relationship between warming sea temperatures and squid distribution and biomass has been the conclusion of the study by van der Kooij *et al.* (2016) who analysed a 35-year time series of squid catches, mainly from the North Sea International Bottom Trawl Survey (IBTS) between 1980 and 2014. The recent evidence of a summer spawning stock for *Illex coindetti* in the North Sea is also thought to be linked to increased temperatures (Oesterwind *et al.* 2020); this species has a tropical, sub-tropical and temperate distribution and the northernmost area previously known for spawning is in Galician waters.

A1a.3.11.2 Ocean acidification

A number of recent studies have examined the impact of ocean acidification on the cuttlefish *S. officinalis*, with CO₂ partial pressure demonstrated to affect the calcification of cuttlebone (an important buoyancy regulation device in the animal) (Gutowska *et al.* 2010a, Dorey *et al.* 2013), as well as acid-base transporter mechanisms in the gills of juvenile cuttlefish (Hu *et al.* 2011). However, Hu *et al.* (2011) and Gutowska *et al.* (2010b) both suggest that the adult *S. officinalis* is an efficient acid-base regulator and is relatively tolerant to hypercapnia. Maneja *et al.* (2011) undertook experimental studies reared under three pCO₂ conditions (700 µatm, 1,400 µatm and 4,000 µatm). At 4,000 µatm, statolith morphology was affected leading to

reduced prey capture efficiency, though there was some recovery in hatchlings. The acid-base regulatory system in the epidermis of embryos of the squid *Sepioteuthis lessoniana*, reported and described by Hu *et al.* (2013), suggests a physiological mechanism exists among cephalopods to regulate pH and tolerate acidic conditions caused by high CO₂ levels.

A1a.3.12 Environmental issues

A1a.3.12.1 Ecological importance

Cephalopods are important elements in marine food webs, both as predators and prey. Whales, dolphins, seals, birds and predatory fish consume large quantities of squid.

Estimates of seabird consumption of cephalopods in the north-east Atlantic are low compared to equivalent seabird populations in the southern Atlantic, possibly due to differences in the relative abundances of squid, fish and zooplankton between the two hemispheres (Boyle & Pierce 1994). The main seabird consumers of (predominantly short-finned) squid in north-west Europe are fulmar (*Fulmarus glacialis*) and Manx shearwater (*Puffinus puffinus*). None of the major seabird populations in the north-east Atlantic feeds regularly on long-finned squid (Boyle & Pierce 1994).

Cetaceans probably have a greater impact on cephalopod populations than seabirds or seals. Most species of cetacean consume cephalopods; mainly octopus and bobtail squid in the smaller species, while some larger cetaceans are specialist squid feeders (Pierce & Santos 1996). Risso's dolphin (*Grampus griseus*) is one of a number of species known to take *Loligo* spp. (Boyle & Pierce 1994), and in fact is widely believed to be primarily a squid feeder (e.g. Hammond *et al.* 2006). Although there is evidence of cephalopods in stomach contents, indications are that most dolphins and the harbour porpoise (*Phocoena phocoena*) are primarily fish-eating (Santos *et al.* 1994). The minke whale (*Balaenoptera acutorostrata*) is also thought to take squid (Pierce 1992). An analysis of the stomach contents of sperm whales (*Physeter macrocephalus*) stranded in Denmark revealed that *G. fabricii* is a key prey species for this cetacean (Simon *et al.* 2003). Several cetaceans, including the white beaked dolphin (*Lagenorhynchus albirostris*), the bottlenose dolphin (*Tursiops truncatus*) and Risso's dolphin, are recorded as consuming *E. cirrhosa*.

Seals are known to take several octopus and squid species, including *Loligo* spp. (Pierce & Santos 1996). The grey seal (*Halichoerus grypus*) was found to eat more octopus than other cephalopods in Scottish waters and octopus can play an important part of the diet of harbour seals (*Phoca vitulina*) (Tollit & Thompson 1996).

Sampling of fish stomachs has shown that a small but significant proportion of the diet of juvenile whitefish is composed of cephalopods (Boyle & Pierce 1994), although cephalopods are a major component of the diet of relatively few fish. Hislop *et al.* (1991) noted that, where cephalopods in fish stomachs were identified, they were usually *Alloteuthis* spp.

Cephalopods are fast, mobile and opportunistic predators themselves and feed on a wide range of prey. Squid operate at a relatively high trophic level for such short-lived species. *L. forbesii* feeds primarily on fish (typically gadoids, clupeids, sandeels and gobies), crustaceans and cephalopods (Boyle & Pierce 1994). As *L. forbesii* grows, the proportion of fish in the diet increases and the proportion of crustaceans decreases (Boyle & Pierce 1994). The relative importance of fish and crustaceans in the diet of *L. vulgaris* is similar to those in the diet of *L. forbesii* (Pierce *et al.* 1994b).

The octopus, *E. cirrhosa*, feeds mainly on crustaceans and molluscs, including lobster (*Homarus gammarus*), edible crab (*Cancer pagurus*) and Norway lobster (*Nephrops norvegicus*) (Boyle 1983). Cuttlefish such as *S. officinalis* also prey on a range of crabs, demersal fish and other cephalopods. Bobtail squid will feed on smaller benthic organisms such as shrimps and mysids, although larger individuals may tackle small crabs and fish.

Only a small number of species are targeted and caught in commercial fisheries around UK waters, but their commercial value is significant and increasing. *Loligo forbesii* is a common component of catches, particularly in the northern North Sea (Arkhipkin *et al.* 2015), while the English Channel cuttlefish fishery is currently the most valuable cephalopod fishery in the north east Atlantic (Royer *et al.* 2006, Arkhipkin *et al.* 2015). Cephalopod populations (or stocks) are not formally assessed on a regular basis and there are no quotas in EU waters; while these stocks are not currently thought to be over-fished, responsible management remains important and efforts are ongoing at the national, regional and European level to inform fishery management and regulation (ICES 2019).

A1a.3.12.2 Contamination and disturbance

Some metals, such as copper and zinc are biologically essential but toxic to most species in large amounts, although others have no known biological role. Cephalopods naturally accumulate high levels of a number of trace metals, such as cadmium (Finger & Smith 1987, Stowasser *et al.* 2005). Comparisons of the copper content revealed very high levels of copper in cephalopods relative to vertebrates, with copper levels in the hepatopancreas (a midgut digestive gland) of *O. vulgaris* and *S. officinalis* one hundred times higher than the mean value for vertebrate liver and 10^5 times that of seawater (Rocca 1969). The hepatopancreas appears to be the main organ for the storage of metals and high concentrations of copper, correlated with high levels of silver, cadmium and zinc, have been reported in the hepatopancreas of various cephalopods (Schipp & Hevert 1978). *E. cirrhosa* accumulates mercury (Hg) rapidly, with concentrations within individuals increasing with body length (Rossi *et al.* 1993). High levels of mercury were also found in the mantle muscle of *L. forbesii* and *T. eblanae* from the North Sea (Craig 1996).

The type and amount of accumulation will be related to diet, habitat and behaviour. For example, cadmium concentration in *L. forbesii* generally decreases with increasing body size, as smaller squid have a higher proportion of cadmium contaminated benthic invertebrates in their diet. Mercury however is retained in the tissues and contamination increases with age and size (Pierce *et al.* 2008). The potential to accumulate trace minerals is positively correlated with trophic level, due to biomagnification through the food web and studies have revealed mean mercury levels in *L. forbesii* to be six times greater than those found in *O. vulgaris* (which operates at a lower trophic level) (Montiero *et al.* 1992). Consequently, this bioaccumulation will continue to affect organisms at higher trophic levels which feed on squid, including cetaceans, fish and humans.

Comparisons between cephalopods, suggest cuttlefish have relatively higher concentrations of contaminants in their tissues. Recent studies have further investigated variability in trace element concentration and its effects on juvenile cuttlefish as well as the potential of pharmaceuticals released in the environment to accumulate and affect cuttlefish survival (ICES 2019 and references therein).

Controlled exposure of cephalopod eggs to heavy metal contamination revealed contrasting bioaccumulation capacities between species, due to the retention properties of egg envelopes (Lacoue-Labarthe *et al.* 2011). Eggs of the cuttlefish *Sepia officinalis* have hard shells enclosing

the embryo and these showed the lowest heavy metal contamination, even after a longer period of exposure. Common octopus (*O. vulgaris*) eggs are only protected by a chorionic membrane and these showed the highest levels of contamination.

All cephalopod species in the North Sea will be sensitive to the disturbance of bottom sediments, although this is only likely to have a serious impact if spawning grounds are disturbed. Any factor disrupting spawning aggregations of squid will also have a negative impact on recruitment. Female squid tend not to be as fecund as finfish and, as they have such a short lifecycle, populations fluctuate greatly from year to year depending upon the success of spawning and recruitment.

A1a.3.12.3 Acoustic disturbance

Hearing in cephalopods is exclusively through reception of particle motion by equilibrium receptor systems, involving statocysts¹ (Budelmann 1990); unlike marine mammals and some fish, cephalopods do not possess organs capable of detecting the pressure component of sound. Best hearing sensitivity appears to be between 100-300Hz; a realistic upper range is ca. 500Hz and reported detections for frequencies up to 1.5kHz are thought to have been an artefact of the experimental setup (Kaifu *et al.* 2008, Mooney *et al.* 2010, Hu *et al.* 2010) (,). This raises the possibility of cephalopods detecting and potentially being disturbed by human activities generating low-frequency noise in the marine environment, including boat traffic, seismic exploration, drilling or construction work.

Evidence of effects is relatively limited. Potential for lethal effects appears limited to explosions at close range (Carroll *et al.* 2017), but acute tissue damage has been reported from giant squids (*Architeuthis dux*) at two incidents of multiple strandings on the north coast of Spain in 2001 and 2003; the presence of seismic surveys in the wider area has been used to suggest airgun pulses as a potential contributing factor to the strandings (Guerra *et al.* 2004). Laboratory exposure studies and a field exposure experiment have demonstrated that physical damage to the statocysts can occur following exposure to high-amplitude sound in *S. officinalis* and *O. vulgaris* (André *et al.* 2011, Solé *et al.* 2013b), and *L. vulgaris* and *I. coindetii* (Solé *et al.* 2013a) and *S. officinalis* (Sole *et al.* 2017). Electron microscopy revealed lesions and permanent damage to the hair cells within the statocysts of individuals exposed providing evidence for a potentially important pathway of effect; as the statocysts are vital organs for maintaining balance in the water column, there is potential for anthropogenic noise to cause permanent physical and behavioural damage to cephalopods. How these experimental results may relate to realistic exposure conditions and effects at population level in the field is still to be determined (Carroll *et al.* 2017).

¹ A statocysts is an organ of varying complexity with a calcareous mass and sensory hair cells capable of determining orientation and acceleration (Budelmann 1990)

References

- André M, Solé M, Lenoir M, Durfort M, Quero C, Mas A, Lombarte A, van der Schaar M, Lopez-Bejar M, Morell M, Zaugg S & Houégnigan L (2011). Low-frequency sounds induce acoustic trauma in cephalopods. *Frontiers in Ecology and the Environment* **9**: 489-493.
- Arkhipkin AI & Nigmatullin C (1997). Ecology of the oceanic squid, *Onychoteuthis banksii*, and the relationship between the genera *Onychoteuthis* and *Chaunoteuthis* (Cephalopoda: Onchyoteuthidae). *Journal of the Marine Biological Association of the United Kingdom* **77**: 839-869.
- Arkhipkin AI, Rodhouse PGK, Pierce GJ, Sauer W, Sakai M, Allcock L, Arguelles J, Bower JR, Castillo G, Ceriola L, Chen C-S, Chen X, Diaz-Santana M, Downey N, González AF, Granados Amores J, Green CP, Guerra A, Hendrickson LC, Ibáñez C, Ito K, Jereb P, Kato Y, Katugin ON, Kawano M, Kidokoro H, Kulik VV, Laptikhowski VV, Lipinski MR, Liu B, Mariátegui L, Marin W, Medina A, Miki K, Miyahara K, Moltschaniwskyj N, Moustahfid H, Nabhitabhata J, Nanjo N, Nigmatullin CM, Ohtani T, Pecl G, Angel J, Perez A, Piatkowski U, Saikliang P, Salinas-Zavala CA, Steer M, Tian Y, Ueta Y, Vijai D, Wakabayashi T, Yamaguchi T, Yamashiro C, Yamashita N & Zeidberg LD (2015). World squid fisheries. *Reviews in Fisheries Science and Aquaculture* **23**: 92-252.
- Arvanitidis C, Koutsoubas D, Robin JP, Pereira J, Moreno A, Morais da Cunha 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.
- Boyle PR & Pierce GJ (1994). Fishery biology of northeast Atlantic squid: an overview. *Fisheries Research* **21**: 1-15.
- Boyle PR (1983). *Eledone cirrhosa*. In: PR Boyle (Ed.). *Cephalopod Life Cycles Volume 1*. Academic Press, London, 475pp.
- Boyle PR, Mangold K & Ngoile M (1988). Biological variation in *Eledone cirrhosa* (Cephalopoda: Octopoda): Simultaneous comparison of North Sea and Mediterranean populations. *Malacologia* **29**: 77-87.
- Budelman BU. 1990. The Statocysts of Squid. Chapter 19. In: Gilbert DL, Adelman WJ, Arnold JM (Eds.) *Squid as experimental animals*. Plenum Press, NY & London, pp 421-439.
- Carroll AG, Przeslawski R, Duncan A, Gunning M, Bruce B. 2017. A critical review of the potential impacts of marine seismic surveys on fish & invertebrates. *Marine Pollution Bulletin* **114**, 9-24.
- Chen CS, Pierce GJ, Wang J, Robin JP, Poulard JC, Pereira J, Zuur AF, Boyle PR, Bailey N, Beare DJ, Jereb P, Ragonese S, Mannini A & Orsi-Relini L (2006). The apparent disappearance of *Loligo forbesii* 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.
- Collins MA, Burnell GM & Rodhouse PG (1995). Distribution and demography of *Loligo forbesii* in the Irish Sea. *Biology and Environment: Proceedings of the Royal Irish Academy* **95B**: 49-57.
- Collins MA, Yau C, Allcock L & Thurston MH (2001). Distribution of deep-water benthic and benthic-pelagic cephalopods from the northeast Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **81**: 105-117.
- Craig S (1996). Total mercury concentration in the cephalopods, *Loligo forbesii* (Steenstrup), *Todaropsis eblanae* (Ball) and *Todarodes sagittus* (Lamarck). Zoology Honours Thesis, University of Aberdeen.
- de Heij A & Baayen RP (2005). Seasonal distribution of cephalopod species living in the central and southern North Sea. *Basteria* **69**: 4-6.
- Denis V & Robin JP (2001). Present status of the French Atlantic fishery for cuttlefish, *Sepia officinalis*. *Fisheries Research* **182**: 1-12.
- Dorey N, Melzner F, Martin S, Oberhänsli F, Teyssié J-L, Bustamente P, Gattuso J-P & Lacoue-Labarthe T (2013). Ocean acidification and temperature rise: effects on calcification during early development of the cuttlefish *Sepia officinalis*. *Marine Biology* **160**: 2007-2022.
- Doubleday ZA, Prowse TAA, Arkhipkin A, Pierce GJ, Semmens J, Steer M, Leporati SC, Lourenco S, Quetglas A, Sauer W & Gillanders BM (2016). Global proliferation of cephalopods. *Current Biology* **26**: R387-R407.
- Finger JM & Smith JD (1987). Molecular association of Cu, Zn, Cd and ²¹⁰Po in the digestive system of the squid *Nototodarus gouldi*. *Marine Biology* **95**: 87-91.
- Guerra A & Rocha F (1994). The life history of *Loligo forbesii* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). *Fisheries Research* **21**: 43-69.
- Guerra A, Gonzalez AF & Rocha F (2004). A review of records of giant squid in the north-eastern Atlantic and severe injuries in *Architeuthis dux* stranded after acoustic exploration. ICES Annual Science Conference. ICES CM 2004/CC: 29.

- Gutowska MA, Melzner F, Langenbuch M, Bock C, Claireaux G & Pörtner HO (2010b). Acid-base regulatory ability of the cephalopod (*Sepia officinalis*) in response to environmental hypercapnia. *Journal of Comparative Physiology B* **180**: 323-335.
- Gutowska MA, Melzner F, Pörtner HO & Meier S (2010a). Cuttlebone calcification increases during exposure to elevated seawater Pco₂ in the cephalopod *Sepia officinalis*. *Marine Biology* **157**: 1653-1663.
- Hammond PS & Grellier K (2006). Grey seal diet composition and prey consumption in the North Sea. Report to Department for Environment, Food and Rural Affairs, project ref. MF0319. Sea Mammal Research Unit, University of St. Andrews, UK, 18pp. plus appendices.
- Hastie LC, Nyegaard M, Collins MA, Moreno A, Pereira JMF, Piatkowski U & Pierce GJ (2009a). Reproductive biology of the loliginid squid *Alloteuthis subulata* in the Northeast Atlantic and adjacent waters. *Aquatic Living Resources* **22**: 35-44.
- Hastie LC, Pierce G & Wang J (2006). An overview of cephalopods relevant to the SEA 7 area. Report to the Department of Trade and Industry. Department of Zoology, University of Aberdeen, 43pp.
- Hastie LC, Pierce GJ, Wang J, Bruno L, Moreno A, Piatkowski U & Robin JP (2009b). Cephalopods in the North-eastern Atlantic: Species, biogeography, ecology, exploitation and conservation. *Oceanography and Marine Biology: An Annual Review* **47**: 111-190.
- Hislop JRG, Robb AP, Brown MA & Armstrong DW (1991). The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. *ICES Journal of Marine Science* **48**: 139-156.
- Holme NA (1974). The biology of *Loligo forbesii* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom* **54**: 481-503.
- Hu MY, Lee J-R, Lin L-Y, Shih T-H, Stumpp M, Lee M-F, Hwang P-P & Tseung Y-C (2013). Development in a naturally acidified environment: Na⁺/H⁺ exchanger 3-based proton secretion leads to CO₂ tolerance in cephalopod embryos. *Frontiers in Zoology* **10**: 1-16.
- Hu MY, Tseng Y-C, Stumpp M, Gutowska MA, Kiko R, Lucassen M & Melzner F (2011). Elevated seawater Pco₂ differentially affects branchial acid-base transporters over the course of development in the cephalopod *Sepia officinalis*. *American Journal of Physiology* **300**, doi: 10.1152/ajpregu.00653.2010.
- Hu MY, Yan HY, Chung WS, Shiao JC & Hwang PP (2010). Acoustically evoked potentials in two cephalopods inferred using the auditory brainstem response (ABR) approach. *Comparative Biochemistry and Physiology – Part A: Molecular and Integrative Physiology* **153**: 278-283.
- ICES 2019. Interim Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH), 5–8 June 2018, Pasaia, San Sebastian, Spain. ICES CM 2018/EPDSG:12. 194 pp.
- Jereb P, Allcock AL, Lefkaditou E, Piatkowski U, Hastie LC & Pierce GJ (2015). Cephalopod biology and fisheries in Europe: II. Species accounts. ICES Cooperative Research Report No. 325, 360pp.
- Joy JB (1990). The fishery biology of *Todarodes saggitatus* in Shetland waters. *Journal of Cephalopod Biology* **1**: 1-19.
- Kaifu K, Akamatsu T & Segawa S (2008). Underwater sound detection by cephalopod statocyst. *Fisheries Science* **74**: 781-786.
- Lacoue-Labarthe T, Reveillac E, Oberhänsli F, Teyssié J-L, Jeffrey R & Gattuso J-P (2011). Effects of ocean acidification on trace element accumulation in the early life stages of squid *Loligo vulgaris*. *Aquatic Toxicology* **105**: 166-176.
- Laptikhovskiy 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.
- Lishchenko F, Perales-Raya C, Barrett C, Oesterwind D, Power AM, Larivain A, Laptikhovskiy V, Karatza A, Badouvas N, Lishchenko A & Pierce GJ (2021). A review of recent studies on the life history and ecology of European cephalopods with emphasis on species with the greatest commercial fishery and culture potential. *Fisheries Research* **236**: 105847.
- Montiero LR, Portiero FM & Goncalves JM (1992). Inter- and intra-specific variations of the mercury levels in the muscle of cephalopods from the Azores. *Arquipelago* **10**: 13-22.
- Mooney TA, Hanlon RT, Christensen-Dalsgaard J, Madsen PT, Ketten DR & Nachtigall PE (2010). Sound detection by the longfin squid (*Loligo pealeii*) studied with auditory evoked potentials: sensitivity to low frequency particle motion and not pressure. *Journal of Experimental Biology* **213**: 3748-3759.
- Oesterwind D, ter Hofstede M, Harley B, Brendelberger H & Piatkowski U (2010). Biology and meso-scale distribution patterns of North Sea cephalopods. *Fisheries Research* **106**: 141-150.
- Packard A, Karlsen HE & Sand O (1990). Low frequency hearing in cephalopods. *Journal of Comparative Physiology A* **166**: 501-505.

- Pecl GT & Jackson GD (2008). The potential impacts of climate change on inshore squid: biology, ecology and fisheries. *Reviews in Fish Biology and Fisheries* **18**: 373-385.
- Pierce G, Young I & Wang J (2002). An overview of cephalopods relevant to the SEA 2 and SEA 3 areas. Report to the Department of Trade and Industry. Department of Zoology, University of Aberdeen, 42pp.
- Pierce GJ & Boyle PR (2003). Empirical modelling of interannual trends in abundance of squid (*Loligo forbesii*) in Scottish waters. *Fisheries Research* **59**: 305-326.
- Pierce GJ & Santos MB (1996). Trophic interactions of squid *Loligo forbesii* in Scottish waters. In: SPR Greenstreet & ML Tasker Eds. *Aquatic Predators and their Prey*. Fishing News Books, Cambridge, pp. 58-64.
- Pierce GJ (1992). Cephalopods in the diet of marine mammals. Fishery potential of northeast Atlantic squid stocks. Final report to the Commission of the European Communities on Contract no. MA.1.146, Appendix A.19, Department of Zoology, University of Aberdeen, 22pp.
- Pierce GJ, Boyle PR, Hastie LC & Santos MB (1994b). Diets of squid *Loligo forbesii* in the northeast Atlantic. *Fisheries research* **21**: 149-163.
- Pierce GJ, Hastie LC, Guerra A, Thorpe RS, Howard FG & Boyle PR (1994a). Morphometric variation in *Loligo forbesii* and *Loligo vulgaris*: regional, seasonal, sex, maturity and worker differences. *Fisheries Research* **21**: 127-148.
- Pierce GJ, Stowasser G, Hastie LC & Bustamante P (2008). Geographic, seasonal and ontogenic variation in cadmium and mercury concentrations in squid (Cephalopoda; Teuthoidea) from UK waters. *Ecotoxicology and Environmental Safety* **70**: 422-432.
- Pierce GJ, Valavanis VD, Guerra A, Jereb P, Orsi-Relini L, Bellido JM, Katara I, Piatkowski U, Pereira J & Balguerias E (2009). A review of cephalopod – environment interactions in European Seas. *Hydrobiologia* **612**: 49-70.
- Portiero FM & Martins HR (1994). Biology of *Loligo forbesii* Steenstrup, 1856 (Mollusca: Cephalopoda) in the Azores: samples composition and maturation of squid caught by jigging. *Fisheries Research* **21**: 103-114.
- Rasero M Gonzalez AF, Castro BG & Guerra A (1996). Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Illex coindetti* (Cephalopoda: Ommastrephidae) in Galician waters. *Journal of the Marine Biological Association of the United Kingdom* **76**: 73-87.
- Robinson RA, Learmonth JA, Hutson AM, MacLeod CD, Sparks TH, Leech DI, Pierce GJ, Rehfish MM & Crick HQP (2005). Climate change and migratory species. BTO Research Report 414. Report to DEFRA, 306pp.
- Rocca E (1969). Copper distribution in *Octopus vulgaris* Lam. hepatopancreas. *Comparative Biochemistry and Physiology* **28**: 67-82.
- Rocha F, Guerra A & Gonzalez AF (2001). A review of reproductive strategies in cephalopods. *Biological Reviews* **76**: 291-304.
- Rodhouse PG, Swinfen RC & Murray AWA (1988). Lifecycle, demography and reproductive investment in the myopsid squid *Alloteuthis subulata*. *Marine Ecology Progress Series* **45**: 245-253.
- Rossi A, Pellegrini D, Belcari P & Barghigiani C (1993). Mercury in *Eledone cirrhosa* from the northern Tyrrhenian Sea: contents and relations with lifecycle. *Marine Pollution Bulletin* **27**: 683-686.
- Royer J, Pierce GJ, Foucher E & Robin JP (2006). The English Channel stock of *Sepia officinalis*: modeling variability in abundance and impact of the fishery. *Fisheries Research* **78**: 96-106.
- Sacau M, Pierce GJ, Stowasser G, Wang J & Santos MB (2005). An overview of cephalopods relevant to the SEA 6 area. Report to the Department of Trade and Industry. Department of Zoology, University of Aberdeen, 56pp.
- Santos MB, Pierce GJ, Ross HM, Reid RJ & Wilson B (1994). Diets of small cetaceans from the Scottish coast. ICES Council Meeting Papers. ICES CM 1994/N: 11.
- 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.
- Simon MJ, Kristensen TK, Tendal OS, Kinze CC & Tougaard S (2003). *Gonatus fabricii* (Mollusca, Theuthida) as an important food source for sperm whales (*Physeter macrocephalus*) in the northeast Atlantic. *Sarsia* **88**: 244-246.
- Sims DW, Genner MJ, Southward AJ & Hawkins SJ (2001). Timing of squid migration reflects North Atlantic climate variability. *Proceedings of the Royal Society of London B* **268**: 2607-2611.
- Solé M, Lenoir M, Durfort M, Lopez-Bejar M, Lombarte A & André M (2013a). Ultrastructural damage of *Loligo vulgaris* and *Illex coindetti* statocysts after low frequency sound exposure. *PLoS ONE* **8**: e78825.
- Solé M, Lenoir M, Durfort M, Lopez-Bejar M, Lombarte A, André M, van der Schaar M & André M (2013b). Does exposure to noise from human activities compromise sensory information from cephalopod statocysts? *Deep Sea Research II* **95**: 160-181.

Solé M, Sigray P, Lenoir M, van der Schaar M, Lalander E, André M. 2017. Offshore exposure experiments on cuttlefish indicate received sound pressure and particle motion levels associated with acoustic trauma. *Scientific Reports* 7, 45899

Stephen AC (1944). The cephalopoda of Scottish and adjacent waters. *Transactions of the Royal Society of Edinburgh* 61: 247-270.

Stowasser G, Bustamente P, MacLeod CD, Wang J & Pierce GJ (2005). Spawning areas and selected metal concentrations in squid (*Loligo forbesii*) in UK waters with notes on metal concentrations in other squid species. Report to the Department of Trade and Industry. Department of Zoology, University of Aberdeen, 24pp.

Stowasser G, Pierce GJ, Wang J & Santos MB (2004). An overview of cephalopods relevant to SEA 5 area. Report to the Department of Trade and Industry. Department of Zoology, University of Aberdeen, 40pp.

Taylor MA (1986). Stunning whales and deaf squids. *Nature* 323: 298-299.

Tollit DJ & Thompson PM (1996). Seasonal and between year variations in the diet of harbour seals in the Moray Firth, Scotland. *Canadian Journal of Zoology* 74: 1110-1121.

Van der Kooij J, Engelhard GH & Righton DA (2016). Climate change and squid range in the North Sea. *Journal of Biogeography* 43: 2285-2298.

Wilson E (2006). *Octopus vulgaris*. Common octopus. *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme* [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 10/12/2008]. Available from: <http://www.marlin.ac.uk/species/Octopusvulgaris.htm>