# 6 The future of cephalopod populations, fisheries, culture, and research in Europe

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## 6.1 Cephalopods and climate change

### 6.1.1 Introduction: climate change and climate variation

The term “climate change” is generally currently understood as referring to global warming and the build-up of greenhouse gases in the Earth’s atmosphere, that is, directional and essentially abnormal changes in the expected climate within the Earth's atmosphere and subsequent effects on other parts of the Earth, such as ice caps. It comprises long-term significant changes in the expected patterns of average weather of specific regions and long-term changes in the climate regime at a global scale. These changes are, in part, natural, but increasingly there is an anthropogenic component to “global warming”. They occur against a background of natural climatic variation on temporal-scales ranging from thousands or millions of years (e.g. the alternation of ice ages and interglacial periods) to phenomena that occur over time-scales of days, months, or years (e.g. the *El Niño* Southern Oscillation), although, as commonly understood, the term “climatic variation” probably excludes local weather patterns.

As our own frame of reference tends to span a few years or, at most, a few decades, it is phenomena on these time-scales that are hardest to distinguish from climate change. The extent of climatic variation in any locality is strongly influenced by four geographic factors: (i) latitude, (ii) distance from the sea, (iii) direction of the prevailing winds, and (iv) elevation. The periodic change in atmospheric and oceanic circulation patterns is one important feature in these variations.

Large-scale and regional impacts of climate change on the marine environment that have been observed and/or predicted include increased temperature, higher sea levels, changes in ocean circulation, reduced sea-ice cover, reduced salinity, increased dissolved $CO_2$ concentration (and hence acidity) in seawater, changes in rainfall patterns, changes in climate variability, increased frequency of storms and storm surges, increased windspeeds, changes in wave conditions, and more extreme weather events (Turrell, 1999; Hansen *et al.*, 2001; IPCC, 2001; Sear *et al.*, 2001a, 2001b; Hulme *et al.*, 2002; Fisheries Research Services, 2004; ICES, 2004b).

Impacts of climate change may be seen at global and regional scales and operate through various direct and indirect mechanisms. Effects on marine organisms may be seen at cellular, individual, population, community, and ecosystem levels. Climate impacts may operate either directly, through effects on individual physiology (metabolic and reproductive processes), or indirectly, through effects on prey, predators, and competitors (Stenseth *et al.*, 2002), as well as on disease organisms and parasites. Thus, climate effects can include physiological effects (e.g. on metabolic rate), changes in individual life-history parameters (e.g. rates of growth and maturation), changes in the timing of life-history events (e.g. breeding, migration), changes in migration routes, changes in population parameters (e.g. reproductive success, recruitment success, mortality rate), and effects on abundance and distribution. Effects on individual populations, in turn, may affect community and ecosystem structure and function (IWC, 1997; Tynan and DeMaster, 1997; Harwood, 2001; Würsig *et al.*, 2002).

Climate change may lead to a higher frequency of extreme events, which are often ecologically more relevant than fluctuations in mean climate (Stenseth *et al.*, 2002). For example, changes in the frequency of episodic events (e.g. storms) may affect recruitment. In general, the effects of climate change on the marine environment are difficult to predict because of the complex interactions between ocean processes and climate, and they will vary greatly between areas. Uncertainties about the nature and degree of future climate change make it impossible to know exactly how weather, ocean circulation, and biological productivity will be affected (Weaver and Zwiers, 2000).

Although the most obvious effects of climate change will occur in surface waters, the deep ocean will also be affected. Changes in temperature and acidity may occur very slowly, but abrupt changes in thermohaline circulation in the southern ocean could occur as a result of massive surface freshening from glacial meltwater (Kaiser and Barnes, 2008).

### 6.1.2 Cephalopoda

There is high variability in the annual abundance of many cephalopod populations, which suggests that environmental effects on populations tend to be both pronounced and transient. This reflects the short life, rapid and labile growth and maturation patterns, and the lack of overlap between generations. Physiological features that allow squid to have fast life histories include very efficient digestion, sustained growth, with both increase in muscle fibre size and continual recruitment of new muscle fibres, efficient oxygen use, and low levels of antioxidative defence (Pecl and Jackson, 2008; Rosa and Seibel, 2008).

Metabolic and life-history parameters are sensitive to environmental variation, and there is no reservoir of old adults to buffer the population against fluctuations in spawning and recruitment success. Nevertheless, populations apparently recover relatively quickly after periods of low abundance.

Thus, cephalopods are both sensitive (in terms of rapid response) and resilient (in terms of recovery) to perturbations, including overfishing and, potentially, climate change. It may, therefore, be difficult to distinguish between the effects of directional climate change and local climate variation, and indeed (as is the case for all exploited species) between these effects and the effects of fishing.

Impacts of environmental change and variation may occur at all stages of the life cycle, from egg to mature adult. However, the planktonic early life stages (paralarvae) are thought to be particularly sensitive to both physical and chemical oceanographic factors (e.g. temperature and acidity) and to the biotic environment (e.g. phytoplankton productivity and abundance of zooplankton – prey for the paralarvae – and fish (including prey, predator, and competitor species). Environmental effects on eggs and paralarvae are probably the least well understood. Growth and mortality rates during the paralarval phase of the life cycle are high and potentially highly variable (see Pierce *et al.*, 2008b, for a recent review).

Cephalopods fished in ICES waters include short-finned (ommastrephid) and long-finned (loliginid) squid, octopus, and cuttlefish (Hastie *et al.*, 2009a). Many of these cephalopods, particularly those species that are targeted directly by artisanal or commercial fisheries, have 1- or 2-year life cycles. Paralarvae hatch from eggs, quickly grow into juveniles, and progressively mature into adult animals. In demersal and benthic species, the eggs are secured to a hard substratum, whereas in pelagic species, the eggs are usually floating. Typically, egg-laying occurs in batches, sometimes over a period of weeks (possibly months). However, there is normally no post-spawning regeneration of the gonad, and females often die shortly after the completion of spawning. There are exceptions, however: the females of some octopus guard the eggs, and the moribund females of gonatid squid form a protective capsule around the eggs (Seibel *et al.*, 2000, 2005).

Given their short lifespan and rapid growth rate, individual growth and population abundance in cephalopods are thought to be especially sensitive to changes in environmental conditions, such as seawater temperature (Rodhouse *et al.*, 1992; Boyle and Pierce, 1994; Waluda and Pierce, 1998; Waluda *et al.*, 1999). The sensitivity of cephalopod species to environmental fluctuations is a potentially important factor to consider in stock assessments and fishery management measures (Pierce *et al.*, 2008b). Previous research has suggested that environmental temperature can influence somatic growth rates and final body size, both in captivity and in the natural environment, with accelerated growth rates observed with increasing water temperatures (Jackson *et al.*, 1997; Forsythe *et al.*, 2001; Jackson and Moltschaniwskyj, 2002; Forsythe, 2004; Keyl *et al.*, 2008). Cephalopods could, therefore, be good indicators of environmental change.

### 6.1.3 Cephalopods as indicators of climate change

An ecological indicator is defined as a measure, an index of measures, or a model that characterizes an ecosystem or one of its critical components and may reflect biological, chemical, or physical attributes of ecological condition (Jackson, L. E., *et al.*, 2000). A "good" indicator should meet several types of criteria concerning conceptual foundation, feasibility of implementation, response variability, and interpretation and utility (Barber, 1994). Jackson, L. E., *et al.* (2000) amplified these criteria as follows: (i) relevance to assessment and ecological functions; (ii) feasibility of data-collection methods, logistics, information management, quality assurance, and monetary costs; (iii) response variability, measurement error, temporal variability within the field season and across years, spatial variability, and discriminatory ability; and (iv) interpretation and utility of data in relation to objectives, assessment thresholds, and linkage to management action. Ultimately, a good indicator in the context of anthropogenic phenomena such as climate change is one that can be used to communicate information about an ecosystem, reflecting the impact of human activity on the system, to groups such as the public or government policy-makers. Ecological indicators can help to describe effects in simple terms that can be widely understood and used by non-scientists to make management decisions. Often, no single indicator is ideal, and it is, therefore preferable to combine a suite of indices providing complementary information (Salas *et al.*, 2006).

#### 6.1.3.1 Relevance

Cephalopods are often cited as essential ecosystem components (usually by cephalopod biologists), but it is doubtful whether their role is intrinsically more important than that of any other taxon, except from the viewpoint of specialist teuthophages, such as some of the toothed whales. Certain cephalopods are thought of as pioneer species, which could indicate highly disturbed ecosystems. Thus, a marked and sustained increase in their abundance could indicate a regime shift (Zeidberg and Robison, 2007; Vecchione *et al.*, 2009).

#### 6.1.3.2 Feasibility

Fishery and research survey trawl data are widely available on a range of exploited cephalopod species, and some countries have relatively long dataseries. However, no cephalopods are quota species, and so collection of data is not accorded the same priority as that of many finfish species. The biology of some cephalopod species is well studied, but there are gaps in knowledge, owing, for example, to the difficulty of age determination and the high variability in life cycles. Other possible sources of time-series on cephalopods include predator diets (e.g. Montevecchi and Myers, 1997).

#### 6.1.3.3 Responsiveness

As a consequence of high metabolic rate, rapid growth, and short life cycles, cephalopod abundance can be very sensitive to environmental change, with fishing mortality being a less important component of population dynamics than in long-lived species. This is probably the key point in favour of using cephalopods as climate-change indicators.

#### 6.1.3.4 Interpretation

The flexible nature of cephalopod life histories can make consequences of environmental change unpredictable; they may adapt rather than die. It may also prove difficult to separate the effects of climate variability from those of climate change (although this can apply to any organism). In terms of public profile, cephalopods are charismatic species, for example, because of the very large size of some species, their intelligence, and their "alien" quality. However, at least in northern Europe, the public is more likely to be concerned with the fate of dolphins than that of squid. In southern Europe, however, cephalopods are probably most appreciated as a food resource, and changes in their abundance may therefore excite more public interest.

### 6.1.4 Large-scale climate variability

Large-scale patterns of climate variability, such as the *El Niño*–Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO), account for major variations in weather and climate around the world and have been demonstrated to affect many marine species and fish stocks through both direct and indirect pathways (Stenseth *et al.*, 2002). Effects of short-term events, such as *El Niño* events and the NAO, can provide a valuable insight into the potential effects of longer-term climate change.

Changes in large-scale climate indices, such as the NAO, are often linked to changes in currents, upwelling systems, and water temperature. They also affect the distribution and abundance of animals at the base of the food chain. Thus, temporal and spatial population dynamics of calanoid zooplankton (*Calanus finmarchicus* and *C. helgolandicus*) have been linked to changes in sea surface temperature and the NAO (Planque and Taylor, 1998; Beare *et al.*, 2002; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Beaugrand and Reid, 2003; Beaugrand and Ibanez, 2004). Abundance of these species will, in turn, determine food availability for higher predators, including squid.

Thus, abundance of northern short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic is positively related to a negative NAO index (weak winter, northwesterly winds), high water temperatures off Newfoundland, and a southward shift in the position of the Gulf Stream and the boundary between shelf waters and offshore slope waters (Dawe *et al.*, 2000). The response of the sympatric *Loligo pealeii* population to variation in the NAO appears to be opposite to that seen in *Illex illecebrosus* (Dawe *et al.*, 2007).

*El Niño* events in the Northwest Pacific lead to environmental conditions favourable to recruitment in the western winter–spring cohort of the neon flying squid (*Ommastrephes bartramii*), whereas *La Niña* events result in decreased recruitment through variability of environmental conditions on the spawning grounds. There is also a northward shift in the fishing grounds in *La Niña* years and a southward shift in *El Niño* years (Chen *et al.*, 2007). However, Yatsu *et al.* (2000) reported that recruitment rates of the autumn cohort of *O. bartramii* were lower in *El Niño* years when water temperatures from winter to summer were lower than in normal years in the North Pacific.

Anderson and Rodhouse (2001) suggested that the ENSO phenomenon might influence the variability of abundance of paralarvae of the squid *Dosidicus gigas*, with favourable retention during *El Niño* conditions and unfavourable offshore transportation during *La Niña* and normal conditions.

### 6.1.5 Currents, productivity, and upwelling

Changes in ocean currents and mixing, deep-water production, and coastal upwelling will directly affect the distribution and abundance of plankton and of many fish and cephalopod species, as well as their migrations. Many pelagic fish species are closely associated with mesoscale ocean features, such as fronts, which are hot spots of primary productivity and also tend to have associated high densities of pelagic fish and squid.

An extended or stronger frontal region may possibly act as a barrier to egg mass and larval transport of the Argentinean short-fin squid (*Illex argentinus*) within the area of the Brazil–Falkland Current confluence (Waluda *et al.*, 2001a). Any changes in these ocean currents and fronts as a result of climate change could, therefore, influence the distribution and abundance of this species.

In upwelling systems, fish production appears to be determined by enrichment, concentration, and retention processes, which, in turn, are controlled by climatic factors. An increase in temperature should intensify upwelling, causing a reduction in the concentration and retention processes and therefore resulting in a decline in local fish production (Walther *et al.*, 2002). The reproductive cycle of the common octopus (*Octopus vulgaris*), an important resource species in northwest Spain, is coupled to the coastal wind-driven upwelling, so that females spawn prior to spring months before the upwelling season, and hatching takes place from late summer to early autumn (Otero *et al.*, 2007). This ensures that the newly hatched paralarvae are present in the water column when the ecosystem is still productive. Coastal wind patterns appear to explain up to 82% of the interannual variation in octopus catches in the Galician artisanal fishery (Otero *et al.*, 2008). Analysis rates of change in abundance and biomass of the *O. vulgaris* early larval phase in the northwest Iberian coast, where upwelling events occur with a frequency of 10–20 d from April to September, indicates that the increase in larval abundance and biomass is significantly correlated with the simultaneous decrease in water-column-integrated nitrate, ammonium, and chlorophyll levels. These conditions occur during the early stage of the relaxation phase of coastal upwelling events, when nutrient salts are consumed to produce biogenic matter, which is retained in the system and transferred through the foodweb (Otero *et al.*, 2009).

In the northwest African upwelling areas, *O. vulgaris* recruitment depends on the retention processes when paralarvae are present in the plankton (Faure *et al.*, 2000).

### 6.1.6 Temperature

Seawater temperature is one of the key parameters affecting cephalopods (Rodhouse *et al.*, 1992; Boyle and Pierce, 1994; Waluda and Pierce, 1998; Waluda *et al.*, 1999). Temperature affects all phases of the life cycle, from the development within the egg, paralarval growth, and settlement of demersal species (e.g. Villanueva, 1995; Gowland, 2002; Katsanevakis and Verriopoulos, 2006) to recruitment and reproductive success (e.g. Waluda *et al.*, 2001a, 2001b).

Previous research has suggested that environmental temperature can influence somatic growth rates and final body size, both in captivity and in the natural environment, with accelerated growth rates observed with increasing water temperatures (Jackson *et al.*, 1997; Forsythe *et al.*, 2001; Jackson and Moltschaniwskyj, 2002; Forsythe, 2004). Small increases in temperature (as little as 1°C) could have a significant influence on cephalopod growth, affecting the threshold body mass in *Octopus* spp. by up to 15.5% and the body mass at 100 d by up to 62.6% (André *et al.*, 2009). According to Forsythe (2004), an increase of 1°C in environmental temperature can result in squid that are threefold larger after only 90 d.

High temperatures can also result in more rapid completion of the life cycle and smaller adult size, whereas good food supplies may delay spawning and lead to larger adult size (e.g. Moreno *et al.*, 2005, 2007). However, the precise role of different extrinsic factors differs between species (Mangold, 1987).

Apart from direct effects on metabolism, individual growth rate and, ultimately, population abundance depend on food supply mediated through effects on primary production and other lower trophic levels. Changes in plankton distribution, abundance, and composition are related to climate, including temperature (Southward *et al.*, 1995; Planque and Taylor, 1998; Ducrotoy, 1999; Heath *et al.*, 1999a, 1999b; Edwards *et al.*, 2001, 2002; Beare *et al.*, 2002; Beaugrand and Reid, 2003; Reid *et al.*, 2003; Edwards and Richardson, 2004; Moline *et al.*, 2004).

Kang *et al.* (2002) suggested that increasing zooplankton and changes in the zooplankton community in the Sea of Japan since the 1990s coincided with increasing sea surface temperature (SST) and, in turn, led to increased catches of the squid *Todarodes pacificus*. The recruitment success of higher marine trophic levels depends strongly on synchronization with plankton production.

Temperature variation has also been widely linked to variation in cephalopod movements, distribution, and abundance, and with variation in fishery catches, especially in squid (e.g. Pierce *et al.*, 1998; Waluda and Pierce, 1998; Bellido *et al.*, 2001; Sims *et al.*, 2001; Pierce and Boyle, 2003; Zuur and Pierce, 2004; Sánchez *et al.*, 2008). The link between cephalopod distribution and temperature is not a new concept: invasions of *O. vulgaris* in the English Channel in 1899–1900 and 1950, associated with unusually high temperatures, were described by Garstang (1900), Rees (1950), and Rees and Lumby (1954).

In the English Channel, loliginid squid catches seem to be related with mean SST of the year (Robin and Denis, 1999). Recruitment of the Patagonian squid (*Loligo gahi*) is related to the SST in October of the previous year (Agnew *et al.*, 2002). Annual catch and cpue of diamond squid (*Thysanoteuthis rhombus*) in the Sea of Japan seem to be closely related with SST, salinity changes, and sea level (Miyahara *et al.*, 2005). Variations in the annual biomass of the market squid (*Loligo opalescens*) population in the California Current are related to temperature changes, which influence both prey availability and metabolic rates (Zeidberg *et al.*, 2006).

Temporal variation in peak abundance of squid seen off southwest England represents temperature-dependent movement, which, in turn, is mediated by climatic changes associated with the North Atlantic Oscillation. Such climate-mediated movement may be a widespread characteristic of cephalopod populations worldwide and may have implications for future fishery management because global warming may alter both the timing and location of peak population abundance (Sims *et al.*, 2001). Kishi *et al.* (2009) suggest that the migration route and spawning area of *Todarodes pacificus* might change with global warming, with individual body weight declining as temperatures exceed the optimum for the species.

Effects of temperature can also be seen in data on the occurrence of squid in seabird diets. Montevecchi and Myers (1997) found that, on a decadal scale, a major dietary change in breeding northern gannets (*Sula bassana*) from migratory warm-water pelagic fish and squid to cold-water fish was associated with cold-water perturbations in the Northwest Atlantic during the 1990s.

### 6.1.7 Rainfall, sea level, and salinity

More intensive precipitation events and flash floods will result in increased run-off from land. Increased nutrient input into coastal waters, combined with increases in water temperatures, could cause an increase in toxic algal blooms and eutrophication. Effects on the dynamics of phytoplankton community dynamics, in turn, will affect marine fish and cephalopods (Edwards *et al.*, 2001).

Changes in salinity, for example with changes in river inputs/run-off and melting ice, will influence the distribution and abundance of prey through effects on stratification and circulation, and possibly as the result of limited salinity tolerance (Fiedler, 2002).

Sobrino *et al.* (2002) demonstrated a negative correlation between rainfall and *O. vulgaris* abundance in the Gulf of Cadiz.

Sea level was one of the factors affecting annual variation in catch and cpue of the diamond squid (*Thysanoteuthis rhombus*) in the Sea of Japan (Miyahara *et al.*, 2005).

### 6.1.8 $CO_2$ and ocean acidity

Carbon dioxide accumulating in the atmosphere permeates ocean surface layers where it alters seawater chemistry and may affect marine animals (Pörtner *et al.*, 2004; Fabry *et al.*, 2008), although information on effects on important groups such as fish is lacking (Ishimatsu *et al.*, 2008). Elevated $CO_2$ partial pressures (hypercapnia) can affect acid–base regulation, production of calcareous structures, oxygen transport capacity, growth, respiration, energy turnover, and mode of metabolism. Acid–base parameters, such as pH, bicarbonate, and $CO_2$ levels, are likely to affect metabolic function and, therefore, growth and reproduction. Pörtner (2008) points out that lower marine invertebrates, which are characterized by a low capacity to compensate for disturbances in extracellular ion and acid–base status and a sensitivity of metabolism to disturbances, are likely to be particularly susceptible to ocean acidification, and that one key consequence will be the narrowing of thermal tolerance windows in such species.

Pörtner and Reipschläger (1996) predicted that species with high metabolic rates would be more severely affected by ocean acidification because oxygen binding in their blood is more pH-sensitive. Epipelagic squid (e.g. Ommastrephidae, Gonatidae, Loliginidae) are hypothesized to be most severely affected by the interference of $CO_2$ with oxygen binding at the gills because their metabolic rates are higher than those of other aquatic animals (Seibel, 2007; Seibel and Drazen, 2007) and blood oxygen transport is extremely pH-sensitive. Rosa and Seibel (2008) demonstrated that ocean acidification will substantially depress metabolic rates (31%) and activity levels (45%) in the jumbo squid (*Dosidicus gigas*) and that the effect will be exacerbated by high temperature. However, Gutowska *et al.* (2008) found that juvenile cuttlefish maintained not only calcification, but also their growth rates and metabolism when exposed to elevated partial pressures of $CO_2$. They suggest that active cephalopods possess a certain level of pre-adaptation to long-term increments in $CO_2$ levels.

Although their results were inconclusive, Gutowska and Melzner (2009) highlighted the possibility that elevated $CO_2$ and reduced pH would affect embryonic development in the common cuttlefish (*Sepia officinalis*). Lacoue-Labarthe *et al.* (2008a, 2008b, 2009a, 2009b) studied the effects of increased $CO_2$ and temperature on trace element bioaccumulation in eggs of the common cuttlefish. Decreased pH reduced the accumulation of cadmium and zinc by the eggs, but increased the accumulation of silver. Higher acidity appears to affect the binding properties of the eggshell components and its permeability.

### 6.1.9 Distribution and abundance

All the effects described above, singly or in combination, may ultimately affect the movements, distribution, and abundance of cephalopods. Therefore, as is the case for finfish (e.g. Stebbing *et al.*, 2002), changes in distribution of some cephalopod species are likely in response to climate change. Supporting evidence about the likelihood of such changes arises not only from studies of climatic effects on physiological and life-cycle parameters (as described above), but from distribution changes that appear to be related to climate variation, even when the mechanism is unclear. Hastie *et al.* (1994) proposed that the high incidence of the ommastrephid squid *Todaropsis eblanae* in the North Sea in the early 1990s was the result of climatic variation, coinciding with the entry of various other warm-water species into the North Sea. Chen *et al.* (2006) speculated that the decline in *Loligo forbesii* in Iberian Peninsula waters since the early 1990s, which was correlated with temperature changes, was caused by climatic variation.

Various recent records of new cephalopod species in the Ionian Sea, Adriatic Sea, and Levantine basin (Mediterranean) could reflect distribution changes caused by climate change (E. Lefkaditou, pers. comm.). These species include the bathybenthic octopus *Bathypolypous sponsalis*, bathybenthic sepiolid *Neorossia caroli,* and the epipelagic octopod *Ocythoe tuberculata*, as well as two Indo–Pacific cephalopods, *Sepioteuthis lessoniana* and *Octopus aegina*. Caballero-Alfonso *et al.* (2008) suggest that the appearance of the subtropical cephalopod *Ocythoe tuberculata* in the North Atlantic in 2006 was a reflection of anomalous sea warming.

As seasonal movements of migratory cephalopods are related to the seasonal cycle of environmental variation (e.g. Arkhipkin *et al.*, 2004a), it may be expected that the timing of movements will vary with environmental conditions, as reported by Sims *et al.* (2001).

### 6.1.10 Community-level effects, regime shifts, and ecological replacement

Various recorded changes in marine communities over the last few decades have been attributed to climate change. Thus, Southward *et al.* (1995) described changes in the plankton community in the English Channel over 70 years and noted the increase in warm-water species during warm periods, and vice versa. They predicted that global warming would lead to species from the Bay of Biscay becoming common in the English Channel.

Similarly, the composition of the coastal nekton community along the eastern seaboard of the US has shifted progressively from vertebrates to invertebrates over the last four decades and, especially since 1980, from benthic to pelagic species. These shifts correlated most strongly with spring–summer SST, which increased by 1.6 °C over the 47-year period (Collie *et al.*, 2008).

It has been suggested that cephalopods could replace depleted finfish as part of ecological regime shifts, although to date there are few examples of this having happened. Species with short generation times and high fecundity, such as squid, are well suited opportunistically to replace fish species with late maturity and low fecundity (Zeidberg and Robison, 2007).

Balguerías *et al.* (2000) examined the apparent shifts in species abundance in the Saharan Bank area, concluding that a combination of oceanographic factors and fishing pressure had favoured benthic cephalopods at the expense of most finfish populations. Nevertheless, the change was not nearly as marked as suggested by fishery statistics. The range expansion of jumbo squid (*Dosidicus gigas*) described by Zeidberg and Robison (2007) coincided not only with changes in climate-linked oceanographic conditions and a reduction in competing top predators, but also with a decline in the abundance of the most important commercial groundfish species in the area, Pacific hake (*Merluccius productus*). Vecchione *et al.* (2009) suggest that a persistent high abundance of octopods off Elephant Island (Antarctic), first detected after the cessation of commercial fishing, could be indicative of a regime shift.

### 6.1.11 Concluding remarks and knowledge gaps

Numerous studies reviewed here and elsewhere (see Pierce *et al.*, 2008b) have underlined the high sensitivity of cephalopod species to local, regional, and large-scale environmental conditions and changes. Cephalopods have the intrinsic flexibility to adapt to climate change; their life history and physiological traits allow them to be opportunists in variable environments (Rodhouse and Nigmatullin, 1996). Additionally, we will not have to wait decades to determine these effects. For species where we have established good baseline data, changes will be immediately obvious. In contrast, for longer-lived predators, it will probably take decades to establish cause and effect on their life histories, populations, and abundance (Pecl and Jackson, 2008).

Environmental effects on early life stages of cephalopods can affect life-history characteristics (growth and maturation rates) as well as distribution. Oceanographic conditions are of particular significance for mobile pelagic species such as the ommastrephid squid (Pierce *et al.*, 2008a, 2008b). This suggests that recruitment success of pelagic species or of species with pelagic early life stages could be a possible indicator of variations in the oceanographic environment.

Impacts of climate change may have had positive effects on some populations of commercial squid species, such as *Illex coindetii* in the eastern Ionian (Mediterranean Sea; E. Lefkaditou, pers. comm.). In general, the positive effects of high productivity are likely to be most evident when their timing coincides with the hatching period, thus ensuring high survival of hatchlings.

Understanding climatic effects depends on knowledge of ecology and natural history. Thus, *O. vulgaris* females apparently migrate towards the coast before spawning, presumably in search of rocky substrata with caves and holes that facilitate the protection of the eggs. Nevertheless, it is not known whether or not this behaviour is related to other factors, such as temperature, which, by affecting the rate of embryonic development, can determine hatching time and hence the environmental conditions experienced by the hatchlings.

In many cephalopods, the energy required for reproduction appears to be derived directly from exogenous sources rather than by mobilization of body tissues. Environmental productivity may thus directly affect reproductive investment, in terms of the number and/or size of eggs and, consequently, survival of the paralarvae.

Finally, the increase in acidity in the sea caused by the increase in $CO_2$ might alter the capacity to form calcium carbonate and, hence, affect the formation of calcareous structures, such as the statoliths, which in cephalopods serve as the system of balance, or the cuttlebone, which serves for buoyancy. However, evidence on this point is equivocal, with recent work on cuttlefish (Gutowska *et al.*, 2008) pointing to tolerance of elevated $CO_2$ levels.

The combination of sensitivity and adaptability of cephalopods to climate variation, seen in individual life-history parameters and population processes, and mediated through direct physiological effects and the indirect consequences of effects on other species, makes cephalopods potentially useful indicators of climate change. In addition, the presence of recording structures, such as the beak, gladius, and cuttlebone, means that the environmental conditions experienced over an animal's lifetime, and its responses, are recorded in terms of isotope ratios and increment sizes, etc., affording the prospect of improved understanding of the mechanisms by which the environment affects the individual.

Regarding knowledge and data gaps, in most cephalopods, the planktonic (paralarval) stage is poorly known, notably in relation to how long these animals spend in the plankton. Studies are needed, using appropriate nets, to determine their seasonal, annual, and bathymetric and latitudinal distribution.

The lack of long-term dataseries, even on basic fishery parameters like cpue, is one of the major constraints on improving our understanding of cephalopod population trends. Long-term dataseries will be imperative to the success of any management strategy to cope with climate variability. It will also be critical to consider interactions between different stressors, such as overfishing, habitat destruction, and climate change (Root *et al.*, 2003).

Although life-cycle plasticity has been demonstrated in a range of cephalopods, the ways in which life-history parameters are linked to environmental conditions are not well understood. There is a need to develop integrated population models that consider both life-cycle parameters and environmental drivers, potentially allowing both a better understanding of the mechanisms linking life history and environment, and a way of evaluating the relative importance of different drivers (e.g. global change vs. overfishing). Such models would be facilitated by availability of accurate estimates of age and mortality. It is also necessary to find ways to introduce environmental information into cephalopod stock assessment and fishery management.

Solow (2002) and Lozier *et al.* (2009) have neatly illustrated some of the possible pitfalls involved in interpreting empirical models that identify apparent temporal and spatial relationships between species abundance and environmental conditions. Thus, results of empirical analysis of observational data need to be supported by experimental studies under controlled conditions in order to demonstrate the impact of different environmental factors on the life cycle, physiology, and behaviour of cephalopod species. Various laboratory studies in the last two decades have examined effects of temperature on different stages of the life cycle of various cephalopods, and more recent work has also examined other environmental factors, such as $CO_2$ concentrations (e.g. Rosa and Seibel, 2008). Such data have been used to derive models of individual growth (e.g. Forsythe and van Heukelem, 1987; André *et al.*, 2009), but more work is now needed to link individual-level responses to effects at the population and ecosystem levels.

## 6.2 European cephalopod fisheries

Once located mostly in southern Europe, cephalopod fisheries have grown and expanded northwards along European coastlines. The decline of traditional finfish resources is, without question, part of the reason for this change, but the occasional incidence of high abundance of some cephalopod species may also be important. Also significant is the globalization of supply and demand, so that catches can be transported virtually anywhere around the globe in a very short time. Thus, the limited nature of the northern European market for cephalopod products is easily offset by the expansion of international trade.

Cephalopod fisheries are of two main types: (i) commercial or industrial-scale fisheries taking cephalopods in inshore and offshore waters, particularly by trawling and mainly as a bycatch; and (ii) small-scale, directed coastal fisheries. Although the former have increased in importance in recent years, the increase in the latter is arguably more dramatic. Currently, inshore fisheries targeting cephalopod species yield an equally or even more important proportion of cephalopod landings, particularly in southern European countries, such as Portugal, Spain, Italy, and Greece, where more cephalopod species are consumed as part of the traditional diet and these fisheries represent an important part of the local economy.

Coastal cephalopod fisheries previously used traditional fishing gears, such as clay pots and trammelnets, and until the early 1980s, catches generally were low or moderate, because of the relative inefficiency of the gear employed. However, during the last few decades, more efficient gears have been developed, including modernized traditional gears and newly introduced gears, such as plastic pots and fykenets (Sánchez and Obarti, 1993; Borges, 2001; Lefkaditou *et al.*, 2002; Young *et al.*, 2006a), resulting in higher cephalopod catches, which are becoming particularly important for the income of local, small-scale fishing fleets. Changes in the geographic distribution of cephalopod landings have been noted (e.g. in Portugal). These adjustments are related to changes in the distribution of the resources and are usually suspected to reflect environmental changes. Fishing fleet behaviour, which will respond to factors such as variation in fuel costs and availability of other resource species, can also strongly affect variation in landings.

Where cephalopods are bycatch species, landings reflect only retained catches, and the amount of discards, which depends on market price, the amount of target species caught, the length of the fishing trip, and (at least where minimum landing sizes apply) individual body size, is not regularly reported. In general, there are three different types of discarding patterns, reflecting the degree of commercial interest: (i) species of no commercial interest that are always discarded; (ii) species of low or variable commercial value for which the discard percentages will vary (e.g. between areas and seasons, and depending on the amounts of other species caught); and (iii) species of higher commercial value that are almost always landed. Reporting of discards may improve under the revised sampling programme (European Community's Data Collection Regulation, Commission Decision 2008/949/EC).

Studies to date on commercially important species, such as the octopods *Octopus vulgaris* and *Eledone cirrhosa*, the cuttlefish *Sepia officinalis*, and the squid *Loligo vulgaris, L. forbesii*, and *Illex coindetii*, suggest that there is little discarding (Sartor *et al.*, 1998; Young *et al.*, 2004). However, it should be borne in mind that these studies were regional in focus, and results cannot be generalized to other parts of Europe. Thus, *E. cirrhosa* and *I. coindetii* are not highly valued throughout their range and neither species attracts much interest in Scotland, where they are probably normally discarded.

Despite their high and increasing importance, monitoring of the directed artisanal fisheries targeting cephalopods needs to be improved. These inshore fisheries comprise a high diversity of local fishing gears, catches from which (at least in the past; see Pierce, 1999; Guerra *et al.*, 2000; Pereira, 2001) have not always appeared in official statistics. When recorded, these landings are usually grouped under the category "other fishing gear" in official statistics. In Galicia (northwest Spain), artisanal landings of cephalopods are recorded in some detail by the Xunta de Galicia, with statistics available by species (only the two *Alloteuthis* species are grouped together), port, gear type, month, and year (ICES, 2009).

The Gómez-Muñoz model (which uses data collected during interviews with fishers and is particularly applicable to fisheries with a clear seasonal peak, see Gómez-Muñoz, 1990; Simón *et al.*, 1995) has been used to estimate unreported landings in artisanal fisheries. Some recent applications of the method suggest that official statistics are reasonably good (Rocha *et al.*, 2006; Young *et al.*, 2006b), and that this is an approach that could usefully be more widely applied.

Cephalopod fisheries in Europe are expected to continue to expand as a result of the increasing market demand for these species and the heavy exploitation of traditional coastal finfish resources. To ensure future sustainability, there is a particularly urgent need for studies of the dynamics of species exploited by small-scale fisheries and the effect of different gears on their stocks, as well as studies on the effectiveness of different gears and their contribution to landings and sales at a regional level. To allow this to be done, it is important that the specific fisheries targeting cephalopods (e.g. trammelnets for *Sepia*, fykenets, pots, and specific trawlnets for loliginids) are considered as separate "métiers" under national data collection programmes.

Does the future of cephalopod fisheries look better than the future of finfish fisheries? Populations of cephalopods demonstrate wide fluctuations in abundance, reflecting their "live fast, die young" life history, with non-overlapping generations, and their labile life-history strategies. This makes cephalopod populations sensitive to changes in oceanographic conditions and perhaps susceptible to local overfishing. Boats targeting cephalopods need to be able to diversify in years of lesser abundance. Thus, the directed squid fishery in the Moray Firth in northern Scotland landed exceptionally large amounts of squid in 2005 (Young *et al.*, 2006a), encouraging more vessels to enter the fishery in summer 2006. Initial catches in 2006 were of extremely small individuals, and landings into some Moray Firth ports were as low as 10% of the 2005 value (J. M. Smith, pers. comm.), with total squid landings for Scotland decreasing from ca. 2000 t in 2005 to 1000 t in 2006. The other side of the coin is that cephalopod populations tend to demonstrate great resilience to fluctuations in environmental conditions because of their capacity to vary their growth rate and size at maturity, extend their breeding seasons, vary the depth of their spawning grounds, and maintain complex recruitment patterns (Clarke, 1996). The short generation time means that recovery after periods of low abundance can be very quick. Given this adaptability, their high production-to-biomass ratio, and the acceptability of cephalopods as a human food source, it is reasonable to conclude that cephalopods represent an important renewable resource that should be possible to harvest sustainably.

Relatively few European stocks have been subjected to rigorous assessment, and almost none are assessed on a routine basis. As highlighted in Section 5, various assessment methods have been applied to cephalopods in different parts of the world (see also Pierce and Guerra, 1994). In the last 15 years, several European stocks have been assessed under the auspices of short-term, EU-funded projects, and contributed papers from studies in European waters in Payne *et al.* (2006) demonstrate that it is possible to carry out meaningful assessments. An important caveat, again highlighted in Section 5, is that data collection must be attuned to the assessment, and in the absence of routine assessment, data collection from many (if not most) European cephalopod fisheries has been inadequate to support rigorous assessment.

## 6.3 Cephalopod culture

Commercially viable aquaculture of cephalopods is still in the process of development. Common octopus (*Octopus vulgaris*) is currently considered a priority new species for aquaculture research in Spain, Portugal, and Greece (Vaz-Pires *et al.*, 2004; Iglesias *et al.*, 2007; Lefkaditou *et al.*, 2007). It undoubtedly meets some of the requirements for industrial culture: (i) easy adaptation to captivity, (ii) high growth rate, (iii) good acceptance of frozen food, (iv) high reproductive rate, and (v) high market price (Iglesias *et al.*, 2000). The main barrier to successful culture through the life cycle is the high mortality rate and poor growth of the paralarvae. The main problem to resolve is the identification of suitable food in terms of quality and quantity, long recognized as an issue for culture of this group of carnivorous molluscs (Boletzky and Hanlon, 1983). Research on this topic is considered an area of the highest priority (Iglesias *et al.*, 2007; Villanueva and Norman, 2008).

At present, there are no commercial diets available for cephalopods. For large-scale commercial production, cost analysis of commercial installations for ongrowing *O. vulgaris* demonstrated that food has to be reliable in terms of availability, consistency, and cost (García García *et al.*, 2004). Artificial diets have been used only at experimental scales and with modest success for juvenile and adult cuttlefish and octopus. There are promising recent results from studies using natural frozen diets and semi-humid artificial diets for *Sepia officinalis* (e.g. Sykes *et al.*, 2006; Domingues *et al.*, 2008) and formulated moist diets based on fish and prawn mixed with alginate or gelatine as binders for *O. vulgaris* (e.g. Cerezo Valverde *et al.*, 2008; Quintana *et al.*, 2008). Nevertheless, further research on cephalopod nutrition is needed to develop commercial culture for this group.

Cephalopod paralarvae appear to have more stringent nutritional requirements than juveniles and adults. Some success has been achieved, again at experimental scales, for *O. vulgaris* paralarvae using laboratory-reared crab zoeae as prey (Villanueva, 1995), crab zoeae combined with *Artemia* (Iglesias *et al.*, 2004; Carrasco *et al.*, 2006), and *Artemia* combined with fish flakes (Okumura *et al.*, 2005). Again, further research is needed to improve current knowledge of ecophysiological and nutritional requirements of *O. vulgaris* paralarvae before commercial-scale culture is possible.

Improved knowledge of cephalopod metabolism and digestion remains crucial. Future research should also determine the influence of environmental factors, such as light and temperature; the relationships between immunological parameters, nutritional status and growth; diet; and absorptive capacities. Furthermore, studies on reproduction, behaviour, and pathology of *O. vulgaris* and *S. officinalis* under culture conditions are needed.

## 6.4 Use of cephalopod by-products in aquafeed

Large quantities of cephalopod by-products are available from processing factories. The viscera have previously been considered as waste, but, because of their biochemical composition, they could form the basis of various products (e.g. Tavakoli and Yoshida, 2006; Souissi *et al.*, 2008), including dietary supplements for aquaculture (Le Bihan, 2006).

Silage is a liquid product made from animal material. Liquefaction is caused by the action of enzymes already present in the animal and is accelerated by acid, which creates the right conditions for enzymes to help break down hard tissues and limit the growth of spoilage bacteria. The high concentration of free amino acids in silage makes it suitable as a food additive in aquaculture. The silages currently used as food additives in aquaculture are made from fish wastes. However, enzymological and biochemical studies demonstrate a high potential for the use of cephalopod viscera as raw material for silage production. Silage obtained from cuttlefish viscera contains 63% protein, of which 89% is peptides and 14% lipids (comprising 37% saturated, 15% mono-unsaturated, and 47% polyunsaturated fatty acids). Searches for bioactive molecules in cuttlefish viscera silage have revealed the presence of growth factor-like, digestion-regulator, and immuno-stimulator molecules.

The addition of low levels of cuttlefish silage to diets of crustacean post-larvae, juvenile molluscs, and fish has been demonstrated to lead to an increase in zootechnical parameters (i.e. weight gain, feedfood consumption, and feedfood–conversion ratio) and to stimulate ontogenesis. The enrichment of the diet of juvenile cuttlefish with cuttlefish silage leads to a reduction in the required food ration, an increase in weight, and an improved food-conversion rate. The inclusion of 2% cuttlefish silage in the diet of young shrimps enhanced weight gain by 170% compared with control animals (which received an unenriched diet) after 60 days of rearing. Results on enrichment of the diet of *Artemia* have also been encouraging. Supplementing the diet of juvenile *Dicentrarchus labrax* with the autolysate of cuttlefish, rather than the hydrolysate of fish, also induces better growth (Le Bihan, 2006). In future, others ways of using processing wastes should be explored because this not only maximizes the utilization of fished cephalopods, but the use of the wastes as raw material contributes to better waste management and protection of the environment.

## 6.5 Fishery forecasting

With the exception of *Nautilus*, large interannual fluctuations in abundance are a common feature of populations of species in the class Cephalopoda. They are short-lived, ecological opportunists, generally semelparous, and their life-history characteristics are labile (e.g. Boyle and Rodhouse, 2005). As a consequence, recruitment variability is driven, to a greater or lesser extent, by the environment (e.g. Rodhouse, 2001). Because the extant population of most cephalopods normally consists of only one or two year classes, population size and fishery success are generally more vulnerable to recruitment variation associated with climatic variation than is the case for longer-lived species (Rodhouse, 2001).

One of the main problems with reconstructing the historical recruitment time-series and predicting future recruitment of fished stocks (of fish or cephalopods) is the low signal-to-noise ratio in the stock–recruitment relationship, which may reflect both the difficulty of accurately measuring stock size and recruitment and the inherent variability of the relationship. Predictions can be improved by including environmental predictors (e.g. sea surface temperature) in the models and by taking into account the quality of spawners (e.g. considering the links between the number and quality of the eggs and the size, age, and condition of the spawning females; Marshall *et al.*, 2003, 2006), but uncertainty remains. Fuzzy-logic models represent a method of capturing the uncertainty and variability inherent in these processes, and work is needed to compare results from such models with those from both traditional stock–recruitment models and artificial neural-network models. To date, such comparisons seem to demonstrate the superior capability of fuzzy-logic models to address problems of uncertainty in the data and variability in the stock–recruitment relationship. The fuzzy-logic model approach is recommended as a useful addition to the analytical tools currently available for cephalopod stock assessment and management.

The mechanisms that link cephalopod abundance to the atmosphere–ocean system are still not well understood, despite numerous studies that demonstrate empirical relationships between post-recruit distribution–abundance and environmental factors (see Section 6.1; also Pierce *et al.*, 2008b for a recent review). Models based on such empirical relationships need to be validated using independent datasets (e.g. from different areas or future years), and this step is often lacking in published studies. Determination of the underlying mechanism obviously affords greater confidence in the persistence of the relationship and, hence, in its future utility as a forecasting tool (see Solow, 2002, for a brief critique of the purely empirical model-fitting approach). Nevertheless, empirical models represent potentially powerful tools for fishery forecasting. For example, fishery managers can use the predictions to set the number of licences issued at the start of a fishing season.

To date, most research effort related to the underlying mechanisms has been focused on pelagic squid stocks, whose abundance appears to be linked to fluctuations in large current systems. In these cases, recruitment variability can be partly explained by environmental effects on the pelagic paralarval stage (González *et al.*, 1997; Waluda *et al.*, 1999, 2001a, 2001b; Miyahara *et al.*, 2005).

Recent research on demersal and benthic species, notably on *Octopus vulgaris* and *Loligo vulgaris* in Spain, offers improved understanding of the mechanisms underlying relationships between environmental conditions and post-recruit abundance, and suggests that there is scope for successful fishery forecasting in these groups.

Monthly landings of *L. vulgaris* demonstrate a marked seasonality in both Atlantic and Mediterranean areas (Sánchez and Martin, 1993; Guerra *et al.*, 1994). The amounts landed depend strongly on recruitment of paralarvae of the year and on a combination of environmental factors that can control distribution and abundance within their essential habitat, where growth and reproduction occurs. Along the Catalonian coast (northwestern Mediterranean), it appears that relatively cool weather conditions in the early part of the year favour higher landings in autumn, with habitat-model results indicating a negative effect on landings for sea surface temperatures higher than 17.5°C (Sánchez *et al.*, 2008). Optimal temperature conditions were more common in the northern and central parts of the study area than in the southern (Ebro Delta) area during 2000–2005, a difference reflected in historical catch-per-unit-effort data.

Upwelling areas are nutrient-rich systems and often the sites of major fisheries. Theoretically, three major processes must combine to yield favourable reproductive habitats: (i) nutrient input, (ii) concentration of food, and (iii) larval retention (Bakun, 1996). The status of an upwelling system in a given year can be quantified using simple wind-based, upwelling indices and measurements of nutrient and food availability. In upwelling areas, when fish larvae are present in the water column, the frequency of calm periods in a given year strongly influences larval survival (Peterman and Bradford, 1987). Variations in productivity of eastern boundary current ecosystems lead to natural variations in fish biomass (Chavez *et al.*, 2003; Ware and Thomson, 2005), and fluctuations in plankton may result in long-term changes in fish recruitment (Beaugrand *et al.*, 2003).

The common octopus (*O. vulgaris*) is a benthic species and one of the most important harvested cephalopods worldwide. Major interannual changes in its local abundance have been related to upwelling (through its effect on paralarval retention; Faure *et al.*, 2000), sea temperature (Balguerías *et al.*, 2002), and rainfall (Sobrino *et al.*, 2002).

Galicia constitutes the northern boundary of the Iberian–Canary Current upwelling system and almost the northern limit of the distribution of *O. vulgaris*. The artisanal fishery for *O. vulgaris* in Galicia has considerable socio-economic importance and involves almost 1500 vessels. Landings from the artisanal sector may be substantially under-reported (Pierce, 1999; Guerra *et al.*, 2000; Otero *et al.*, 2005). Nevertheless, if this bias is reasonably constant, interannual trends in landings may indicate changes in abundance because there has been no major change in the number of vessels registered during recent years.

The catches of *O. vulgaris* in Galicia seemed to follow cycles of 5–6 years' duration, with recent peaks in 1997 and 2004 and troughs in 1994–1995, 2000–2001, and 2005. Annual catches are positively correlated with the frequency of relaxation/moderate downwelling episodes during October–March, as well as with the frequency of upwelling episodes. Excessive upwelling strength over the upwelling season is negatively correlated with octopus landings. A regression model of *O. vulgaris* catches as a function of three upwelling indices and a density-dependent effect (i.e. the previous year's catches) provides a good fit to the data ($r^2 > 0.85$). Conditions during downwelling could favour the coastal retention and survival of the pelagic paralarvae, whereas upwelling episodes deliver nutrients to the foodweb. Strong upwellings are characterized by extremely high flushing rates that do not allow phytoplankton adaptation (Otero, 2006; Otero *et al.*, 2008).

A model for the effect of upwelling chemistry on paralarval abundance indicated that the decrease in nitrate, ammonia, and chlorophyll could explain up to 88% of the increase in abundance of *O. vulgaris* paralarvae. These conditions occur during the relaxation of upwelling events, when nutrient salts are consumed to produce biogenic matter, which is retained in the system and transferred through the foodweb

(Otero *et al.*, 2009). A negative density-dependent effect contributed 6% to the overall variability in octopus catches (Otero *et al.*, 2008). Taking into account that, after settlement on the bottom, octopus remain in more or less the same limited area throughout their life (Domain *et al.*, 2000), and that the availability of shelters is a limiting factor for octopus distribution (Katsanevakis and Verriopoulos, 2004), competition for habitat between adults and new recruits is plausible – and cannibalism is also known to occur (Smith, 2003). Large changes in catches can arise from small variations in the local windfield (Faure *et al.*, 2000; Otero *et al.*, 2008) and could be of major importance in the context of the predicted increasing intensity of upwelling conditions as atmospheric carbon dioxide concentrations increase (Diffenbaugh *et al.*, 2004).

## 6.6 Future fishery management

It is almost inevitable that, as more European fishers move into cephalopod fishing, some management measures will need to be introduced. Arguably, the best-managed cephalopod fishery in the world, for the squid *Illex argentinus* in Falkland Islands waters, has been run using restricted entry, real-time assessment, and the option of early closure to ensure sufficient escapement. Despite the evident and demonstrable success of this approach, the fishery is to move to an individual transferable quota (ITQ) system. In general, however, quota management is not thought appropriate to such short-lived species, and the shift in EU fishery policy towards an ecosystem approach to fishery management means that all participants in the fishing industry, from ICES, national governments, and regulatory authorities to fishery scientists and fishers, are currently more receptive to alternative approaches than ever before.

Ecosystems are complex and dynamic natural units that produce many goods and services other than those of direct benefit to fisheries. As fisheries have an impact on the ecosystem, which is also affected by other human activities, they need to be managed in an ecosystem context. The meanings of terms such as the "ecosystem approach to fishery management" (EAFM) are still not universally agreed, and the concepts will continue to evolve as the EAFM is implemented in the ICES Area. Nevertheless, the justification for the EAFM is evident in the characteristics of exploited ecosystems and the impacts resulting from fisheries and other activities. Indeed, practically all aspects of the EAFM were foreseen in the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) and, before that, in the World Conservation Strategy (IUCN *et al.*, 1980).

Stakeholder involvement is one key component of the EAFM and, indeed, of sustainable resource utilization in general. History suggests that top–down imposition of measures to control the exploitation of fish and shellfish has usually failed and that bottom–up and demand-led regulation may have more chance of success (D. J. Starkey, pers. comm.) As seen in Section 5, there is already some regulation of many small-scale European fisheries for coastal cephalopods, often at a local or regional scale, and such fisheries could provide an ideal testing bed for fisher participation and co-management.

Successful fishery management is inherently multidisciplinary because it must be underpinned both by sound biological and ecological knowledge and by a clear understanding of the human (social, economic, and institutional) dimensions of the fisheries. Ecosystem models, such as the Ecopath suite of programmes, facilitate simulation of the ecological consequences of management scenarios and can potentially be coupled to hydrodynamic models, thus allowing the local environmental consequences of climate change to be explored. Approaches such as cognitive maps, based on interview or observer data, can be used to simulate fishers' decisions (e.g. Wise *et al.*, 2009) under various resource abundance, economic, and regulatory scenarios.

Meanwhile, even if implementation lags behind, concepts and the associated terminology continue to evolve. Integrated coastal-zone management recognizes the need to manage interactions between multiple human activities, of which fishing is just one, and the wider-scale application of this concept, which embraces the whole marine sector (not just the coastal zone), has been christened "marine spatial planning".

### 6.6.1 Galician octopus fishery

Fishing for common octopus (*Octopus vulgaris*) in Galicia is one of the main socio-economic activities within the small-scale fisheries in this area, with more than 1500 vessels licensed to catch octopus (32% of the artisanal fleet). Annual catches from this fishery from 1997 onwards ranged from 1800 to 3800 t, and were worth €10–17 million per year. The fishery is under pressure for various reasons, including increased fishing costs (fuel, fishing material, bait, etc.), variability of the resource, product price in the market, and a lack of human resources in many key positions within the fishery. Therefore, although this small-scale fishery is well managed through regional laws, there is a need to develop a management plan to ensure sustainable exploitation of *O. vulgaris* in future, with participation by researchers, government, fishers, and other stakeholders. Objectives could include:

- development of a management plan tailored to the current situation in the artisanal *O. vulgaris* fishery, based on previous scientific studies and ensuring the sustainability of the resource while maximizing net income in the fishery sector and protecting the interests of other stakeholders;
- ongoing review and revision of the management regime, supported by research on alternative management options, including the creation of protected areas of different kinds;
- active participation of stakeholders in the development and implementation of management, reflecting their valuable experience in this sector; in many existing systems involving "consultation" and "participation" of industry, true co-management is rare and, in practice, fishers often still have little or no say in management decisions (Mikalsen and Jentoft, 2008);
- detailed study of the real costs of octopus fishing, and looking for the best way to minimize costs and, in parallel, be more conservative with the resource and its environment;
- development of a monitoring and surveillance plan to ensure compliance with regulations;
- informing the public and stakeholders about the management scheme adopted.

### 6.6.2 Directed squid fishing in Scotland

In Scotland, 2005 saw a dramatic increase in interest in squid fishing, with new fisheries emerging on the Aberdeenshire coast and in the Inner and Outer Hebrides, in addition to the existing fisheries in the Moray Firth and Firth of Forth. There is also increased interest in other parts of the UK. Two management objectives already identified by the UK industry are to (i) limit catches of new recruits, and (ii) protect spawning grounds. Another potential issue, because small-mesh codends are used when targeting squid, is the incidence of fish bycatches in squid nets.

Some of the suggested research priorities listed here have already been incorporated into an industry-funded study of squid fishing in Scotland (funded by SEAFISH, 2007–2009).

- Monitoring of catches during experimental squid-fishing trials. In Scotland, the industry proposes exploration of the use of a near-bottom trawl gear that can be deployed over hard ground. As *Loligo forbesii* spawns on hard ground, particular care must be taken to avoid disruption of spawning and damage to the eggs. Additionally, the industry has identified the need to establish a protocol for handling squid on board, and to ensure that sustainable fishing practices are adopted. Young squid are known to recruit close inshore on the east coast of Scotland in early autumn before moving into deeper waters. However, it is now necessary to obtain a detailed picture of their movements, both to ensure effective fishing and to avoid overfishing. On-board observers and GPS data could be used to monitor catch composition (including bycatch) in relation to gear type and deployment, date, time of day, depth, turbidity, and seabed substratum. Data collected would also be used in depletion and cohort analysis to estimate stock size and exploitation rate.
- Collection of data on spawning areas. Fishers will be asked to report all occurrences of squid eggs in their gear. Information gathered will be used to model the physical characteristics of spawning areas.
- Collection of data on nursery areas. During a limited directed programme of research sampling, near-bottom deployment of bongo nets will be used to survey paralarvae. Cephalopod paralarvae are poorly sampled during normal plankton tows, and the current consensus is that this reflects their location in the water column.
- Gear selectivity trials. To date, there have been few studies of gear selectivity for squid (e.g. Hastie, 1996; Fonseca *et al.*, 2002; Belcari *et al.*, 2007). An investigation of the application of a square-mesh panel in front of the trawlnet codend in the northern Tyrrhenian Sea (Italy) demonstrated some potential benefits for the exploited population of *Illex coindetii* (Belcari *et al.*, 2007). British trawler fishers trialled specially modified "squid" nets in 2005. Further and more extensive studies are needed in order to evaluate the selectivity of gears currently in use and to develop new selective gears able to provide a compromise between not losing commercial specimens and, at the same time, allowing as many juveniles as possible, as well as non-target species, to escape.
- Modelling of recruitment success. Stock–recruitment relationships in cephalopods are thought to be weak (e.g. Pierce and Boyle, 2003). However, inclusion of appropriate environmental indicators can substantially improve predictions, as demonstrated by studies in the Southwest Atlantic (Waluda *et al.*, 2001a, 2001b).
- Investigation of optimum on-board storage and handling methods.
- Studies of discarding. Although limited work on cephalopod discarding has previously been carried out in several areas, the information available is incomplete and probably out of date, and there are no such data available from directed cephalopod fisheries.

- Evaluation of the potential for targeting oceanic squid. Ommastrephid (short-finned) squid are regularly taken as bycatch by trawlers in southern European waters. However, historically, there was also an important fishery for *Todarodes sagittatus* in Norway, as well as some interest in this species in the Shetland Islands (UK) in the late 1980s. More recently, the potential for fishing *Gonatus fabricii* has been explored in Greenland waters, although trials were considered unsuccessful. Population abundance in ommastrephids may be "episodic" in nature, although one of the world's biggest squid fisheries, for *Todarodes pacificus* off Japan, has sustained commercially viable catches over several decades. It is likely that ommastrephid abundance in Northeast Atlantic shelf waters will increase as sea temperatures increase (see Hastie *et al.*, 1994), and little is known of the abundance of these squid in offshore waters.
- Scenario modelling to explore ecological and socio-economic consequences of alternative management measures.
- Development of protocols for sustainable directed squid fisheries with fisher participation.

### 6.6.3 Larger-scale cephalopod fisheries

Various management approaches are currently applied to larger-scale cephalopod fisheries across the world (e.g. in North America, in both the ICES and PICES areas), which could be applicable in European waters. For example, in California, market squid (*Loligo opalescens*) is the focus of one of the most important fisheries, and fecundity, egg escapement, and mortality-based biological reference points are currently being developed (Dorval *et al.*, 2009).

In Europe, the fisheries in which cephalopods are an important bycatch are usually multispecies fisheries, which present managers with significant challenges. Any measures applied to catching cephalopods are constrained by measures applied to the capture of the target finfish species. Similarly, bycatch of fish may be an issue when small-mesh codends are used on trawls targeting squid (as in fisheries for *Loligo* spp. in the US and Scotland). New research in several areas could prove valuable.

The characterization of essential fish and cephalopod habitats should provide a much more detailed understanding of the spatial distributions of exploited species, facilitating seasonal and spatial regulation of fishing activity so as to maximize the efficiency and sustainability of the exploitation of fished species, for example by protecting major spawning grounds. Empirical statistical models of habitat requirements (e.g. Sánchez *et al.*, 2008) can assist in predicting the locations of important habitats and, for species requiring particular seabed conditions for spawning, acoustic surveys can be used to identify spawning areas (Foote *et al.*, 2006).

Modifications to gear design or fishing practice to take account of the behaviour of cephalopods can be used to reduce bycatch of non-target species. Thus, loliginid squid are capable of holding station in the mouth of a moving trawlnet for extended periods, but once exhausted, can be drawn into the bag or attempt to escape sideways, hence becoming trapped in the wings of the net. *Loligo pealeii* have been observed to rise when dropping back towards the codend and, in some cases, to turn and rise on tiring. Thus, introduction of separator panels can separate squid from finfish bycatch (Glass *et al.*, 1999). In addition, trawling speed may have a significant effect on squid catches.

Squid shoals are potentially identifiable acoustically (e.g. Starr and Thorne, 1998; Kawabata, 1999, 2005; Kang *et al.*, 2005; Madureira *et al.*, 2005), and this acoustic signature could be used to inform decisions about whether or not to fish at a particular time and place.

## 6.7 Selected topics for future research

The following sections describe a range of possible research directions that would improve our knowledge of cephalopod biology and ecology and contribute directly or indirectly to their sustainable exploitation. It is worth pointing out that, although cephalopods are invertebrates, they have highly organized nervous systems, and research on captive cephalopods raises ethical and welfare issues (see Boyle, 1991; Moltschaniwskyj *et al.*, 2007). To a greater or lesser extent, such concerns have led to regulation of experimental studies on cephalopods, notably in the UK, where it falls under the Home Office licensing system.

### 6.7.1 Status of cuttlefish stocks

Since the early 1980s, there has been a rapid increase in the landings of cuttlefish by UK vessels in the English Channel, with landings peaking in 2003 at 5135 t. Cuttlefish constitute a significant part of the earnings from mixed fisheries in the Channel, the fishery being an important source of employment. At the European scale, cuttlefish are currently the most important cephalopod fishery resource.

Tagging experiments and spatio-temporal trends in fishery statistics suggest that the cuttlefish in the Channel and those in the Bay of Biscay are separate stocks. However, preliminary investigations of genetic differences revealed very low differentiation between these areas. In the English Channel, cuttlefish spawn in separate coastal areas, but their contributions to stock renewal are unknown. Further studies are required to clarify issues related to stock identification.

Aspects of the stock dynamics and exploitation of cuttlefish in the English Channel were described by Dunn (1999). A modelling study of the impact of exploitation on the stock suggested that it may be fully exploited (Royer *et al.*, 2006). A preliminary investigation of the state of the stock, based on the application of a two-stage biomass model, suggested an increasing trend in stock biomass in recent years (B. A. Roel and G. H. Engelhard, pers. comm.). The ongoing research project CRESH (2009–2012), funded under the INTERREG programme, aims to determine essential habitats for reproduction and prerecruit stages and to develop modelling approaches for a full evaluation of the English Channel cuttlefish stock.

### 6.7.2 Small-scale cephalopod fisheries

Small-scale fisheries contribute to a significant fraction of cephalopod catches in European waters, particularly in some fishing areas around the Iberian Peninsula, the northwest coast of Africa, and in the Mediterranean Sea (Lefkaditou and Adamidou, 1997; Lefkaditou *et al.*, 2003b). In these areas, cuttlefish catches by static nets (gillnets or trammelnets) and octopus catches by traps, pots, or fykenets are the major component of the total catches. The squid *Loligo vulgaris* and *Todarodes sagittatus* also occur seasonally in the catches in some of the Italian *ad hoc* developed artisanal fishing activities.

The availability of new fishing gears that are easily used by small artisanal vessels, such as plastic pots and fykenets, resulted in the rapid development of octopus coastal fisheries. For cuttlefish, however, expansion of the traditional net fisheries was mainly related to an increase in the species' abundance in many coastal fishing grounds and to the change in the target of artisanal fisheries owing to the depletion of coastal finfish resources.

In spite of the unavailability of specific statistics, these fisheries probably constitute a substantial source of income for local fishing communities not associated with the big trawl fishery. They also represent important local social traditions and are the only source of income for some small, scattered, Mediterranean communities. Decreasing trends in such fishery landings, recently observed in some areas, are probably related to the decrease in the small-scale fishing fleets (e.g. in Italy) and/or to the high fishing pressure recently imposed on cephalopod populations in many areas.

Despite their increasing interest in targeting cephalopods, and their economic and social importance for local fishing communities, monitoring of these small-scale fisheries is still limited, and there are important gaps in the available knowledge of the biology and population dynamics of octopus and cuttlefish.

In order to support sustainable artisanal exploitation of coastal cephalopod resources, a sector of considerable economic and social importance for local populations, the following actions are urgently needed:

a ) systematic monitoring of fisheries targeting cephalopods;
b ) detailed analysis of the economic and social importance of these fisheries at local levels as well as at national levels;
c ) thorough study of different life stages and population dynamics of targeted cephalopod species;
d ) bioeconomic studies of small-scale fishery activities, including fleets targeting cephalopods; and
e ) evaluation of possible ecological and socio-economic implications of alternative management strategies at the local level.

### 6.7.3 Essential habitat modelling

During the last decade, the importance of identifying, designating, and protecting essential fish habitats (EFHs) has been widely recognized. The mapping and designation of EFHs applies to the spatial component of fishery management, a component that has often been neglected in previously enforced fishery policies. The new framework regulation in the European Community's Common Fisheries Policy requires the introduction of habitat identification and protection into developing new fishery policies.

The EC-funded FP6 Project (EnviEFH: Environmental Approach to Essential Fish Habitat Designation, December 2005–February 2008) was based on the latest advances in EFH mapping and identification, which are characterized by a broad approach to EFH designation. This includes all the physical, chemical, and biological properties of marine areas, and the associated sediment and biological assemblages that sustain fish populations throughout the various stages of their life cycle. Species life-history information was introduced in an integrated EFH mapping effort, which involved the mapping of ocean production processes, species spawning, nursery and feeding aggregations, overexploited areas, and alternative fishing grounds. The overall objective of the EnviEFH project was to facilitate the spatial component of fishery management, especially the designation of essential fish habitats and their protection through new fishery policies.

Among several other species, the EnviEFH project included commercial cephalopod resources in the Mediterranean. Cephalopods are very sensitive to environmental changes. Spatio-temporal environmental variations strongly affect the biological processes and characteristics of cephalopods during their short life cycles. Cephalopods seem to respond to environmental variation both “actively” (by migrating to areas with more favoured environmental conditions) and “passively” (by using optimum environmental conditions to reach certain life stages at different growth rates between different generations). In many demersal and benthic species, distribution is related to bathymetry. Different groups dominate at different depth ranges, with benthic octopus species tending to occur in the deepest waters. In some demersal species, notably cuttlefish and loliginid squid, inshore–offshore migrations are seen within the range of occurrence. Pelagic species, such as ommastrephid squid, tend to be highly migratory and are likely to be strongly affected by changes in current systems and large-scale oceanographic phenomena (e.g. *El Niño*). Coastal species may be affected by variations in water quality (e.g. turbidity and oxygenation) and salinity (related to rainfall and river flow). Local abundance of many species, both demersal and pelagic, is related to temperature and/or productivity, although these links can often be displaced in both time and space, with conditions experienced by eggs and paralarvae affecting recruitment to the adult population, which may occur several months later in a completely different area. The timing of cephalopod life cycles is often related to the seasonal cycle of environmental conditions, raising the issue that climate change may result in a mismatch between the timing of critical life stages and optimum environmental conditions (see Pierce *et al*., 2008b).

In addition, Lefkaditou *et al.* (2008) reported depth to be the principal variable associated with the distribution of *Illex coindetii* populations in the Ionian Sea, demonstrating diversification of recently recruited juveniles and immature individual depth preferences. Mature individuals were more likely to be found at depths of 200–330 m, at greater distances from thermal fronts, and in locations characterized by highly positive surface chlorophyll *a* anomaly. Also, Sánchez *et al.* (2008) argue that *Loligo vulgaris* couples its life cycle with environmental features and takes advantage of the hydrographic characteristics of the area. Fishing grounds for squid are mainly located in the northern and central parts of the Catalan coast where the EFH for paralarvae is optimal. Low landings per unit effort in the southern part may be related to the export/migration of paralarvae from north to south, following the north–south current water that flows parallel with the coast.

Future research themes should include in-depth research on the responses of cephalopods to a combination of changing environmental habitat descriptors. There is a need to take account of surface and subsurface oceanographic processes that are not readily captured in static models (e.g. current systems), and of interactions between large-scale climate processes and local oceanography.

Unless local oceanography is understood, empirical relationships between species distributions and environmental processes may not explain the underlying mechanism(s) controlling species abundance, and models will not be applicable in other areas. Environmental relationships, clearly spatial and temporal components (e.g. environmental conditions), affect both recruitment strength and the subsequent distribution of post-recruits. It is also necessary to consider that cephalopods will be affected indirectly by environmental effects on other species.

A promising generic approach is the coupling of large- and local-scale oceanographic models with ecosystem models, although fully spatially explicit versions of such models may be hugely complex. Single-species studies still can reveal subtleties and details of interactions between animals and their environment that are not necessarily apparent from oceanography–ecosystem models.

Research is needed to improve our understanding of what exactly determines the distribution of cephalopod habitats in an ever-changing marine environment, to identify certain species as important environmental change indicators, to provide an important contribution to stock assessment methods, and to contribute to the environmental approach to fishery management (EAFM). A first picture of fisheries–environment interactions in the Mediterranean arose from the EnviEFH project, and there is a need for similar research in European Atlantic waters.

### 6.7.4 Cephalopods as vectors for pollutants and physiological effects of pollutants

Chemical substances constitute the greatest pollutant burden on natural ecosystems. Such pollutants can affect the marine environment by directly affecting individual animals exposed to the contamination. They can also contaminate a fishery resource and thereby affect species higher in the food chain, such as humans.

Many molluscs bioconcentrate chemical substances more than other animal groups by virtue of their high storage capacities and limited excretory abilities, as well as being less able to metabolize organic chemicals. This suggests there will be a lower effect threshold for molluscs compared with other invertebrate groups.

Cephalopods are known to accumulate and detoxify several trace metals in their digestive gland (Bustamante *et al.*, 2002a), branchial hearts (Ueda *et al.*, 1979), and renal and pericardial appendages (Bustamante *et al.*, 2000). Silver, for example, is absorbed mainly from seawater (Bustamante *et al.*, 2004; Miramand *et al.*, 2006), whereas cadmium is accumulated mainly from the diet (Koyama *et al.*, 2000; Bustamante *et al.*, 2002b). Cephalopods are a major vector for the bioaccumulation of trace metals in animals higher up the food chain, such as whales and humans (Muirhead and Furness, 1988; Bustamante *et al.*, 1998a, 2006; Lahaye *et al.*, 2005).

Despite its short lifespan, *Eledone cirrhosa* can accumulate high levels of mercury, such as those seen in the mantle muscle tissue of animals from the northern Tyrrhenian Sea, which are related to the cinnabar anomaly of Mount Amiata (Tuscany; Barghigiani and De Ranieri, 1992; Rossi *et al.*, 1993). Biomass estimates indicate very high densities of this octopus along the Tuscany coast (Wurtz *et al.*, 1992). The species is common in the diet of local people and could be detrimental to human health. Studies on metal concentrations in *Octopus vulgaris* in Portuguese waters also highlight possible health risks to human consumers (e.g. Seixas and Pierce, 2005a, 2005b; Seixas *et al.*, 2005a, 2005b).

In giant squid (*Architeuthis dux*) from the Mediterranean and Atlantic Spanish waters, the highest concentrations of mercury, cadmium, cobalt, copper, iron, nickel, selenium, vanadium, and zinc were found in the digestive gland and branchial hearts, highlighting their major role in the bioaccumulation and detoxification processes. With the exception of mercury, the muscles contained relatively low concentrations of trace elements. Nevertheless, this tissue still contained the main proportion of the total arsenic, chromium, mercury, manganese, nickel, and zinc in the body because muscles represent the main proportion of the squid mass. These findings suggest that, overall, metal metabolism is the same as in other cephalopod families from neritic waters. In female squid, zinc concentrations in the digestive gland increased with increasing body weight, probably reflecting physiological changes during sexual maturation. A comparison of trace element concentrations in the tissues of *Architeuthis* showed that silver, copper, mercury, and zinc concentrations were higher in squid from the Mediterranean than from the Atlantic, reflecting different exposure conditions. In comparison with other mesopelagic squid from the Bay of Biscay, cadmium concentrations recorded in the digestive gland suggest that *Architeuthis* may feed on more contaminated prey or that it has a longer lifespan that other cephalopods (Bustamante *et al.*, 2008).

Organic chemicals are known to affect cephalopods physiologically, causing changes in respiration, reproduction, etc. Studies have demonstrated that squid and cuttlefish accumulate organochlorine compounds (Sato *et al.*, 2000; Danis *et al.*, 2005), including PCBs (Butty and Holdway, 1997; Yamada *et al.*, 1997), in concentrations similar to those measured in the environment.

Chemical pollutants are also known to affect molluscs physiologically, for example, by reducing growth and reproductive fitness, and depleting energy reserves (Oehlmann and Schulte-Oehlmann, 2003). In addition, cellular, molecular, and genetic alterations have been reported for molluscs (e.g. DNA damage caused by chemical pollution and resulting in genetic mutations; reviewed by Oehlmann and Schulte-Oehlmann, 2003).

Preliminary research has demonstrated that, although low concentrations of some heavy metals are blocked by the egg membrane, high concentrations inhibit egg development and cause high mortality of the embryos (E. Le Bihan, pers. comm.). It is important to study the sensitivity of cephalopod eggs to pollutants as well as the effects of pollutants on digestive physiology and its consequences for the hatchlings.

Perrin *et al.* (2004) have demonstrated that some heavy metals can affect the digestive enzymes of the digestive gland. Bustamante *et al.* (2002b, 2004) and Miramand *et al.* (2006) have demonstrated the bioaccumulation of some heavy metals and confirmed the storage function of the digestive gland. The results indicate that it is necessary to know the toxic concentrations and the toxic effects on juvenile cephalopod physiology (nutrition, digestion, growth survival).

Research on the suppression or stimulation of the immune system of invertebrates indicates that exposure to various contaminants, including metals, adversely affects the immune system so that disease is contracted earlier and infection rates are higher (Cheng, 1988a, 1988b; Oliver and Fisher, 1999; Pipe *et al.*, 1999; Galloway and Depledge, 2001). In relation to cephalopods, temperature and physical stress are known to affect the immune system, although there is very little information on the effect of chemical pollutants – including endocrine disruptors – on the health of cephalopods (see Malham and Runham, 1998; Malham *et al.*, 2002). The effect of these pollutants on the various cephalopod fisheries as a whole is also unknown, although individual animals will undoubtedly be affected.

Finally, it should be noted that pollutants bioaccumulated by cephalopods are passed on to the consumers of cephalopods, including humans. Whereas some fish species are known to accumulate high levels of mercury, it is the accumulation of cadmium that is more frequently noted in cephalopods. Although metal concentrations in cephalopods are relatively well documented and generally thought to be below levels that are toxic to humans, much less information is available on other types of contaminants and marine toxins. Some information exists on the accumulation of domoic acid, which is responsible for amnesic shellfish poisoning, and high levels have been recorded in the octopus *Eledone moschata* (Costa *et al.*, 2005a, 2005b).

In order to understand the effects of pollutants on cephalopods and the potential loss to the fishery, proposed new research should include the following.

- Targeted sampling trips (cephalopods and water) along known cephalopod migratory routes to assess potential accumulation (efforts would be concentrated at juvenile stages as being the most vulnerable to pollution, although most bioaccumulation will occur in adults).
- Laboratory experiments to assess the physiological, biochemical, immunological, and transgenomic responses of different cephalopod life-history stages to selected pollutants.
- The production of models of the effects of pollutants on cephalopods, including reduction in fitness and potential loss to the fishery.
- Assessment of the amounts of contaminants passing from cephalopods up the food chain, including contaminant levels entering the human food chain.
- Verification of the use of cephalopods as bio-indicators of environmental mercury for comparing both the levels of the metal in different areas and the variations in the same area between different periods.

### 6.7.5 Age determination using growth-recording structures

Studies and monitoring of growth in cephalopods are complicated by the high variability of individual growth rates. Length–frequency distributions are generally polymodal, making it difficult to clearly single out cohorts or microcohorts, and growth estimation by means of length–frequency methods is difficult (e.g. Sánchez, 1984; Caddy, 1991; Jereb and Ragonese, 1995; Arvanitidis *et al.*, 2002). Therefore, conventional methods for determining growth, such as length–frequency analysis, used in the assessment of traditional resources such as short-lived fish and crustaceans, are inappropriate to cephalopods. This, in turn, is the main reason why statoliths have attracted increasing attention in the last two decades and are considered among the most promising tools for age determination in cephalopods (e.g. Jereb *et al.*, 1991; Jackson, 1994).

Generally speaking, age estimates from statolith analysis may result in strikingly different values from those obtained by length–frequency analysis (see e.g. Jereb and Ragonese, 1995; Arkhipkin *et al.*, 1998). In particular, much shorter lifespan estimates are obtained. Recent studies are very much in favour of a very fast life cycle for most squid, because of the combination of efficient digestion and a protein-based metabolism, along with the ability to sustain continuous growth by a combination of hypertrophia (muscle fibre size) and hyperplasia (muscle fibre number), the efficient use of oxygen, and low levels of antioxidative defence (Jackson and O'Dor, 2001).

However, other evidence supports longer lifespans, and there are problems related to interpreting increments in statoliths. These include changes in statolith structure and growth increment deposition rate with growth and maturity, and potential bias caused by loss of growth increments deposited in statoliths during paralarval life (see González *et al.*, 2010), environmentally derived changes in increment width (Moreno, 2001), and biases related to statolith preparation and differences in the methods for interpreting and enumerating increments (e.g. Lipinski and Durholtz, 1994; González *et al.*, 2000; Bettencourt and Guerra, 2001). There is also a rather broad consensus that the use of other hard structures, such as beaks or gladii, to investigate growth and age in cephalopods is less likely to lead to a simple and routinely applied methodology.

Many aspects of cephalopod life history have been elucidated in the absence of reliable age data, including seasonality of breeding and recruitment and the relationships between somatic growth and maturation (e.g. in *Loligo forbesii*; see Smith *et al.*, 2005). However, the evident complexities, including multiple microcohorts, alternative size-at-maturity strategies, apparent mismatches between recruitment and spawning seasons, multiple breeding seasons, and interactions between body size, fecundity, and seasonality (e.g. in *L. forbesii*, see Boyle *et al.*, 1995; Collins *et al.*, 1997, 1999; Pierce *et al.*, 2005b), make clear that age is a key parameter and that length is a very poor proxy.

Based on these considerations, we propose new broad-scale, collaborative studies on statoliths. At a basic level, these would evaluate precision and increase consistency among investigators. This would require scientists from different countries meeting, discussing, and carrying out the necessary procedures in order to make comparisons and evaluations possible. In such a context, additional techniques and/or tools, such as image analysis systems, already applied individually, could be used and results evaluated (Eltink *et al.*, 2000).

Second, there is a need for further data collection. This includes experimental studies on increment deposition. Although several studies indicate that increments are normally daily, it is far from clear that this is always the case. The collection of new age data, both from historical collections and new samples, is also necessary. Finally, a workshop-based approach would facilitate the use of statolith data to generate new insights into life-history processes in cephalopods and ultimately inform improved fishery management.

It is now about two decades since the first international statolith workshop was held in Mazara del Vallo (Sicily, Italy, 1989; Jereb *et al.*, 1991). Therefore, it is suggested that a new series of workshops on the analysis of statoliths and interpretation of data on growth increments should be organized. The first such event would involve:

- participation of experts on statoliths and experts on cephalopod life cycles and growth;
- expertise from otolith research and guidelines from fish age-reading intercalibration workshops;
- investigation of statoliths of several different species, especially squid (i.e. ommastrephids and loliginids) from different areas around the world;
- existing collections of statoliths of animals of known age to address problems related to accuracy and precision;
- evaluation of the use of additional techniques, such as image analysis systems;
- discussion on how to deal with the many problems related to statolith structure modification with growth and maturation;
- investigation of the application and use of models, taking into consideration the above-mentioned sources of bias and problems.

It is important that the use of other recording structures to reconstruct individual growth trajectories and age continues to be explored. Several recent studies have demonstrated that age determination is possible using increments in the beak and stylus of octopus (Hernández-López *et al.*, 2001; Doubleday *et al.*, 2006; Leporati *et al.*, 2008; Doubleday, 2009; Hermosilla *et al.*, 2009; Perales-Raya *et al.*, 2009). Hughes (1998) demonstrated the potential for using increments in the gladius of *L. forbesii* to reconstruct recent growth trajectories. The clear advantage of the squid gladius is that increments can be related to actual growth in ML (with almost a 1:1 ratio). In species, which demonstrate such wide variability of individual growth trajectories, growth patterns reconstructed from putting together age and size data from different animals can give a highly misleading picture of individual growth (Alford and Jackson, 1993; Arkhipkin, 2005; Arkhipkin and Roa-Ureta, 2005).

### 6.7.6 Life-history reconstruction using growth increments in recording structures

Statoliths can provide a variety of information about squid biology and ecology. Growth increments and other patterns within the statolith microstructure may be used to identify age, hatching date, and the growth of an individual as well as to date and estimate the duration of ontogenetic events, such as the paralarval phase and number of spawning events. Furthermore, the chemical composition of statoliths has extensive relevance to many ecological questions.

The uptake of minor and trace elements in carbonate structures of many marine animals is influenced by chemical and physical parameters of the ambient water. Element incorporation can vary with temperature, salinity, and element concentration in the surrounding water. Therefore, essential information on distribution and migration pathways of the individual animal is stored in the bio crystal. Microchemical analyses have become a standard method in fish otoliths to reconstruct environmental histories of individuals and as natural tags of stock structure.

Compared with fish otoliths, there have been only a handful of studies examining the chemical composition of cephalopod statoliths, but statolith chemistry is obviously a field of growing interest. Chemical signatures of statoliths have been used as a tool to determine environmental life histories of the neon flying squid (*Ommastrephes bartramii*; Yatsu *et al.*, 1998), the Japanese common squid (*Todarodes pacificus*; Ikeda *et al.*, 2003), and the boreo-atlantic armhook squid (*Gonatus fabricii*; Zumholz *et al.*, 2007a), as well as to discriminate between stocks of the Patagonian longfin squid (*Loligo gahi*; Arkhipkin *et al.*, 2004b). Experimental studies found good evidence for environmental influences (e.g. temperature, salinity, food intake) on several minor and trace elements (Zumholz, 2005; Zumholz *et al.*, 2006, 2007b), providing an essential basis for further investigation in the field.

Such a project might include the following components.

- stock separation
- location of spawning and nursery grounds
- reconstruction of migration routes
- changes in the microstructure and chemical signature of statoliths caused by climate-change effect on chemical and physical parameters of the ambient water

The focus would be on commercially important species such as *Loligo forbesii, Loligo vulgaris, Sepia officinalis,* and ommastrephids for which older statolith collections might also be available.

### 6.7.7 Genetic biodiversity and genetic stock structuring in European cephalopods

Research employing molecular genetic methods conducted during previous EU and allied projects on European cephalopods uncovered two fundamentally different patterns of distribution of genetic diversity: (i) genetic homogeneity of populations of loliginid and ommastrephid squid across large geographical scales; and (ii) distinct genetic population substructuring over relatively small geographical scales (hundreds of kilometres) in cuttlefish and octopus species (Shaw *et al.*, 1999; Pérez-Losada *et al.*, 2002, 2007; Garoia *et al.*, 2004; Dillane *et al.*, 2005; Cabranes *et al.*, 2008). These data indicate that, whereas highly migratory squid species may be safely considered to represent single stocks at large geographical scales (certainly at infranational scales), more sedentary species, such as cuttlefish and octopus, mostly comprise highly localized genetic stocks. As distinct genetic stocks suggest very low levels of gene flow (i.e. effective migration) within a species, the observation of locally structured genetic diversity within some cephalopod species indicates that such species should be managed on a corresponding local scale.

Previous genetic studies of cephalopods also indicate that no single factor may be responsible for the observed population substructuring in some species. For example, the scale and pattern of structuring in *Sepia officinalis* hints at species life-history effects on dispersal, such as localized breeding grounds, whereas in *Octopus vulgaris*, oceanographic features that affect larval dispersal may be more important.

Existing genetic studies of European cephalopods represent very basic initial surveys of genetic diversity. A full understanding of the distribution of genetic biodiversity in these species, and, therefore, the data upon which to base realistic management models, can only be achieved with further, carefully targeted studies.

Population genetic studies, utilizing a combined approach with microsatellite DNA and mtDNA markers, of *Sepia officinalis*, *Octopus vulgaris*, and *Loligo vulgaris* should be conducted in European waters, especially within Mediterranean waters.

- The primary aim for *L. vulgaris* would be to assess whether regional genetic differentiation occurs, indicating localized spawning groups, or whether, like other loliginids, it can be assumed to comprise a single population or genetic stock, at least throughout Mediterranean waters.
- The primary aim with *S. officinalis* and *O. vulgaris* would be to determine the geographical scale of subpopulation structuring and the relation of such structuring to geographical distance (i.e. isolation-by-distance determinants of species dispersal) and/or to oceanographic features (i.e. distinct physical barriers to dispersal). To achieve these aims for *S. officinalis* and *O. vulgaris*, a hierarchical sampling scheme incorporating different spatial scales and relevance to oceanographic features would be required. An ideal combination would be to study both species simultaneously as a comparative study of the influence of species biology on stock structuring.
- To provide a complete picture of fished European species, genetic studies of population/stock structuring should be carried out for *Todarodes*, *Alloteuthis*, *Eledone*, and *Sepia* species of commercial or biodiversity importance.

Population genetic studies can be conducted in isolation, but would be significantly more powerful in their outcome if combined in a multidisciplinary study alongside other population-level methodologies, such as statolith microchemistry or approaches such as essential habitat modelling.

### 6.7.8 The role of cephalopods in the ecosystem

In the context of the EAFM, it is important to understand how cephalopods interact with other ecosystem components, including prey, predators, competitors, pathogens, and parasites.

#### 6.7.8.1 Ecosystem models

Models of the trophic structure of ecosystems built using Ecopath/Ecosim/Ecospace (Christensen and Walters, 2000) are a useful tool to explore the consequences of increased fishing on cephalopods, but few applications to date consider cephalopods as a distinct functional group (or groups). The Ecopath approach allows characterization of foodweb structure through integration of disparate ecosystem information derived from many years of study. Ecosim and Ecospace allow us to explore various hypotheses about system dynamics as well as potential solutions to conservation concerns about overfishing. After defining functional groups in the ecosystem and obtaining a "balanced" model, simulated depletion or removal of functional groups allows estimation of interaction strengths and "keystone" potential for each group. Relative interaction strengths in a pristine unfished system are likely to be quite different from interaction strengths indicated by this present-day model. The effects of human extraction of food from different trophic levels in the ecosystem can be tested, as can the consequences of creating protected areas.

Ecopath represents just one tool available to analyse the complex network of trophic relationships in an ecosystem. Other possible approaches include neural network and fuzzy-logic models (Wasserman, 1989; Spooner *et al.*, 2002). In general, such tools create representations of the system that facilitate analysis of the similarities and differences between complex systems of very different natures, ranging from the technological to the biological and social.

Complex network, neural network, and fuzzy-logic models of ecosystems all require historical series of both biological and oceanographic data, and/or data from the whole ecosystem. Historical data on catches and/or cpue for cephalopods and accompanying species are essential. This kind of information is contained in databases that some European agencies, institutes, or organizations have constructed from research cruises carried out annually over many years in the same geographic area. Additional information may also be available from some research cruises undertaken in specific areas (e.g. submarine canyons, deep coral grounds). Making such databases accessible to the research community should be a future priority.

#### 6.7.8.2 Parasites

One of the main tasks in the study of cephalopod parasites and their effects on cephalopod stocks is to understand how parasites are being recruited to host populations. It is generally thought that potentially harmful cephalopod parasites are those transmitted via trophic interactions, but much more information is needed. It would be interesting to investigate the parasitic forms present in cephalopod prey, especially in paralarvae and juvenile cephalopods. Additionally, it would be very informative to compare the physical and chemical characteristics of water body masses with the zoogeographical distribution of cephalopod parasites.

Variability in recruitment of parasite infracommunities tends to be associated with major current systems of the world's oceans. It appears that instability in water masses caused by physical perturbations (e.g. water mass convergence and turbulent mixing in upwelling systems) is associated with instability of trophic interactions over time, which in turn leads to a paucity of parasite communities. Various reports indicate the crucial role of oceanographic processes on the recruitment of different parasitic aggressors that affect stocks of commercial species (Marcogliese, 2001; Pascual *et al.*, 2007a) in areas as diverse as the Humboldt upwelling affected by *El Niño* (Luque and Oliva, 1999), changes in Antarctic ice cover (Agnew *et al.*, 2003), or the variability of other upwelling systems or productive areas (Esch and Fernández, 1993). Nevertheless, studies of the larval phases constituting the vector by which the parasitic infection enters are currently lacking for both cephalopods and fish. Knowledge of the relationship between parasite recruitment and the oceanographic regime could be very useful in providing an indicator of ecosystem health, as well as being relevant to the understanding of the status of fished cephalopod stocks (Pascual *et al.*, 2007b).

#### 6.7.8.3 Determining trophic relationships using biochemical and molecular techniques

In support of stomach content analysis, both fatty acid and stable isotope analysis have been used to study the trophic ecology of cephalopods (as reviewed by Jackson *et al.*, 2007). Although neither technique easily provides detailed data on diet composition – although quantitative fatty acid signature analysis (Iverson *et al.*, 2004) has the potential to do so – both are suitable for demonstrating differences and trends in diet. They can be applied to animals with empty stomachs and provide dietary information integrated over an extended period, the length of which depends on the turnover rate of the tissue sampled.

Most stable isotope studies analysed cephalopod species regarding their role as prey to higher trophic levels (e.g. Hobson *et al.*, 1994; Ruiz-Cooley *et al.*, 2004, 2006). Several studies, however, have used stable isotopes to investigate the role of cephalopods as predators. Although analysis was generally carried out on whole animals or muscle tissue (Takai *et al.*, 2000; Landman *et al.*, 2004; Chen *et al.*, 2008; Parry, 2008), the most recent studies also successfully demonstrated the usefulness of beaks (Cherel and Hobson, 2005; Zimmer *et al.*, 2007; Cherel *et al.*, 2009a), gladii (Cherel *et al.*, 2009b), and shells (Lukeneder *et al.*, 2008) in describing the relative trophic position within and between cephalopod species. The underlying principle was that sequential sampling along the growth increments of squid beaks and gladii can be used to produce a chronological record of dietary information throughout an individual's history. Overall, stable isotope studies have identified changes in feeding with size (Ruiz-Cooley *et al.*, 2004; Cherel and Hobson, 2005; Zimmer *et al.*, 2007; Lukeneder *et al.*, 2008; Parry, 2008; Cherel *et al.*, 2009b), variations in habitat use (Landman *et al.*, 2004; Chen *et al.*, 2008), and species migration patterns (Ikeda *et al.*, 1998; Takai *et al.*, 2000; Cherel and Hobson, 2005; Lukeneder *et al.*, 2008).

Although a large number of cephalopod species have been analysed for their fatty acid composition, only a few of these analyses were aimed at studying the feeding ecology of the species (Jackson *et al.*, 2007). The purpose of the earliest studies was to identify the species energy requirements in the wild (e.g. Jangaard and Ackman, 1965). Recent research focused predominantly on the nutritional requirements of cephalopods with regard to rearing in captivity (e.g. Navarro and Villanueva, 2003; Domingues *et al.*, 2004; Almansa *et al.*, 2006) and their nutritional value for human consumption (e.g. Nakazoe, 2000; Ozogul *et al.*, 2008). Studies investigating the trophic ecology of cephalopods have used fatty acids as biomarkers to identify habitat (Phillips *et al.*, 2001, 2003a; Chen *et al.*, 2008), seasonal (Phillips *et al.*, 2003b), ontogenetic (Piatkowski and Hagen, 1994; Phillips *et al.*, 2003c), and between-species (Rosa *et al.*, 2005) variation in feeding.

The usefulness of both methods in studying the trophic ecology of cephalopod species was further verified through several controlled feeding experiments (Hobson and Cherel, 2006; Stowasser *et al.*, 2006; Fluckiger *et al.*, 2008). As with all techniques, limitations and technical difficulties have been noted (see Pierce *et al.*, 2004, for a review). Thus, it is increasingly apparent that differences in stable isotope ratios between tissues can reflect biochemical and physiological differences rather than simply differences in turnover, thus undermining the concept that diet is averaged over different lengths of time in different tissues. For example, the large amounts of chitin in beaks and gladii are likely to influence their isotopic signatures when compared with those of soft tissues, and the varying chitin contents within beaks are likely to affect the interpretation of ontogenetic isotopic variations (discussed in Cherel *et al.*, 2009b). A promising approach to overcoming the chitin effect is to undertake compound-specific isotopic analyses of individual amino acids isolated from cephalopod tissues (e.g. Lorrain *et al.*, 2009).

A limitation of the fatty acid method is that the prey must contain large amounts of lipids. Also, in some cases, the fatty acid signatures were a modification of those seen in the fatty prey, necessitating the derivation of "correction factors" if a quantitative picture of diet was sought. Finally, it is important to note that inferences about trophic relationships from both the stable isotope and fatty acid methods can be greatly strengthened by the assembly of reference libraries of the isotopic and lipid signatures of potential prey of studied predators. Nevertheless, both techniques have great power to help elucidate trophic interactions and thus quantitatively define the role of cephalopods in the ecosystem. The most fruitful approach is to combine, for the same individuals, the direct method of stomach content analysis with the two complementary indirect methods that are based on protein (stable isotopes) or lipid (fatty acids) metabolism.

Another suite of techniques developed for, or applicable to, dietary analysis is based on the identification of species-specific components of prey tissues. This includes the use of antisera to detect specific proteins, which has been attempted for cephalopods (Grisley and Boyle, 1988; Kear, 1992), and, more recently, the application of molecular genetic techniques (e.g. for marine mammals, see Symondson, 2002; Tollit *et al.*, 2009). DNA-based species identification quantification techniques have been developed for a range of applications (e.g. plankton identification, Pan *et al.*, 2008, and references therein), and the concept of molecular bar-coding continues to be developed, potentially with applications for cephalopods (Strugnell and Lindgren, 2007). As with fatty acid and stable isotope techniques, a library of prey species signatures is essential when applying DNA-based identification to diet analysis, and the use of this approach for full quantification of the diet is still in the future. However, advances in techniques, from use of the polymerase chain reaction (PCR) to automated DNA sequencing, and falling costs should bring these techniques within reach of researchers studying cephalopod trophic interactions.

## Acknowledgements

Much of the material presented in this report was originally compiled for the report of the CEPHSTOCK project (Q5CA-2002-00962, 2002–2005). We thank all the project participants for their input. GJP acknowledges support from the EU during the editing of this report, through the ANIMATE project (MEXC-CT-2006-042337). We also thank the staff at ICES Secretariat for their encouragement, advice, and patience during the extended gestation of this report.