ICES COOPERATIVE RESEARCH REPORT
RAPPORT DES RECHERCHES COLLECTIVES

NO. 303

AUGUST 2010

Cephalopod biology and fisheries in Europe

Editors

Graham J. Pierce • Louise Allcock • Isabel Bruno
Paco Bustamante • Ángel González • Ángel Guerra
Patrizia Jereb • Eugenia Lefkaditou • Shelagh Malham
Ana Moreno • João Pereira • Uwe Piatkowski • Mario Rasero
Pilar Sánchez • M. Begoña Santos • Marina Santurtún
Sonia Seixas • Ignacio Sobrino • Roger Villanueva

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer
H. C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

Recommended format for purposes of citation:

Pierce, G. J., Allcock, L., Bruno, I., Bustamante, P., González, Á., Guerra, Á., Jereb, P., *et al*. 2010. Cephalopod biology and fisheries in Europe. ICES Cooperative Research Report No. 303. 175 pp.

Series Editor: Emory D. Anderson

ISBN 978-87-7482-078-9

ISSN 1017-6195

Contents

Executive summary

Over the past two decades, cephalopod molluscs have attracted increased attention from marine biologists and fishery scientists. Several species are important for European fisheries, as targets of small-scale coastal fisheries and/or as bycatch in multispecies fisheries for demersal fish. The present report draws on a series of reviews prepared in 2005 for the CEPHSTOCK project (see Section 1). The taxonomy of the main resource species is reviewed (Section 2), and brief descriptions of each species are provided, along with information from studies of population genetics, habitat requirements of paralarvae and adults, and health and ecotoxicology (Section 3). The main fisheries are described, including illustration of gears used in specialized small-scale fisheries and a discussion of the socio-economic importance of the fisheries. The current status of cephalopod aquaculture is reviewed, highlighting notable advances in commercial culture of octopus and cuttlefish (Section 4). Current fishery data collection and fishery management are described, noting that there is no setting of landings quotas and no routine assessment of stock status. Options for stock assessment are discussed, drawing on one-off assessments made during specific projects and current practice elsewhere in the world. The "live fast, die young" life-history strategies of cephalopods present particular challenges, but parallels can be drawn with short-lived fish (Section 5). Finally, the report looks to the future, reviewing possible effects of climate change on cephalopods. It discusses the future development of aquaculture and fisheries for cephalopods, including prospects for fishery forecasting and fishery management – especially in relation to the small-scale directed fisheries. Various knowledge gaps are identified, and ideas for research to fill these gaps are presented.

1 General introduction

Graham Pierce and Peter Boyle

Historically, cephalopods in European waters have always been considered a minor fishery resource, although undoubtedly of local economic importance, especially in southern Europe's artisanal fisheries (Shaw, 1994). Interest in cephalopods as a fishery resource in northern Europe is evident only from a small number of publications in the 1970s (Wiborg, 1972, 1978, 1979a, 1979b; Thomas, 1973; Arnold, 1979; Howard, 1979).

Interest in cephalopods as a fishery resource in Europe has, however, grown substantially since the 1980s, when, in 1987, ICES first established, the Study Group on Squid Biology, the forerunner of the present ICES Working Group on Cephalopod Fisheries and Life History (WGCEPH), and two of the earliest academic studies on the squid *Loligo forbesii* took place (Ngoile, 1987; Lum-Kong, 1989). By the 1990s, increased interest in the potential of cephalopod resources to supplement or even to replace overexploited finfish stocks, as a source of both protein and revenue, led to a series of collaborative research and fisheries data-collection projects on cephalopod biology and fisheries, funded through the European Commission's Research and Fisheries support programmes.

- Fishery Potential of Northeast Atlantic Squid Stocks (FAR MA 1.146, 1990–1992)
- Stock Dynamics, Interactions and Recruitment in Northeast Atlantic Squid Fisheries (AIR1-CT92-0573, 1993–1995)
- Experimental squid jigging with light attraction (Study Project 93/19, 1994–1995)
- Data collection for assessment of fished cephalopod stocks (Study Project 96/81, 1996–1998)
- Cephalopod Resources Dynamics: Patterns in Environmental and Genetic Variation (FAIR-CT96-1520, 1997–2000)
- Cephalopods resources dynamics and fisheries trends in the Algarve and Gulf of Cadiz (Study Project 97/86, 1997–2000)
- Development of software to estimate unreported or misreported catch and effort data and to apply fishery management models (Study Project 97/107, 1997–1999)
- Analysis and evaluation of the fisheries of the most commercially important cephalopod species in the Mediterranean Sea (Study Project 97/54, 1998–2000)
- Data collection for assessment of cephalopod fisheries (Study Project 99/063, 1999–2001)
- Cephalopod Stocks in European Waters: Review, Analysis, Assessment and Sustainable Management (Q5CA-2002-00962, 2002–2005)

This research activity was reflected in a series of symposia on cephalopods, held under the auspices of ICES and the Cephalopod International Advisory Council, and generated a substantial number of new publications on cephalopod biology, ecology, and fisheries, including contributions to several special issues of peer-reviewed journals dedicated to cephalopod biology and fisheries (e.g. Boyle and Pierce, 1994;

Payne, A. I. L., *et al.*, 1998; Piatkowski *et al.*, 2001; Boyle *et al.*, 2002; Pierce *et al.*, 2005a; Payne, A. G., *et al.*, 2006; Koueta *et al.*, 2006).

Currently, cephalopod fisheries in European waters are of substantial importance. Total cephalopod landings from the Northeast Atlantic and Mediterranean have routinely exceeded 100 000 t since 1980 and were more than 116 000 t in 2006 (FAO statistics), comprising 49 000 t landed into Europe from the Northeast Atlantic and ca. 67 000 t landed from the Mediterranean by all nations (including those African and Asian countries with Mediterranean coastlines). However, no cephalopods are treated as quota species under the Common Fisheries Policy, and there are few restrictions specifically related to fishing for these species. Several southern European countries have introduced a range of technical measures and effort controls for cephalopod fishing, including restrictions on the type of gear used and minimum landing sizes (see Section 4 for details). Nevertheless, to date, there has been no move to fully regulate cephalopod fishing in European waters.

As cephalopods are short-lived and increment deposition on recording structures (where present) is daily or indeterminate, age determination is difficult. Furthermore, stock–recruitment relationships have generally not been determined (or do not exist), so most traditional methods of stock assessment have been thought unsuitable, although, as some authors have pointed out (e.g. Pauly, 1998), similar problems also arise for assessment of short-lived fish. To make real advances in stock assessment of cephalopods in European waters, there is a need to ensure that "stocks" are defined, that adequate biological and fisheries data are collected, and that appropriate biological and management reference points are identified for the various stocks (as done already in the Northwest Atlantic; see e.g. Hendrickson and Hart, 2006).

European cephalopod landings statistics refer to broad commercial categories (long-finned squid, short-finned squid, octopus, and cuttlefish), which all include two or more species. Limited routine biological data collection became mandatory under Council Regulation (EC) No. 1543/2000 and continues to be required under Council Regulation (EC) No. 199/2008. In the past, WGCEPH has expressed concern that there was no provision for data collection on several commercially important cephalopod "stocks" and, even for those included in the regulations, the level of data collection could be insufficient for assessment and management purposes (ICES, 2008). Now that data collection has switched to a métier-based system, coverage of landings of most cephalopod species is likely to improve, but it remains uncertain whether the data collected will be sufficient to determine stock status (see ICES, 2009).

The present report is based on material originally compiled for the final report of the EU-funded CEPHSTOCK project, a Concerted Action (Q5CA-2002-00962, 2002–2005) involving scientists from 22 European research institutions in seven countries (UK, France, Germany, Spain, Portugal, Italy, and Greece). This project (2002–2005) aimed to review current knowledge and issues in cephalopod fishery science; to assemble, organize, analyse and synthesize data from national and EC-funded research and development projects; and to recommend future actions for scientists and cephalopod-fishery managers in European waters. The project work involved a series of literature reviews, development of common databases and associated geographic information system (GIS) analysis capability, and meetings and workshops at which the status of fished European cephalopod stocks was discussed, retrospective stock assessments carried out, and management recommendations proposed. Specific objectives of the project were to:

1) review the current state of knowledge of exploited cephalopods (biology, fisheries, environmental relationships, stock identity) in European waters, on a stock-by-stock basis, in order to identify gaps in knowledge and the best methods available to collect necessary data;
2) review and document current data collection, stock assessment, and management practices for cephalopod capture fisheries worldwide;
3) review the current status of cephalopod culture and the prospects for commercial aquaculture;
4) review socio-economic issues related to cephalopod fisheries: economic and social value of cephalopod fishing, contribution to income and employment;
5) review current knowledge of aspects of cephalopod biology and ecology related to their suitability as resource species for capture and culture fisheries, including life-history and ecological data and assessment of environmental factors that affect the immunocompetence and physiology of cephalopods;
6) review management options for currently unregulated cephalopod fisheries in order to meet ecological, economic, social, and institutional goals for sustainable utilization, considering issues such as gear selectivity, minimum landing sizes, closed areas and seasons, stock enhancement;
7) design appropriate data-collection protocols for each stock in order to fill perceived gaps and ensure availability of the appropriate data to underpin management decisions (e.g. catch and effort data, stock identification studies, socio-economic data collection, gear trials);
8) hold workshops on assessment and management, with invited experts, using existing data to make assessments of stock status, including explicit evaluation of associated uncertainties, and to provide baseline precautionary management proposals and recommend future research directions;
9) develop a common database and GIS of biological, fishery, and bibliographic data on European cephalopod stocks;
10) use the database and GIS to develop models of interactions between cephalopod fisheries, cephalopod stocks, and the environment;
11) disseminate the information synthesized and results generated by the Concerted Action as peer-reviewed papers and conference presentations, in addition to reports to the Commission of the European Communities Directorate General for Research; and
12) develop new research proposals to address perceived gaps in the information required for sustainable management of fished cephalopod stocks.

The project contributed to three special issues of international peer-reviewed journals. A special issue of *Aquatic Living Resources* (Pierce *et al.*, 2005a) arose from a theme session on cephalopod life history and fisheries held at the 2004 ICES Annual Science Conference in Vigo, Spain, a session proposed and chaired by members of the project. A special issue of *Fisheries Research* arose from a workshop on cephalopod stock assessment, held at Imperial College, London, also in 2004 (Payne *et al.*, 2006). Lastly, the project contributed to a special issue of *Vie et Milieu* about the cuttlefish *Sepia officinalis* (Koueta *et al.*, 2006).

Publication of project results continues, including recent reviews of the biology of the planktonic stages of benthic octopods (Villanueva and Norman, 2008) and of cephalopod−environment interactions (Pierce *et al.*, 2008b). However, a substantial portion of that report has not been published, and the present report assembles (and updates) the parts of the project output that are most relevant to European cephalopod fisheries.

Following this general introduction, the report continues with a brief review of the thorny subject of cephalopod taxonomy, as applied to the European species of commercial importance (Section 2), before presenting summary accounts of the biology and ecology of the main fished species and some short reviews of specific topics in biology (Section 3). Full accounts will be published as a separate report. Section 4 comprises a description of the current status of fisheries and culture for cephalopods in Europe, while Section 5 examines assessment and management options for European cephalopod fisheries. Finally, we offer perspectives on future prospects for cephalopod fisheries and culture, with particular emphasis on possible effects of climate change, and attempt to identify new research directions and knowledge gaps (Section 6).

2 Taxonomy

Louise Allcock

2.1 Introduction

The taxonomy of the Cephalopoda has undergone something of a revolution in recent years as new results, particularly from molecular genetic studies, demonstrate the need for revision of classical divisions and relationships that were based on comparative morphology. Much of this work concerns revision of non-commercial and/or less abundant taxa, many of which are either deep-sea dwellers, e.g. the genus *Opisthoteuthis* (Villanueva *et al*., 2002b), Northeast Atlantic *Bathypolypus* (Muus, 2002) and *Benthoctopus* (Allcock *et al*., 2006), or inhabit more remote regions of the world, e.g. the several still-undescribed species of the group known as "mimic octopuses" of the Indian Ocean and South Pacific.

2.2 Long-finned squid

The loliginid squids (represented in this report by four species (*forbesii* Steenstrup, 1856; *vulgaris* Lamarck, 1798; *subulata* Lamarck, 1798; and *media* Linnaeus, 1758) have been under constant systematic revision for many years. The latter two species were traditionally placed in the genus *Alloteuthis* Wülker, 1920. Indeed, *media* was placed in *Alloteuthis* from the inception of the genus (Wülker, 1920) and is the designated type species of the genus, whereas *subulata* was included within *Alloteuthis* just a few years later by Naef (1923). This taxonomy was fairly stable and survived several major revisions of the Loliginidae (Natsukari, 1984; Brackoniecki, 1986). However, a systematics workshop held in 1988 (Vecchione *et al*., 1998) recognized only five genera and assigned *Alloteuthis* subgeneric status within the genus *Loligo*. This revision was overturned in a subsequent systematics workshop in 2003 (Vecchione *et al*., 2005), where evidence from gladius structure (Alexeyev, 1989, 1991) and mitochondrial DNA analysis (Anderson, 2000a, 2000b) was considered sufficient to elevate *Alloteuthis* back to generic status. Recent molecular data from *Alloteuthis* specimens across the geographic range of the species have demonstrated that the character most commonly used to distinguish European species (relative tail length) is unreliable (Anderson *et al*., 2008). The data confirmed that two species exist in European waters but, given that the type specimen of *subulata* is not extant and the whereabouts of the type specimen of *media* has not been confirmed, taxonomic issues abound. Redescriptions and a neotype designation are essential to stabilize the taxonomy.

The taxonomy of *Loligo vulgaris* is relatively stable. Children (1823) designated *vulgaris* as the type species of the genus *Loligo* Lamarck, 1798. Although there have been nomenclatural issues surrounding the validity of both the genus and species names, these have been resolved by submissions to the International Commission on Zoological Nomenclature (ICZN, 1954, 1997). A full discussion of these issues can be found in Sweeney and Vecchione (1998). A subspecies of *L. vulgaris, L. v. reynaudii* was created when Augustyn and Grant (1988) concluded that *L. reynaudii* Orbigny, 1839–1841 was a subspecies of *L. vulgaris*. This conclusion, based on morphological analyses and allozyme electrophoresis, was apparently accepted by the 1988 systematics workshop (Sweeney and Roper, 1998). The nomenclature was adopted by many fishery biologists (e.g. Sauer *et al*., 2000; Oosthuizen *et al*., 2002; Roberts *et al*., 2002; Shaw and Sauer, 2004), but not by taxonomists (e.g. Anderson, 2000a, 2000b). The latest revision of the Loliginidae did not specifically address this problem

(Vecchione *et al*., 2005), but Table 2 in that paper refers to *reynaudii* and *vulgaris* as distinct species. As *L. reynaudii* is restricted to South African waters, it does not concern us directly, but its apparent re-elevation to specific status (Vecchione *et al*., 2005) removes the need to refer to *L. vulgaris* in the ICES Area as *L. v. vulgaris*.

The most problematic species is *forbesii* Steenstrup, 1856. There are two issues surrounding it. First and simplest is the issue of the *–ii* at the end of the name. Virtually all authors for this species, from Joubin (1895) to the present day, have used "*forbesi*". However, Steenstrup (1856) clearly states that he is naming the species after Professor Edward Forbes; the Latinization of Forbes is Forbesius, and the genitive of this is *forbesii*, and Steenstrup consistently ends the species name *–ii* throughout the manuscript. Although it is permissible for the describer not to Latinize the name (which would produce the spelling *forbesi*), the spelling is fixed at the time of description, if the describer (i.e. Steenstrup in this case) constructed the name correctly (see Articles 31–32 of the ICZN), which he clearly did.

The second and more difficult issue is the generic placement of *forbesii*. It was placed in *Loligo* by Steenstrup and remained there until the 1990s. Reports of photophores (Alexeyev, 1992) and potential luminescence (Naef, 1921; Lum-Kong and Hastings, 1992) have led some researchers to believe that *forbesii* would be better placed in *Uroteuthis* Rehder, 1945 (see Vecchione *et al*., 1998 for discussion). Again, this issue is not explicitly discussed in the report of the most recent (2003) loliginid workshop (Vecchione *et al*., 2005), but Table 2 in that report places *forbesii* within *Loligo*. We elect to treat *forbesii* as a species of *Loligo*.

Nomenclature used herein for long-finned squid

Loligo vulgaris Lamarck, 1798

Loligo forbesii Steenstrup, 1856

Alloteuthis media Linnaeus, 1758

Alloteuthis subulata Lamarck, 1798

2.3 Short-finned squid

The family Ommastrephidae is well characterized and most former controversies have been resolved. Both *Todaropsis eblanae* (Ball, 1841) and *Todarodes sagittatus* (Lamarck, 1798) are the type species of their respective genera, and their nomenclature is unlikely to change in the future. *Illex coindetii* (Verany, 1839) is one of three North Atlantic species of *Illex*, as confirmed by recent DNA analyses (Carlini *et al*., 2006).

Nomenclature used herein for short-finned squid

Illex coindetii Verany, 1839

Todarodes sagittatus Lamarck, 1798

Todaropsis eblanae Ball, 1841

2.4 Octopus

The systematics of the commercially fished octopus species is not controversial. Controversies over usage of the genus name *Eledone* and senior synonyms of *Octopus vulgaris* Cuvier, 1797 are long since resolved (ICZN, 1954, 1997).

Nomenclature used herein for octopus

Eledone moschata Lamarck, 1798
Eledone cirrhosa Lamarck, 1798
Octopus vulgaris Cuvier, 1797

2.5 Cuttlefish

The family Sepiidae is another group with extensive taxonomic and nomenclatural issues. The 1988 systematics workshop is the most recent thorough revision of the sepiids. This revision identified several species complexes within the genus *Sepia* Linnaeus, 1758, one of which was the "species complex *Rhombosepion*" (Khromov *et al.*, 1998). The workshop proceedings concluded with a classification of all recent Cephalopoda (Sweeney and Roper, 1998), which treated Khromov's species complexes, including *Rhombosepion* Rochebrune, 1884, as subgenera of *Sepia* Linnaeus, 1758. Two of the species in the ICES Area, *elegans* Blainville, 1827, and *orbignyana* Férussac in Orbigny, 1826, are placed in this subgenus, and *elegans* is the type species of this subgenus. The third species in the ICES Area, *officinalis* Linnaeus, 1758, is the type species of *Sepia* Linnaeus, 1758, and its taxonomy is relatively stable. Sanjuan *et al.* (1996) proposed that *Rhombosepion* should be elevated to generic status, based on Nei's genetic distance (calculated from 32 allozyme loci) between *Sepia (Rhombosepion) elegans*, *Sepia (Rhombosepion) orbignyana*, and *Sepia (Sepia) officinalis.* There are approximately 100 species in the genus *Sepia*, and, in the absence of further data, this revision, based on only three species, has not been widely accepted and we retain the classification proposed by Khromov *et al.* (1998) and clarified in Sweeney and Roper (1998).

Nomenclature used herein for cuttlefish

Sepia (Sepia) officinalis Linnaeus, 1758
Sepia (Rhombosepion) elegans Blainville, 1827
Sepia (Rhombosepion) orbignyana Férrusac in Orbigny, 1826

3 Biology and ecology of cephalopod species commercially exploited in Europe

3.1 Species accounts

Patrizia Jereb, Uwe Piatkowski, Louise Allcock, Paola Belcari, Manuel Garcia Tasende, Angel González, Angel Guerra, Lee C. Hastie, Eugenia Lefkaditou, Ana Moreno, Santiago Pascual, João Pereira, Graham J. Pierce, Pilar Sánchez, Paolo Sartor, Sonia Seixas, Ignacio Sobrino, and Roger Villanueva

3.1.1 Introduction to the main groups of fished cephalopods in Europe

In nearly all commercial situations throughout Europe, there is no species determination in catches of cephalopods. This has been underlined in WGCEPH reports over the years because it is reflected in the official statistics made available to the scientific community. In addition, cephalopods are landed by both commercial and artisanal fleets, and landings from the latter have been relatively poorly documented in the past. As a result of these problems, the utility of cephalopod landings data for assessment of stock status has been called into question (ICES, 2008, 2009). The new métier-based data-collection system introduced in 2009 may help overcome these issues, in that all species caught in sampled métiers should be identified and, indeed, all important métiers should be sampled (see Section 5).

Official cephalopod landing statistics in Europe generally refer to four groups of species that are analogous from country to country, varying only to the extent that their composition reflects species distribution: (i) long-finned squid, (ii) short-finned squid, (iii) cuttlefish, and (iv) octopus. In some countries (e.g. Sweden), the two squid groups are lumped together.

Although there has been little or no official species determination, the identity of the species comprising each of the groups is, largely, known from current or previous scientific sampling. In some cases, the proportions of the main species in each of the groups have been determined, usually within the scope of short-term projects. Proportions of the different species are found to vary seasonally and annually and may also differ according to the gear used (see Bruno, 2008, in relation to landings of *Illex coindetii* and *Todaropsis eblanae* in Galicia, Spain).

In this section, short accounts of each of the main species that occur in commercial catches within European waters are presented, and the countries where species are landed are identified. Each of these species is briefly described, and their main biological and ecological characters are highlighted. Information is drawn from mainstream scientific publications, "grey" literature, and unpublished sources, including original research conducted by the authors. Full descriptions of the main species will be presented in a separate report.

3.1.1.1 Long-finned squid

This group is composed exclusively of species belonging to the family Loliginidae. All of the species exploited in Europe occur in relatively shallow water and are mostly caught by demersal gear. They are among the most valued squid species and generally command higher prices in the market than short-finned squid.

Four species are caught and landed in Europe, of which two are relatively large and two are very small. Adults of the two larger species are similar in size and appearance but can normally be distinguished from each other, whereas the two smaller species are difficult to distinguish from each other and from the juveniles of the two larger species. They can occur sympatrically, and their identification, therefore, poses problems.

Post-recruit specimens of *Loligo forbesii* can be superficially distinguished from *L. vulgaris* principally by the larger size of the medial suckers on the tentacular club in *L. vulgaris*, whereas in *L. forbesii*, all the suckers are subequal in size (Roper *et al*., 1984). In addition, the papillae present on the terminal portion of the hectocotylus of mature male *L. forbesii* are not found in mature males of *L. vulgaris. Loligo forbesii* has prominent longitudinal stripes of dark chromatophores on the anterior and ventro-lateral surfaces of the mantle. Even though large specimens of *L. vulgaris* can sometimes display similar stripes, these are smaller than in *L. forbesii*, less numerous and different in appearance (Jereb and Ragonese 1986); those of *L. forbesii* are very characteristically "flame-like": each stripe is surrounded by white tissue (devoid of chromatophores) after which a line or border of slightly darker chromatophores is visible to delimit the area surrounding the stripe. In life, *L. forbesii* is usually coloured with more orange tones and *L. vulgaris* with more purple tones.

Alloteuthis spp. can be separated from other members of the family Loliginidae on the basis of their small size as adults and the fact that the mantle length (ML) is 6–15 times greater than its width, i.e. it has a narrower body than all other species. Adult male *A. subulata* and *A. media* possess tentacular club suckers similar to those found in *L. vulgaris*, but the fins do not extend beyond 50% of the total ML, except possibly in male *A. subulata*. Until recently, relative tail length was the characteristic most commonly used to distinguish *A. media* and *A. subulata*. However, molecular data from *Alloteuthis* specimens across the geographic range of the species have demonstrated this characteristic to be unreliable (Anderson *et al*., 2008). As this raises doubts about the reliability of previous identifications, we treat these two species under *Alloteuthis* spp. in this section, although we continue to refer to previous studies using the species name as determined by the author(s) of those studies.

3.1.1.2 Short-finned squid

This group comprises species mainly belonging to the family Ommastrephidae. Occasionally very abundant and very important in catches, landings, and exports from Europe, short-finned squid are less valuable in the market than long-finned squid and more prone to extreme variations in abundance. They all have pelagic distributions and, although sometimes caught demersally, are mainly taken from the water column by trawling and from high-rising gill- and trammelnets.

Three species are most commonly landed in Europe. *Illex coindetii* and *Todaropsis eblanae* mainly occur in the south, but both are occasionally frequent in the north. *Todarodes sagittatus* is more abundant in the north. Particularly in the northern extremes, *Gonatus fabricii* Lichtenstein, 1818, a short-finned squid of the family Gonatidae, is taken. We have not included an account for this species, or for other less frequent or occasional species, but the fact that other species may be landed means that specimens that do not appear to fit the descriptions of the most common species require careful identification.

3.1.1.3 Octopus

Landings in this category consist exclusively of species belonging to the family Octopodidae. Catches and landings are dominated in weight and number by a single species, *Octopus vulgaris*, which is taken in greater numbers in the southern part of the ICES Area and farther south. Landings of the two *Eledone* species in the area are increasing. The genus *Octopus* is easy to distinguish from the genus *Eledone*, primarily by the presence of a double row of suckers on the arms of the former vs. a single row on the arms of the latter. However, the two *Eledone* species may be difficult to distinguish from each other if specimens are preserved or have been dead for some time. Several other European octopus species may be landed as catch from commercial vessels, but their low abundance makes it hard to determine the extent to which they are representative of regular catches.

3.1.1.4 Cuttlefish

Of the cephalopod categories landed in Western Europe, cuttlefish landings are the highest, mostly from catches concentrated over the continental shelf in the region of the southern Celtic Sea, the approaches to the English Channel, and the northeastern Bay of Biscay. Most landings are composed of catches of a single species, *Sepia officinalis*, but landings of at least two other species are also common in some European countries. Catches are made demersally by means of trawling and artisanal trapping.

The distinction between species can pose difficulties, particularly in juveniles, and more acutely in some geographical areas than in others, because the external appearance of *S. officinalis* varies across its distributional range.

Formerly, *S. officinalis* included two subspecies, *S. o. officinalis* and *S. o. hierredda*, the first distributed in the ICES Area and the second just outside, to the south. Although they are very similar in general appearance, morphological and genetic analysis has demonstrated that *S. officinalis* Linnaeus, 1758 and *S. hierredda* Rang, 1837, are clearly different species of the same genus (Guerra *et al.*, 2001). As *S. hierredda* may also be found within the ICES Area, it is useful to know how to tell them apart. The mantle of *S. hierredda* is narrower than in *S. officinalis*, and the unmodified arms and the hectocotylized arm are shorter. The number of transverse rows of reduced suckers on the hectocotylus is generally larger (8 or 9 to 14) in *S. hierredda* than in *S. officinalis* (4 or 5 to 8 or 9). The striated zone of the cuttlebone of *S. officinalis* is somewhat smaller (41% of the ML) than in *S. hierredda* (47%). The cuttlebone of *S. officinalis* is slightly wider and thicker (38% and 13% of the ML, respectively) than that of *S. hierredda* (35% and 12%, respectively). The phragmocone and the outer cone of *S. officinalis* are wider than in *S. hierredda*. The cuttlebone of *S. officinalis* is slightly acuminate at the anterior end, whereas it is very acuminate in *S. hierredda*. The spine of the cuttlebone in *S. officinalis* is usually covered by chitin, especially in adults, whereas that of *S. hierredda* is never covered by chitin. As *S. hierreda* has only recently been recognized as a separate species, few landings data have been attributed to this species. A species account is therefore not included.

Sepia elegans and *S. orbignyana* are also sometimes confused with each other and with *S. officinalis* (particularly younger individuals). *Sepia elegans*, however, is the narrowest of the three, whereas *S. orbignyana* has a more pronounced spine at the terminal end of the cuttlebone than either of the other two.

3.1.2 *Loligo vulgaris* Lamarck, 1798

Common names. European squid (English); encornet (French); Europäischer Langflossenkalmar (German); calamary (Καλαμάρι; Greek); calamaro comune[1] (Italian); lula-vulgar (Portuguese); calamar común (Spanish).

3.1.2.1 Adult diagnostic features

Cornea present. Fins rhomboidal, their length up to ca. 66 % of dorsal ML. Arms with two rows of suckers; sucker rings with 20 teeth, the distal ones large and pointed and the proximal ones minute or absent. Tentacular clubs with four longitudinal rows of suckers in the "manus", the suckers in the central rows being larger than the marginal ones. Buccal membrane with 15 tiny suckers on the extremity, each with chitinous rings. Left ventral arm (IV) of male hectocotylized. Simple funnel-locking cartilage (Roper *et al.*, 1984).

3.1.2.2 Distribution and habitat

Loligo vulgaris occurs along the eastern Atlantic from the British Isles (55°N) to the Gulf of Guinea (20°S; Roper *et al.*, 1984), extending out to Madeira (Clarke and Lu, 1995), and throughout the Mediterranean Sea (Belcari, 1999a). Adults are occasionally reported off the northwest coast of Scotland at 57°N (Pierce *et al.*, 1994a; Hastie *et al.*, 2009a), the North Sea (De Heij and Baayen, 2005), and the Kattegat and western Baltic Sea (Jaeckel, 1937; Muus, 1959; Hornborg, 2005). Paralarvae are absent north of the English Channel (Yau, 1994; Collins *et al.*, 2002). *L. vulgaris* is a nectobenthic species that lives in the circumlittoral and upper bathyal zones (Worms, 1983).

3.1.2.3 Life history

Loligo vulgaris demonstrates high geographic variability of reproductive and growth parameters, and temperature is one of the main factors inducing such variability (Moreno *et al.*, 2002). Males attain greater lengths (640 mm ML) than females (540 mm ML), with the maximum values recorded on the Saharan Bank (Raya, 2001). The life cycle may be completed within approximately one year, with maximum lifespans of 15 months recorded in western Iberia (Moreno *et al.*, 1996; Rocha and Guerra, 1999).

Loligo vulgaris is a terminal spawner, but oocyte maturation and egg-laying occur in separate batches during the spawning period (Rocha and Guerra, 1996; Rocha *et al.*, 2001). Fecundity has been estimated at between 10 150 and 42 000 eggs (Baddyr, 1988; Coelho *et al.*, 1994; Guerra and Rocha, 1994; Laptikhovski, 2000). Mean spawning age is ten months, and mean age-at-maturity is nine months. Hatching time significantly influences mean age-at-maturity, which is higher in winter cohorts than in summer cohorts (Moreno *et al.*, 2005).

The spawning season is shorter in the northern part of the distribution (Moreno *et al.*, 2002; Sifner and Vrgoc, 2004). Elsewhere, spawning occurs throughout the year, with two main peaks between November and June, although these occur earlier in more southern latitudes and earlier in the Atlantic than in the Mediterranean (Baddyr, 1988; Coelho *et al.*, 1994; Guerra and Rocha, 1994; Moreno *et al.*, 1994, 2002; Rocha, 1994; Bettencourt *et al.*, 1996; Villa *et al.*, 1997; Raya *et al.*, 1999; Belcari, 1999a). Spawning areas are poorly known, but egg-mass recoveries indicate that spawning occurs at depths of 2–120 m (Baddyr, 1988; Villa *et al.*, 1997; Pereira *et al.*, 1998).

---

[1] All Italian common names are taken from Bello and Borri (1990).

3.1.2.4 Trophic ecology

Predators. Various cetaceans, seals, large pelagic fish, and some demersal fish have been reported to prey on *L. vulgaris* (e.g. González *et al.*, 1994a; Orsi-Relini, 1994; Morte *et al.*, 1997; Börjesson *et al.*, 2003; Salman, 2004; Peristeraki *et al.*, 2005).

Prey. Paralarvae feed mainly on crustacean larvae, small mysids, and fish larvae (Boletzky, 1979a). Vertical migrations of paralarvae and juveniles are linked to feeding, and juveniles consume more planktonic prey than bentho-pelagic prey (Nigmatullin, 1975; Worms, 1983; Turk *et al.*, 1986). Fish species increase in importance with increasing squid size and are the most frequent prey for adults (Rocha *et al.*, 1994; Coelho *et al.*, 1997; Lefkaditou, 2006).

3.1.2.5 Fisheries

In the Atlantic and Mediterranean, *L. vulgaris* is mainly a bycatch in the multispecies bottom and pelagic trawl fisheries. In the English Channel and French waters, landings of *Loligo* are normally a mixture of *L. vulgaris* and *L. forbesii* (the species are normally not separated in the official statistics). Farther south (e.g. off Spain and Portugal), *L. vulgaris* is the dominant long-finned squid in the landings (see Chen *et al.*, 2006). It is a secondary target species in the Saharan Bank cephalopod trawl fishery (Raya *et al.*, 1999) and in the western Portuguese coastal demersal trawl fishery (Fonseca *et al.*, 2008). There are also small-scale, hand-jig artisanal coastal fisheries at depths of 20–350 m, especially in Spain and Portugal (Guerra *et al.*, 1994). Near the coasts, where the species concentrates during autumn and winter for spawning, small-scale professional and sport fishers usually target the species using hand-jigs.

On the Greek, Portuguese, and northwest Spanish coasts, spawning aggregations are also occasionally targeted by a limited number of fishing vessels using beach-seine (a gear that catches higher quantities than hand-jigs and other artisanal gears), gillnets, and trammelnets. In Galicia (northwest Spain), a seasonal (mainly July–September) fishery targeting juvenile *L. vulgaris* takes place inside the Rías Bajas in waters of 3–40 m depth using seinenets with a bag ("boliche"; Guerra *et al.*, 1994; Tasende *et al.*, 2005). Juveniles generally recruit to the fishery at approximately 5 months of age (Moreno *et al.*, 2007). Nevertheless, the age and size at recruitment to the fishery obviously depends on the fishing gear used. There is no regular assessment and management for *L. vulgaris* fisheries, but landing size restrictions are imposed in Portugal (and in Spain).

The species has been identified in commercial landings in the UK, France, Portugal, Spain, Italy, and Greece.

3.1.3 *Loligo forbesii* Steenstrup, 1856

Common names. Veined squid (English); encornet veiné (French); Langflossenkalmar (German); calamary (Καλαμάρι; Greek); calamaro venato, occhione (Italian); calamar veteado (Spanish); lula-riscada (Portuguese).

3.1.3.1 Adult diagnostic features

Cornea present. Rhomboidal fins of length ca. 75% of dorsal ML, posterior borders slightly concave. Arms with two rows of suckers. Suckers on the manus of the tentacular club are subequal in size; sucker rings with 13–18 sharp conical teeth. Unlike *L. vulgaris*, it lacks enlarged medial suckers on the tentacular club (suckers in all four rows are fairly similar in size). In males, the left ventral arm (IV) is hectocotylized in its distal third by modification of suckers into long papillae that gradually decrease in size distally. Simple funnel-locking cartilage. Diagnosis adapted from Roper *et al.* (1984).

3.1.3.2 Distribution and habitat

Loligo forbesii is a neritic and largely demersal species occurring in coastal waters and the continental shelf from the Faroe Islands to 20°N in the eastern Atlantic, including the North Sea, extending into the Mediterranean and out to Madeira, the Canary Islands, and the Azores. The species is relatively rare south of the Bay of Biscay and is absent from the Baltic Sea (Roper *et al.*, 1984).

3.1.3.3 Life history

Loligo forbesii is commonly assumed to have an annual life cycle, with pulses of recruitment in April and August–November (Lum-Kong *et al.*, 1992; Pierce *et al.*, 1994a; Collins *et al.*, 1995, 1997; Belcari, 1999b), although some individuals may reach an age of ca. 18 months (Rocha and Guerra, 1999). As in other loliginid squid, the growth pattern comprises an early rapid "exponential" phase followed by a slower "logarithmic" phase (Forsythe and van Heukelem, 1987; Forsythe and Hanlon, 1989). Males can reach sizes larger (610 mm ML on the continental shelf; 940 mm in Azores) than females (420 mm and 460 mm), although some males mature at much smaller sizes (from ca. 120 mm; Boyle *et al.*, 1995), apparently representing alternative growth and maturation strategies, and leading to the presence of (at least) two microcohorts in the fished population (Collins *et al.*, 1999).

Loligo forbesii is semelparous, displaying "intermittent, terminal spawning", in which the females lay eggs in batches and die shortly after spawning (Rocha *et al.*, 2001). Many studies describe an extended spawning season, although it is unclear how long an individual continues to spawn (Guerra and Rocha, 1994; Moreno *et al.*, 1994; Collins *et al.*, 1995). Female *L. forbesii* produce only a few thousand (up to 23 000) eggs in their lifetime, with larger females producing more eggs.

Clusters of eggs are normally attached to substrata that include algae, shells, rock crevices, nets, ropes, creels, and other fishing gear that remains submerged and undisturbed. There are few reports of eggs from offshore waters, but this may be because the squid spawn over rocky substratum, making spawning areas largely inaccessible to trawling (Holme, 1974; Lordan and Casey, 1999).

3.1.3.4 Trophic ecology

Predators. Various cetacean species, seals, and large demersal fish have been reported to prey on *L. forbesii* (e.g. Pierce and Santos, 1996; Santos *et al.*, 2004a; De Pierrepont *et al.*, 2005).

Prey. A large number of prey species, including various fish, crustaceans, polychaetes, and molluscs have been identified in *L. forbesii* stomachs. As in most squid, fish are more important in adults, and crustaceans more important in juvenile stages (e.g. Pierce *et al.*, 1994d).

3.1.3.5 Fisheries

Loligo forbesii is the dominant squid species fished north of the English Channel, mainly as bycatch from demersal trawls (Pierce *et al.*, 1994b), although various small directed trawl fisheries exist in coastal waters (e.g. Young *et al.*, 2006a) and are becoming increasingly important. It is the only squid species of economic importance in the Azores, where it is fished by an artisanal fleet equipped with handlines and homemade jigs (Martins, 1982; Porteiro and Martins, 1994). South of the English

Channel, the species is currently less common, but is taken both as a trawl bycatch and by coastal artisanal boats using jigs (Cunha and Moreno, 1994; Guerra *et al.*, 1994; Rocha *et al.*, 1994). Analysis of morphometric variation and the use of allozyme and microsatellite markers suggest that there is no significant separation of stocks throughout the range of its distribution on mainland coasts. The Azores population probably represents a separate subspecies, and animals from offshore banks (e.g. Rockall) demonstrate some differences from the coastal population (Pierce *et al.*, 1994c; Brierley *et al.*, 1995; Shaw *et al.*, 1999). It is also consistently present in the eastern Mediterranean trawl catches (Machias *et al.*, 2001).

The species has been identified in commercial landings in the UK, France, Portugal, Spain, Italy, and Greece.

3.1.4 *Alloteuthis* spp.

Common names

Alloteuthis subulata Lamarck, 1798. European common squid (English); casseron commun (French); Gepfriemter Langflossenkalmar (German); calamaretto puntuto (Italian); lula-bicuda-comprida (Portuguese); calamarín picudo (Spanish).

Alloteuthis media Linnaeus, 1758. Midsize squid (English); casseron bambou (French); calamaretto comune (Italian); lula-bicuda-curta (Portuguese); calamarín menor (Spanish).

3.1.4.1 Adult diagnostic features

Elongated mantle. Rhomboidal fins attenuate posteriorly into a long, slender tail, which can be more than 50% of the ML in males. Arms with two rows of suckers. Tentacle clubs with four rows of suckers. The central rows of suckers are 3–4 times larger than the marginal suckers (Yau, 1994; Laptikhovsky *et al.*, 2002). The left ventral arm (IV) can be hectocotylized in mature males, with 6–8 pairs of normal suckers proximally followed by two longitudinal rows of fine papillae distally (Yau, 1994). Maximum ML of *A. subulata* is 20 cm (Rodhouse *et al.*, 1988).

3.1.4.2 Distribution and habitat

Alloteuthis subulata and *A. media* are sympatric throughout much of the range of both species (Roper *et al.* 1984), extending from approximately 60°N to 20°N (Guerra, 1992). They are found in the North Sea and the Mediterranean (Belcari, 1999 c, 1999d). They both occur primarily in shelf waters and are demersal, although *A. media* is reported to migrate offshore in winter (Roper *et al.*, 1984) and to make diel vertical migrations (Zuev and Nesis, 1971).

3.1.4.3 Life history

Hatchlings of both species are 2–3 mm long (Zuev and Nesis, 1971; Yau, 1994). In *A. subulata*, sexual maturation can be achieved at 4–5 cm ML in both sexes, although mature males have a wider range of sizes than mature females and reach 50% maturity at a slightly smaller size (7–7.5 cm, compared with 7.5–8 cm in females). *Alloteuthis media* has an ML of up to 12 cm in females and 9 cm in males. Individuals hatching in spring grow 7–8 mm month^{-1} during summer and reach an ML of 7–8 cm the following spring (Zuev and Nesis, 1971). Both species are thought to live for approximately one year (Rodhouse *et al.*, 1988; Mangold-Wirz, 1963; Alidromiti, 2007).

The average estimated potential fecundity of female *A. subulata* is 2200–13 500 eggs per female (mean ~5900 ± 970 s.e.; Hastie *et al.*, 2009b). In *A. media*, the potential fecundity has been estimated at 950–1400 eggs for the western Mediterranean and 1500–2500 for the eastern Mediterranean. Oocyte maturation occurs in batches.

Spawning occurs throughout the year, generally with larger numbers of mature squid in spring–summer and smaller numbers in autumn–winter (Rodhouse *et al.*, 1988; Nyegaard, 2001; Hastie *et al.*, 2009b). A predominance of small squid (<50 mm ML) is observed during autumn (Hastie *et al.*, 2009b). Adults of *A. media* migrate to shallow water, spawning at depths of 10–100 m on sand, seagrass meadows, etc. from March to October in the western Mediterranean (Mangold-Wirz, 1963) and year-round in the central and eastern region (Lo Bianco, 1909; Naef, 1923; Laptikhovsky *et al.*, 2002; Lefkaditou, 2006). In the North Sea, spawning takes place in June–July (Zuev and Nesis, 1971). Recruits of *A. media* are present practically all year-round in shallower waters of their distribution (Relini and Orsi-Relini, 1984). Seasonal peaks of recruitment are more evident in areas with a wider continental shelf (Mangold-Wirz, 1963; Papaconstantinou *et al.*, 1994).

3.1.4.4 Trophic ecology

Predators. *Alloteuthis subulata* has been identified from the stomach contents of several species of marine mammal (Santos *et al.*, 2001a, 2001b, 2004a, 2005a, 2005b; González *et al.*, 1994a; Meynier, 2004) and from hake (*Merluccius merluccius*; Daly *et al.*, 2001), and *Loligo* spp. (Pierce *et al.*, 1994d; Rocha *et al.*, 1994). *Alloteuthis media* is eaten by various gadid and elasmobranch fish (Zuev and Nesis, 1971; Bello, 1997), and is an important food for demersal fish in the southern Bay of Biscay (Velasco *et al.*, 2001).

Prey. The main prey of *A. subulata* in the Irish Sea comprises clupeid fish and crustaceans (Nyegaard, 2001). The diet of *A. media* consists of larvae and juveniles of fish, copepods, and euphausiids (Zuev and Nesis, 1971).

3.1.4.5 Fisheries

Both *A. media* and *A. subulata* can be caught and misidentified as juvenile *Loligo* and can occur among long-finned squid catches throughout their range. In the Gulf of Cadiz, *Alloteuthis* spp. are caught as a bycatch of the multispecies bottom-trawl fleet, and recorded annual landings varied between 55 and 290 t during 1996–2006. Both *Alloteuthis* species are landed, probably in similar amounts (I. Sobrino, pers. comm.). In the Rías Bajas of Galicia (northwest Spain), *Alloteuthis* is a bycatch of the boat-seine fishery directed at *L. vulgaris* (Tasende *et al.*, 2005). Studies on bottom-trawl discards have demonstrated that, in the northeastern Mediterranean, *A. media* is totally discarded (Machias *et al.*, 2001), whereas in the western Mediterranean, it is normally landed (Sartor *et al.*, 1998).

These species have been identified in commercial landings in Spain and are regularly landed in Italy (Belcari, 1999c, 1999d).

3.1.5 *Illex coindetii* Verany, 1839

Common names. Broadtail shortfin squid (English); faux encornet (French); thrapsalo (Θράψαλο; Greek); totano, todaro (Italian); pota voladora (Spanish); pota-voadora (Portuguese).

3.1.5.1 Adult diagnostic features

Mantle width 15–25% of the ML. Rhomboidal fins of width 45–60% of dorsal ML. Arms with two rows of suckers. Tentacular club with eight transverse rows of minute subequal suckers. Left or right ventral arm of male hectocotylized with distal trabeculae modified to papillose flaps. Inverse T-shaped funnel cartilage. Funnel groove with anterior foveola and without side pockets. Diagnosis adapted from Roper *et al.* (1984, 1998) and Roper and Mangold (1998).

3.1.5.2 Distribution and habitat

Illex coindetii is found in the Mediterranean Sea, the eastern Atlantic from 60°N to 17°S and 30°W, and in western Atlantic waters from the Gulf of Mexico to Venezuela (Roper *et al.*, 1998; Belcari, 1999e). It is demersal in the middle and lower sublittoral and upper bathyal in temperate latitudes, and it undertakes diel vertical migrations.

3.1.5.3 Life history

Illex coindetii is a medium-sized squid (Sánchez, P., *et al.*, 1998). The maximum ML is generally larger in females than males. The largest sizes are found in Northeast Atlantic populations, with males growing to 370 mm and females to 320 mm (González *et al.*, 1996; Sánchez, P., *et al.*, 1998). The life cycle is probably annual, although lifespan estimates vary from six months (based on statolith increments; Arkhipkin *et al.*, 1998) to 24 months (length frequency analyses; Mangold-Wirz, 1963).

The age at which *I. coindetii* matures is variable: 100–271 days in males and 140–285 days in females (González and Guerra, 1996; González *et al.*, 1996; Arkhipkin *et al.*, 2000). The number of mature eggs in the ovary and oviducts ranges from 50 000 to 200 000. It is an "intermittent spawner", with females spawning several times during a prolonged spawning period lasting from a few days to a few weeks (González and Guerra, 1996). Spawning may occur year-round, but seasonal peaks exist and vary widely through the geographic range (e.g. Sánchez, 1984; Tursi and D'Onghia, 1992; Sánchez and Martin, 1993; Jereb and Ragonese, 1995; Belcari, 1996; Arvanitidis *et al.*, 2002; Hernández-Garcia, 2002; Ceriola *et al.*, 2006).

3.1.5.4 Trophic ecology

Predators. *Illex coindetii* has been found in the stomachs of various marine mammals, including Risso's dolphin (*Grampus griseus*), bottlenose dolphin (*Tursiops truncatus*) (Santos, M. B., *et al.*, 1997, 2007), long-finned pilot whale (*Globicephala melas*), and common dolphin (*Delphinus delphis*) (González *et al.*, 1994a; Silva, 1999). It has also been recorded from swordfish (*Xiphias gladius*; Bello, 1985), greater forkbeard (*Phycis blennoides*; Morte *et al.*, 2002), and the sharpnose sevengill shark (*Heptranchias perlo*; Henderson and Williams, 2001).

Prey. The diet of *I. coindetii* is composed of fish, crustaceans, and cephalopods; it is also cannibalistic. It is mainly a neritic, nekto-benthic predator with a wide spectrum of prey, but adults perform significant vertical migration and also take pelagic prey (Sánchez, P., *et al.*, 1998).

3.1.5.5 Fisheries

Illex coindetii is taken throughout the year as bycatch in bottom and pelagic trawls, and, to a lesser extent, in gill- and trammelnets, at depths of 100–400 m in the Mediterranean, off West Africa, and in the Northeast Atlantic. Its fishery value is increasing. Although separate statistics are generally not reported, the annual catch for the last decade probably ranged from 5000 t to 12 000 t. There is thought to be a single stock throughout the region.

The species has been identified in commercial landings in Ireland, the UK, France, Spain, and Portugal (in the Northeast Atlantic), and Spain, Italy, and Greece (in the Mediterranean).

3.1.6 *Todarodes sagittatus* Lamarck, 1798

Common names. European flying squid (English); toutenon commun (French); Pfeilkalmar (German); katamachi (Καταμάχι; Greek); beitusmokkur (Icelandic); totano viola (Italian); akkar (Norwegian); pota-europeia (Portuguese); pota europea (Spanish).

3.1.6.1 Adult diagnostic features

Tentacle club suckers on dactylus are arranged in four rows, suckers on elongate carpus in 10–12 pairs; entire club relatively long, extending along stalk. Arm suckers with enlarged central tooth, 7–9 regular teeth, and virtually no small alternating teeth. Funnel groove with anterior foveola and without side pockets. Reference: Roper *et al.* (1984).

3.1.6.2 Distribution and habitat

Todarodes sagittatus is found throughout the eastern Atlantic to ca. 40°W, and from the Arctic Ocean to ca. 13°S. The range includes the North Sea and the Mediterranean (Clarke, 1966; Zuev *et al.*, 1976; Roper *et al.*, 1984). They occur in both the open ocean and coastal waters, and from the surface to near-bottom at depths up to 2500 m. They migrate vertically between the surface at night and near-bottom waters during the day (Mangold-Wirz, 1963; Korzun *et al.*, 1979; Nesis, 1987).

3.1.6.3 Life history

The largest reported male from northern Europe had an ML of 640 mm, and the largest unsexed specimens an ML of 750 mm (in Clarke, 1966). More recent records indicate that females reach a maximum ML of 520 mm (males 426 mm) off northern Europe (Lordan *et al.*, 2001a) and 600 mm (males 385 mm) in the Mediterranean (Cuccu *et al.*, 2005). However, the records given by Cuccu *et al.* (2005) represent quite unusual findings for Mediterranean populations (e.g. Quetglas *et al.*, 1999) and for Italian waters (e.g. Jereb and Ragonese, 1990; Belcari, 1999f). It was hypothesized that such large sizes may result from unusually old animals. Age-at-maturity has been estimated at 15 months, although Nesis (1987) suggested that individuals larger than 50 cm are at least 2 years old, a hypothesis also proposed by Lordan *et al.* (2001a). Generally speaking, however, individuals in the Mediterranean and the southern part of the distributional range mature at much smaller body sizes than those in the North Atlantic (Hernández-García *et al.*, 1998a; Piatkowski *et al.*, 1998; Arkhipkin *et al.*, 1999). Females produce 12 000–18 000 eggs (Laptikhovsky and Nigmatullin, 1999).

Spawning probably takes place on the continental slope in late winter or early spring off northern Europe, in March and April off France, and between September and November in the western Mediterranean (Piatkowski *et al.*, 1998; Quetglas *et al.*, 1998a; Arkhipkin *et al.*, 1999; Lordan *et al.*, 2001a). Females always outnumber males. Ripe males seem to be present throughout the year, whereas mature females are present exclusively during the spawning period.

3.1.6.4 Trophic ecology

Predators. *Todarodes sagittatus* has been found in the stomachs of various cetaceans (González *et al.*, 1994a; Clarke and Pascoe, 1997; Santos, M. B., *et al.*, 2001b, 2007; Öztürk *et al.*, 2007) and large fish, such as swordfish (*Xiphias gladius*; Bello, 1985, 1991, 1993; Guerra *et al.*, 1993; Salman, 2004; Peristeraki *et al.*, 2005).

Prey. The diet of *T. sagittatus* is composed of fish, crustaceans, and cephalopods; the presence of cannibalism has also been noted. In northern waters, *T. sagittatus* feeds primarily on small herring (*Clupea harengus*) and cod (*Gadus morhua*; Hernández-García, 1992; Piatkowski *et al.*, 1998; Quetglas *et al.*, 1999).

3.1.6.5 Fisheries

A directed fishery off Norway has taken 10 000 t in some years (e.g. Wiborg, 1972, 1978, 1979b, 1987; Besteiro, 1985; Sundet, 1985; Bjørke and Gjøsæter, 2004). In the Mediterranean, the main fishery is operated by Italian bottom-trawl vessels, with annual catches (mainly bycatches) of ca. 3000 t. In other parts of its distributional range, it is taken as bycatch in trawl fisheries (e.g. Joy, 1990; Jónsson, 1998; Lordan *et al.*, 2001b; González and Sánchez, 2002; Lefkaditou *et al.*, 2003a). The fishery is concentrated from August to December in ICES Division IIa. Common fishing methods include jigging off Norway (Sundet, 1985) and in the Mediterranean (Ragonese and Bianchini, 1990) and purse-seines around the Canary Islands (Clarke, 1966). No landings data for this species alone are reported; it is grouped with other short-finned squid. It is probable that two separate stocks exist, one in the northern and another in the southwestern part of the range.

The species has been identified in commercial landings in Norway, Ireland, Spain, Portugal, Italy, and Greece.

3.1.7 *Todaropsis eblanae* Ball, 1841

Common names. Lesser flying squid (English); toutenon souffleur (French); thrapsalo (Θράψαλο; Greek); totano tozzo (Italian); pota-costeira (Portuguese); pota costera (Spanish).

3.1.7.1 Adult diagnostic features

Mantle width larger than 33% of the total ML. Rhomboidal fins of length less than 50% of dorsal ML, width 75–90% of dorsal ML. Arms with two rows of suckers. Dactylus of tentacular club with four longitudinal rows of small suckers. Manus of club with six transverse rows of four suckers, each with median pairs up to fourfold larger in diameter than lateral suckers. Left and right ventral arms (IV) of mature males are hectocotylized. Inverse T-shaped funnel-locking cartilage. Funnel groove without anterior foveola and without side pockets. Reference: Roper *et al.* (1984).

3.1.7.2 Distribution and habitat

The geographical distribution is discontinuous. The species is known from the Mediterranean Sea, the eastern Atlantic from 61°N to 40°S, the southwestern Pacific, and the southwestern Indian Ocean off Australia. It is demersal and associated with sandy and muddy bottoms, mainly in the lower sublittoral and upper bathyal over the continental shelf, inhabiting depths of 20–780 m (Adam, 1952; Belcari, 1999g).

3.1.7.3 Life history

Eggs of mature females are 0.8–2.5 mm in length (Mangold-Wirz, 1963; Hastie *et al.*, 1994; Laptikhovsky and Nigmatullin, 1999). The hatching season extends from

October to March in British waters (Hastie *et al.*, 1994; Collins *et al.*, 2002) and from March to July, with a peak in May, in northwestern African waters (Laptikhovsky and Nigmatullin, 1999). Growth rates vary with the season of hatching and are higher in later-hatched individuals. French fishery data suggest monthly growth rates of 0.76 cm (males) and 1.22 cm (females; Robin *et al.*, 2002). Maximum ML is 290 mm and 220 mm for females and males, respectively (Robin *et al.*, 2002). Lifespan is approximately 1–2 years for both males and females.

Size-at-maturity varies with geographic location (González *et al.*, 1994b; Hastie *et al.*, 1994; Belcari *et al.*, 1999; Zumholz and Piatkowski, 2005), with an ML of 120–130 mm in males and 140–200 mm ML in females. Total fecundity in mature females varies from 4500 to 28 000 eggs in Scottish waters (Hastie *et al.*, 1994) and from 43 000 to 275 000 eggs off West Africa (Laptikhovsky and Nigmatullin, 1999). *Todaropsis eblanae* is an intermittent terminal spawner. The spawning season varies geographically.

3.1.7.4 Trophic ecology

Predators. The main predators of *T. eblanae* are toothed whales and dolphins (Clarke and Pascoe, 1985; Pascoe, 1986; Blanco *et al.*, 2001; Santos, M. B., *et al.*, 2001a, 2001b, 2007), sharks (Clarke and Stevens, 1974), and several teleost fish species (Meyer and Smale, 1991; Lipinski *et al.*, 1992).

Prey. The diet is composed of fish, crustaceans, and cephalopods (Rasero *et al.*, 1996; Lordan *et al.*, 1998; Zumholz, 2000; Form and Oelschlägel, 2004).

3.1.7.5 Fisheries

Juveniles recruit to the fishery at ca. 3 months of age. *Todaropsis eblanae* is taken throughout the year as bycatch in otter-trawl fisheries and, to a lesser extent, with gill- and trammelnets, longlines, and jigging at depths of 100–400 m in the Mediterranean, off West Africa, and in the Northeast Atlantic (Robin *et al.*, 2002). Most catches are made at a depth of ca. 200 m. As for other ommastrephids, in general, no separate landings data are available for this species; landings are pooled with those of other ommastrephid squid species. *Todaropsis eblanae* is less important than *I. coindetii* in French short-finned squid landings (Robin *et al.*, 2002) and more important than *I. coindetii* in Spanish and Portuguese short-finned squid landings, although seasonal variation occurs (Bruno, 2008).

The species has been identified in commercial landings in Ireland, UK, France, Spain, and Portugal (in the North Atlantic), and Spain, Italy, and Greece (in the Mediterranean).

3.1.8 *Eledone moschata* Lamarck, 1798

Common names. Musky octopus (English); elédone musquée (French); Moschuskrake (German); moshios (Μοσχιός; Greek), moscardino muschiato (Italian); polvo-mosqueado (Portuguese); pulpo cabezón (Spanish).

3.1.8.1 Adult diagnostic features

Arms uniserial. Living animal exudes a very prominent, musk-like odour, reportedly from glands in the skin. Live colour greyish-brown, with blackish-brown blotches on dorsum. Skin smooth to very finely granulose. No ridge occurs around the lateral periphery of the mantle. Web moderately deep – 30% of arm length. Right arm III hectocotylized, length only 60–70% of left arm III. Ligula short (3% of arm length); calamus absent. Distal tips of all other arms of males modified by subdivision of universal suckers into two parallel rows of flattened laminae or platelets. Gill demibranch with 11–12 lamellae. Reference: Roper *et al.* (1984).

3.1.8.2 Distribution and habitat

This species is distributed at depths of 15–200 m in Mediterranean and Iberian waters, with the greatest abundance down to 100 m (Lefkaditou *et al.*, 1998a; Belcari and Sbrana, 1999; Belcari *et al.*, 2002a; Silva *et al.*, 2004). It is relatively abundant on the southern Portuguese coast and in the Gulf of Cadiz, where it extends to 450 m (Guerra, 1984; Reis *et al.*, 1984).

3.1.8.3 Life history

Hatchlings of *Eledone moschata* are 25–30 mm long (ML 10–12 mm), eventually reaching a maximum length of 150 mm in the Gulf of Cadiz and along the Portuguese coast and 190 mm in the Mediterranean (Mangold, 1983; Silva *et al.*, 2004; E. Lefkaditou, pers. comm.; S. Lourenço, pers. comm.). Females reach maturity at an ML of 12 cm in the Gulf of Cadiz and 11 cm in Tunisian waters (Ezzeddine-Najai, 1997; Silva *et al.*, 2004). Males mature at slightly smaller sizes. Estimates of fecundity (oocytes per female) include ca. 450 ± 150 for the Gulf of Cadiz (Silva *et al.*, 2004) and 100–500 for the northwestern Mediterranean populations, where egg length ranged between 12 and 16 mm (Mangold, 1983).

In the Gulf of Cadiz, the spawning season extends from October to July (Silva *et al.*, 2004). Peak spawning occurs from February to May, with a secondary peak in October. The southern Mediterranean populations spawn from November to July (Ezzeddine-Najai, 1997). In the northwestern Mediterranean waters, the reproductive season is shorter, from January to May–June (Mangold, 1983; Belcari *et al.*, 2002a).

The life-cycle model of this species in the northwestern Mediterranean is based on the alternation of short-lived and long-lived life cycles (Mangold, 1983; Silva *et al.*, 2004), whereby populations hatched at different times vary in growth rate and rate of sexual development according to prevailing environmental conditions.

3.1.8.4 Trophic ecology

Hatchlings are able to feed on live crabs of their own size. Their preference for crustaceans is clear from the very early stages onward (Boletzky, 1975). Captive studies confirm a preference for crustaceans over molluscs and fish (Şen, 2007).

3.1.8.5 Fisheries

This species is caught mainly as bycatch of bottom-trawl fisheries; in the Gulf of Cadiz it is often discarded by the Spanish fleet because of its low commercial value. In the main ports of this region, annual landings of *E. moschata* averaged ca. 100 t during 1996–2004, with a maximum from January to April. In the Mediterranean, this species is of considerable economic importance, especially on the south and east coasts and in the Adriatic Sea (Belcari and Sbrana, 1999; Belcari *et al.*, 2002a).

The species has been identified in commercial landings in Spain, Italy, and Greece.

3.1.9 *Eledone cirrhosa* Lamarck, 1798

Common names. Horned octopus, lesser octopus (English); élédone commune, poulpe, poulpe blanc (French); moshios (Μοσχιός; Greek); moscardino bianco (Italian); polvo-do-alto (Portuguese); pulpo blanco (Spanish).

3.1.9.1 Adult diagnostic features

Suckers uniserial. Orange-red and reddish-brown dorsally; greenish iridescence ventrally. Dorsal side covered with numerous warts. A whitish line encircles the lateral periphery of the mantle. A cirrus is present near each eye. Right arm III of males is hectocotylized, shorter (69–76%) than its opposite, with a very short ligula (3–4% of the length of the hectocotylus), calamus absent; terminal suckers of the other arms of males modified and transversely compressed. Diagnosis adapted from Roper *et al.* (1984).

3.1.9.2 Distribution and habitat

Eledone cirrhosa is a common species in the Northeast Atlantic, extending from 67°N to the northwest African coasts (Guerra, 1992) and throughout the Mediterranean Sea. It appears occasionally in the Kattegat (west of Sweden; Hornborg, 2005) and in the Marmara Sea (Unsal *et al.*, 1999). It is a typical soft-bottom eurybathic species that lives to a depth of 770 m (Massy, 1928), although it is mainly distributed between 50 and 300 m (Belcari and Sartor, 1999a; Belcari *et al.*, 2002a).

3.1.9.3 Life history

Females reach a maximum size of 190 mm ML compared with 135 mm ML in males. They attain maturity at smaller sizes in the Mediterranean than in the Atlantic, and males mature at smaller sizes than females (Belcari and Sartor, 1999a; Belcari *et al.* 2002a; A. Moreno, pers. comm.).

A combination of a 1- and 2-year life cycle (fast-growing, early-maturing animals vs. slower-growing, late-maturing animals) is proposed for the North Sea (Boyle and Knobloch, 1982; Boyle, 1983; Boyle *et al.*, 1988). In the Mediterranean, the lifespan of most individuals is estimated to be approximately 2 years (e.g. Moriyasu, 1981, 1983; Belcari *et al.*, 1990, 2002a; Sánchez *et al.*, 2004), with less than 10% reaching maturity at ca. 3 years old (Lefkaditou and Papaconstantinou, 1995; Cuccu *et al.*, 2003; Orsi-Relini *et al.*, 2006). Note, however, that these conclusions are based on length frequency analysis, the validity of which has been called into question (E. Lefkaditou, pers. comm.)

Fecundity estimates vary widely: ~9000 eggs in the North Sea, ~5500 eggs in the Catalan Sea (Boyle *et al.*, 1988), and ~2000 eggs in the Tyrrhenian Sea (Rossetti, 1998). *E. cirrhosa* spawns in summer–autumn in the North Sea (Boyle, 1983; Boyle and Knobloch, 1983) and in spring–summer farther south (A. Moreno, pers. comm.). In the Mediterranean, the spawning season is earlier in the western basin (spring–summer) than in the eastern basin (summer–autumn; Belcari and Sartor, 1999a; Lefkaditou *et al.*, 2000).

3.1.9.4 Trophic ecology

Predators. Whales, seals, and fish are considered to be the most important predators of *E. cirrhosa* (e.g. Pierce *et al.*, 1991; Tollit and Thompson, 1996; Santos *et al.*, 1999; Brown *et al.*, 2001; Daly *et al.*, 2001; Velasco *et al.*, 2001).

Prey. *Eledone cirrhosa* is a carnivorous species and active predator. The diet is mainly composed of decapod crustaceans, mostly alpheids and brachyurids (Boyle and Knobloch, 1981; Sánchez, 1981; Auteri *et al.*, 1988). The species also feeds on molluscs and cephalopod eggs, and cannibalism has been observed (Moriyasu, 1981; Guerra, 1992).

3.1.9.5 Fisheries

Eledone cirrhosa has great commercial value in the western Mediterranean and usually less than 10 % of catches is discarded (Mangold and Boletzky, 1987; Sartor *et al*., 1998; Relini *et al*., 1998). Across Europe, landings come almost entirely from bottom-trawl fisheries, and *E. cirrhosa* appears together with *E. moschata* and *Octopus vulgaris* in the catch statistics. It is marketed in two distinct commercial categories in the Mediterranean, where small specimens (<50 mm ML) have higher economic value (Belcari *et al*., 1998; Belcari and Sartor, 1999). In some regions, these small octopus are a target of the multispecies trawl fishery in spring and summer that coincides with the recruitment period of the species (Relini and Orsi-Relini, 1984; Belcari *et al*., 1998, 2002a; Belcari and Sartor, 1999; Sánchez *et al*., 2004). Recently, this fishery was banned in the Catalan Sea (P. Sánchez, pers. comm.). *Eledone cirrhosa* is the only *Eledone* species present in northern Spanish waters, where it is landed by the bottom-trawl fishery (ca. 700 t year^{-1} on average, 1998–2006) as bycatch, although its commercial value is very low. It is occasionally landed in small quantities in Scotland, but there appears to be little commercial interest in the species (G. Pierce, pers. comm.).

The species has been identified in commercial landings in Portugal, Spain, Italy, and Greece.

3.1.10 *Octopus vulgaris* Cuvier, 1797

Common names. Common octopus (English); pieuvre, poulpe (French); chtapodi (χταπόδι; Greek); Gemeiner Krake (German); polpo comune (Italian); pulpo común (Spanish); olagarro (Spanish, Basque); pop roquer (Spanish, Catalan); polbo (Spanish, Galician); polvo-vulgar (Portuguese).

3.1.10.1 Adult diagnostic features

Suckers biserial. ML to 40 cm; total length to 140 cm. Arms robust at base, lateral arms longest, dorsal arms shortest. Suckers 15–17 of arms II and III enlarged in adults, especially males. Right arm III of mature males hectocotylized; ligula short and spoon-shaped. Gill demibranch with 7–11 lamellae, including terminal lamellae. Four papillae in the dorsal part of the mantle (one situated in the anterior part, another posterior and two laterals). Reticulated skin with four whitish spots, two between the eyes and two below the first dorsal papilla. Diagnosis adapted from Guerra (1992).

3.1.10.2 Distribution and habitat

Octopus vulgaris is especially abundant in the Mediterranean Sea and the eastern Atlantic (Belcari and Sartor, 1999b). Molecular genetic work has demonstrated that the distribution of *O. vulgaris* in the Atlantic extends to southern Brazil (Söller *et al.*, 2000) in the west, to Lanzarote and Senegal in the east, and as far south as Tristan de Cunha and False Bay, South Africa (Warnke *et al.*, 2004). Samples from Japan and Taiwan in the Pacific also appear to be conspecific with *O. vulgaris.* A benthic species, *O. vulgaris* inhabits the coastline to the outer edge of the continental shelf (200 m). It undertakes limited seasonal migrations.

3.1.10.3 Life history

Octopus vulgaris has a life cycle of 12–14 months (Domain *et al.*, 2002; Iglesias *et al.*, 2004) and terminal spawning with egg care by the female. The incubation period of the eggs is 22–25 days at 25 °C (Mangold, 1997), but longer at lower temperatures (36 days at 23 °C, 60 days at 21 °C, 80 days at 17 °C, and 120 days at 13 °C; Mangold and Boletzky, 1973; Caverivière *et al.*, 1999; Martins, 2003). Paralarvae are planktonic for 1–3 months, depending on the effect of temperature on growth rate, and adopt the benthic life mode of the adults at ca. 7.5 mm ML (Villanueva, 1995). The mortality on the paralarvae phase is thought to be very high and dependent on environmental conditions, with highly variable recruitment success (Faure, 2002).

Growth is very rapid, and large individual variation in growth rates has been observed both in culture experiments (Iglesias *et al.*, 2004) and in wild populations (Domain *et al.*, 2000). Juveniles can reach 0.5–0.6 kg within six months of hatching, and 1.4–1.8 kg within eight months, at a mean temperature of 18 °C (Iglesias *et al.*, 2004). Maximum size is 400 mm ML.

The potential fecundity of mature females ranges from 100 000 to 500 000 oocytes. The eggs are small, approximately 2.5 mm long (Mangold, 1997). The spawning season extends throughout the year, with two peaks in Atlantic populations within the main upwelling regions: winter and summer in western Portuguese waters (Moreno, 2008), and spring and autumn in Moroccan waters (Faraj and Bez, 2007) and the Canary Islands (Hernández-García *et al.*, 2002). A single spawning peak occurs in late winter/spring in northwest Spain (Fernández-Rueda and García-Flórez, 2007; Otero e*t al.*, 2007) and in summer in the northern Gulf of Cadiz (Rodríguez-Rúa *et al.*, 2005; Moreno, 2008) and the Mediterranean (Sánchez and Obarti, 1993; Mangold, 1997; Belcari *et al.*, 2002b).

3.1.10.4 Trophic ecology

Predators. Fish, marine mammals, birds, and other cephalopods prey on *O. vulgaris* (Hanlon and Messenger, 1998). Marine mammals include common dolphin (*Delphinus delphis*; López, 2002; Santos *et al.*, 2004b), bottlenose dolphin (*Tursiops truncatus*; Blanco *et al.*, 2001*)*, Risso's dolphin *(Grampus griseus*), long-finned pilot whale *(Globicephala melas*; López, 2002), and Mediterranean monk seal (*Monachus monachus*). Fish predators of adults and juveniles include conger eel (*Conger conger)* and Mediterranean moray eel *(Muraena helena*), whereas Mediterranean dusky grouper (*Epinephelus marginatus*), serranid fish (*Serranus* sp.) and the sand smelt (*Atherina presbyter*) prey on hatchlings (Villanueva and Norman, 2008).

Prey. Paralarvae feed mainly on decapod crustacean larvae (Villanueva and Norman, 2008). Diet of juveniles and adults may include crustaceans, teleost fish, other cephalopods, and polychaetes. On the Mediterranean coast of Spain in Cataluña, 80 % of the diet comprises crustaceans (Guerra, 1978; Sánchez and Obarti, 1993; Quetglas *et al.*, 1998b), but in the Algarve (Portugal), a similar proportion comprises bivalves (Rosa *et al.*, 2004).

3.1.10.5 Fisheries

Octopus vulgaris is taken throughout the year as a target species in bottom and pelagic trawls and via hand-jigs, pots, trammelnets, and traps in small-scale coastal fisheries at depths of 20–200 m in the Mediterranean (Belcari *et al.*, 2002b), off West Africa, and in the Northeast Atlantic. Although some countries report landings of this species separately, others group all landings of Octopodidae together. In Galicia (northwest Spain), where annual landings for 1998–2006 were ca. 1500 t, the species is targeted by the artisanal fleet using traps (called "nasa de polbo"), which are fairly specific to octopus (which forms 80–90 % of the total catches in this gear); it is also caught in traps set for other species, in trammelnets ("trasmallos" and "miños"), and on hooked lines ("raña"; Bañón *et al.*, 2007). In the Gulf of Cadiz, both bottom trawlers and artisanal vessels take this species, and annual landings have fluctuated widely, from 500 t to more than 2000 t in 1994–2006.

The species has been identified in commercial landings in Spain, Portugal, Italy, and Greece.

3.1.11 *Sepia officinalis* Linnaeus, 1758

Common names. Common cuttlefish (English); seiche commune (French); Gemeiner Tintenfisch (German); soupia (Σουπιά; Greek); seppia comune (Italian); sepia común (Spanish); choco-vulgar (Portuguese).

3.1.11.1 Adult diagnostic features

Up to 450 mm ML. Mantle oval. Tentacular club with five or six suckers in each transverse row, the medial one moderately enlarged; swimming keel not extending proximally beyond the base of the club. Hectocotylus on left arm IV of males: after the 5–7 proximal sucker rows, there are from 4–5 to 8–9 (medial) horizontal rows of reduced suckers. Cuttlebone posteriorly rounded with parallel sides. Anterior striae are inverted U-shape, or shallow M-shape. Colour light brown. Head with scattered white spots and with dark pigment around eye orbits. Arms I–III have a broad, longitudinal brownish band medially, extending onto head. Dorsal mantle has bold transverse zebra-stripe pattern during the breeding season; paired dorsal eye spots absent. Fins with narrow white band along outer margin and with small white spots, becoming larger toward junction of mantle and fins. Mature males with arms IV emboldened by white and black zebra bands and white arm spots. Diagnosis adapted from Roper *et al.* (1984), Guerra (1992), and Reid *et al.* (2005).

3.1.11.2 Distribution and habitat

Sepia officinalis extends through the eastern Atlantic and Mediterranean Sea (Belcari, 1999i). In the eastern North Atlantic, it extends from the Shetland Islands and southern Norway (not present in the Baltic Sea, except for occasional incursions with the northeasternmost Atlantic waters), south through the Mediterranean Sea (including Aegean Sea, Sea of Marmara, and Levantine Sea), to northwest Africa, with the southern boundary coinciding approximately with the border between Mauritania and Senegal (16°N; Reid *et al.*, 2005). Seasonal migrations occur from deeper, offshore overwintering grounds to shallower, coastal spawning and nursery grounds.

3.1.11.3 Life history

Hatchling ML ranges from 6 to 9 mm (Boletzky, 1983). Growth rates vary directly with temperature and inversely with size. In the English Channel, statolith analysis indicates that the growth pattern is exponential in hatchlings and early stages, whereas logistic curves are a better fit for larger size classes (7–106 mm ML; Challier *et al.*, 2005a).

Common cuttlefish attain sexual maturity at a wide range of sizes. In the Mediterranean Sea, mature males of 6–8 cm ML were observed. Males over 10 cm ML, however, may still be immature. A similar situation exists in females. Length at first maturity is ca. 13 cm ML in females. Females produce 150–4000 eggs, depending on their size. The main spawning season covers spring and summer, but there is also winter spawning, which is especially pronounced on the Atlantic coast. The length of time spent under optimal conditions in the early juvenile phase (inshore spring and summer conditions) determines whether an individual becomes sexually mature during the first winter and, hence, determines the lifespan, which may vary from ca. 14 to 24 months. The species has an intermittent terminal spawning strategy

(Boletzky, 1983; Guerra and Castro, 1988; Boucaud and Daguzan, 1990; Boucaud-Camou *et al.*, 1991; Gauvrit *et al.*, 1997; Belcari, 1999h; Dunn, 1999; Rocha *et al.*, 2001).

3.1.11.4 Trophic ecology

Predators. *Sepia officinalis* has been found in the stomachs of marine mammals, including Risso's dolphin (*Grampus griseus*; Clarke and Pascoe, 1985), the Mediterranean monk seal (*Monachus monachus*; Salman *et al*., 2001), and (in South Africa) fur seals (*Arctocephalus pusillus*; Castley *et al*., 1991). It is also eaten by elasmobranchs, including the blue shark (*Prionace glauca*; Clarke and Stevens, 1974) and smooth hound (*Mustelus mustelus*; Morte *et al*., 1997).

Prey. The diet mainly consists of small crabs, shrimps, demersal fish, cephalopods, and polychaetes. A significant change from crustaceans to fish occurs with growth. Cannibalism is relatively common at all sizes.

3.1.11.5 Fisheries

Sepia officinalis is an important species for the commercial fisheries of many countries. The main producer countries in the last decade were France in the Northeast Atlantic, followed by Italy and Tunisia in the Mediterranean Sea (Belcari *et al*., 2002c). In northern fisheries (English Channel, Bay of Biscay), cuttlefish are primarily caught by otter and beam trawlers, either as a target species or as bycatch when the target is demersal finfish. In southern fisheries, artisanal gears dominate, and cuttlefish are caught by gillnets, trammelnets, and a great variety of highly selective gears, such as traps, lures, jigs, and spears. Generally, trawlers operate in inshore and offshore fishing grounds, taking both juvenile and adult specimens, whereas artisanal gears (e.g. traps) catch spawning animals mainly inshore. In Galicia, cuttlefish is mainly caught with trammelnets from January to May (during the main reproductive period) on inshore fishing grounds (Arnáiz *et al*., 2001). In the inner area of the rías, cuttlefish is also caught with fykenets ("butróns") and traps ("nasa de choco"). Management options of interest for this resource include effort regulations (licences are issued in inshore artisanal fisheries) and minimum landing size. Catches of this species are not recorded separately by all countries, often being grouped with other cuttlefish, although FAO records separate catch statistics for this species along the Spanish Atlantic coast, and separate statistics are probably also available for the French Atlantic coast.

The species has been identified in commercial landings in the UK, France, Spain, Portugal, Italy, and Greece. *Sepia elegans* Blainville, 1827

3.1.12 *Sepia elegans* Blainville, 1827

Common names. Elegant cuttlefish (English); seiche elegante (French); seppia elegante (Italian); choco-elegante (Portuguese); choquito sin punta (Spanish).

3.1.12.1 Adult diagnostic features

Up to 89 mm ML (Adam, 1952). Mantle oblong, length more than twice width. Club short, oval; sucker-bearing surface flattened, with 6–8 suckers in transverse rows; suckers differ markedly in size: 3–4 greatly enlarged suckers toward posterior end of club and several dorsal suckers enlarged, but not as large as medial suckers. Hectocotylus present on left ventral arm of males: 1–2 rows of normal size suckers proximally, 9–11 rows of reduced minute suckers medially, then normal size suckers to arm tip; suckers in two dorsal and two ventral series displaced laterally. Cuttlebone outline oblong. Anterior striae are inverted U-shape. Spine absent, but ridge and small lateral wings present. Dorso-posterior end of cuttlebone with short, rugose, calcareous keel. Colour reddish brown. Dorsal mantle pale, peppered with scattered purple-black chromatophores. Fins and ventral mantle pale. Reference: Reid *et al*. (2005).

3.1.12.2 Distribution and habitat

Sepia elegans extends through the eastern Atlantic from western Scotland in the north to Namibia (21°S) in the south and is present throughout the Mediterranean Sea (Jereb and Roper, 2005). It is a sublittoral species, living on sandy and sandy–muddy bottoms at depths to ca. 450 m (Jereb and Ragonese, 1991). The species is tolerant of fluctuations in salinity and has been found in brackish waters (salinity 18–25) in the Sea of Marmara (Unsal *et al*., 1999) and the estuarine waters of the Ria de Vigo (Guerra, 1984).

3.1.12.3 Life history

After hatching, juveniles immediately adopt a benthic lifestyle. Growth was calculated at 2.8 mm month^{-1} for males and 3.0 mm month^{-1} for females in the Sicilian Channel (Ragonese and Jereb, 1991), a little faster than that estimated in the western Mediterranean by Mangold-Wirz (1963) and in the Ria de Vigo by Guerra (1984; 2–2.5 mm month^{-1}). Lifespan ranges between 12 and 19 months. The smallest mature males have been reported at 20 mm, and females at 30 mm ML (Guerra and Castro, 1989; Volpi *et al*., 1990). However, most individuals attain maturity at larger sizes (Mangold-Wirz, 1963; Volpi *et al*., 1990; Jereb and Ragonese, 1991), at approximately 1 year of age. Males may carry ca. 95 spermatophores and females ca. 250 eggs.

In the Mediterranean Sea, as well as in the Atlantic, mature males and females are present throughout the year, which suggests a continuous spawning period (e.g. Mangold-Wirz, 1963; Roper *et al*., 1984; Guerra, 1992; Belcari, 1999i). The eggs (maximum diameter 5 mm; Guerra, 1984) are attached to alcyonarians (sea fans), shells, etc., on muddy bottoms or, less frequently, on coral formations (Mangold-Wirz, 1963). Continuous recruitment also occurs, with peaks observed in several Mediterranean areas (Volpi *et al*., 1990; Jereb and Ragonese, 1991; Wurtz *et al*., 1991; D'Onghia *et al*., 1992; Casali *et al*., 1998).

3.1.12.4 Trophic ecology

Predators. *Sepia elegans* has been identified from stomach contents of very few predators, but has been reported from the dolphinfish (*Coryphaena hippurus*; Massuti *et al*., 1998) and the bottlenose dolphin (*Tursiops truncates*; Blanco *et al*., 2001).

Prey. This species feeds mainly on small crustaceans, fish, and polychaetes (Reid *et al*., 2005). Detailed studies on feeding (e.g. Guerra, 1985; Castro and Guerra, 1990) suggest that there is no change in diet with growth and/or maturity and that the variety of prey does not decrease with increasing size.

3.1.12.5 Fisheries

Sepia elegans is taken mainly as a bycatch in Mediterranean and West African trawl fisheries (Roper *et al*., 1984; Belcari, 1999i; Reid *et al*., 2005). Separate statistics are generally not reported for *S. elegans*, which represents a very significant percentage of the catches in some areas of its distributional range (Reid *et al*., 2005). In the Mediterranean Sea, it is marketed along with *S. orbignyana* and small *S. officinalis*, and constitutes a valuable resource locally. In the Sicilian Channel, an exploitation rate of 0.73 was estimated for the species (Ragonese and Jereb, 1991), which suggests very intensive fishing pressure on this resource. It is separately recorded in landings from the Gulf of Cadiz, where it typically forms ca. 7% of cuttlefish landings (the remainder being *S. officinalis*). This species is marketed fresh and frozen.

The species has been identified in commercial landings in Italy and Spain.

3.1.13 *Sepia orbignyana* Férrusac in Orbigny, 1826

Common names. Pink cuttlefish (English); seiche roseé (French); seppia pizzuta (Italian); choco-de-cauda (Portuguese); choquito con punta (Spanish).

3.1.13.1 Adult diagnostic features

Up to 120 mm ML (Mangold-Wirz, 1963). Mantle oval. Club short, oval, with 5–6 suckers in transverse rows. Suckers differ markedly in size: three large suckers medially with one slightly smaller sucker on each side of these. Hectocotylus present on left ventral arm (IV): 1–2 rows of normal size suckers proximally, greatly reduced suckers medially, then normal size suckers distally to arm tip. Suckers of hectocotylus in two dorsal and two ventral series displaced laterally, with a gap between them. Cuttlebone outline oblong. Anterior striae shallow M-shape, or wavy. Spine long, pointed (prominent), straight, directed dorsally, with ventral keel. Colour reddish brown. Reference: Reid *et al.* (2005).

3.1.13.2 Distribution and habitat

Sepia orbignyana occurs in the eastern Atlantic from the Irish Sea in the north to southern Angola (17°S) and is present throughout the Mediterranean Sea (Jereb and Roper, 2005). It is a demersal species that prefers sandy and sandy–muddy bottoms. Its greatest abundance is at depths of 50–250 m (Mangold-Wirz, 1963; Casali *et al.*, 1998). Records from the Sea of Marmara indicate that it can occur in brackish waters (Unsal *et al.*, 1999).

3.1.13.3 Life history

Newly hatched animals observed in the laboratory (Boletzky, 1988) measured 6 mm ML. Females attain larger sizes and grow faster than males (Bello, 2001). Growth was calculated at 2.9 mm month^{-1} for males and 3.0 mm month^{-1} for females in the Sicilian Channel (Ragonese and Jereb, 1991). Lifespan is considered to vary between 12 and 18 months (Mangold-Wirz, 1963). Estimates from length frequency analyses, although widely considered to be unreliable for cephalopods, indicate a longer lifespan of 2 years for males and 3 years for females (Ragonese and Jereb, 1991). Males reach maturity from 35 mm ML, and females from 65 mm ML (Belcari and Sartor, 1993). Mature males, aged 6 or 7 months, carry ca. 100 spermatophores; females aged 9 or 10 months carry ca. 400 eggs (Roper *et al.*, 1984).

In Mediterranean waters, spawning is probably continuous. The eggs, laid individually, whitish or greyish in colour and slightly more elongate than those of *S. officinalis* (Mangold-Wirz, 1963), are deposited in various sponges to form clusters of 30–40 (Reid *et al.*, 2005).

3.1.13.4 Trophic ecology

We found no reports of this species from predator stomach contents. *S. orbignyana* feeds mainly on crustaceans and fish (Auteri *et al.*, 1988).

3.1.13.5 Fisheries

Sepia orbignyana is taken mainly as bycatch throughout the Mediterranean and in the West African trawl fisheries, although targeted fisheries also exist (e.g. Roper *et al.*, 1984; Mangold and Boletzky, 1987; Belcari, 1999j; Reid *et al.*, 2005). Separate statistics are not reported, but *S. orbignyana* represents a very significant percentage of the catches in some areas. In the Mediterranean Sea, it is often marketed along with the congener *S. elegans* and small *S. officinalis* and constitutes a valuable resource locally (Belcari, 1999j). Studies carried out in the Sicilian Channel demonstrated an exploitation rate of 0.60 for this species (Ragonese and Jereb, 1991), which suggests intensive fishing pressure on the resource, as already hypothesized by other authors (e.g. Boletzky, 1983). It is marketed fresh and frozen.

The species has been identified in commercial landings in Italy.

3.2 Application of DNA-based markers in European cephalopod fisheries and biology

Paul Shaw

3.2.1 Introduction

In the past 30 years, DNA-based markers, such as allozymes, mitochondrial DNA (mtDNA), and microsatellites, have made a substantial contribution to many fields of whole organism biology. In particular, population biology (population structuring, individual interactions), phylogenetics, and systematics have benefited from the application of dependable, genetically determined, inherited markers that are not influenced by the environment and individual habits. The value of DNA-based markers has been demonstrated by their widespread use with finfish and their fisheries (see Carvalho and Pitcher, 1995).

Despite the obvious benefits of these markers, their input to cephalopod biology has been limited until the last ten years. Substantial early success was achieved using allozymes to address issues of population structuring (e.g. Brierley *et al.*, 1995), species identification and systematics (e.g. Augustyn and Grant, 1988), and particularly in identifying cryptic species (e.g. Yeatman and Benzie, 1994). The recent development of microsatellite DNA markers for cephalopod species and their application to the study of population structure (e.g. Shaw *et al.*, 1999) and mating strategies (e.g. Shaw and Boyle, 1997) – and the increasing use of DNA sequencing for phylogenetics/systematics purposes (e.g. Strugnell *et al.*, 2005) – has demonstrated the potential for greater contributions to cephalopod biology on a number of levels.

3.2.2 Population genetics of commercially important cephalopods in European waters

3.2.2.1 *Loligo forbesii*

Allozyme (Brierley *et al.*, 1995), microsatellite (Shaw *et al.*, 1999), and mitochondrial DNA data (Norman *et al.*, 1994) all indicate that this species is comprised of a single genetic stock throughout its range along the Atlantic coast of Europe (northwestern Scotland to southern Portugal), but that a significantly differentiated population exists in the Azores archipelago. Shaw *et al.* (1999) also indicated the possibility of genetically differentiated populations on off-shelf banks northwest of Scotland (particularly on Rockall Bank). This genetic pattern of large-scale homogeneity is consistent with what is known of the life-history characteristics of this species, which is highly mobile and migratory as juveniles and adults. The genetic differentiation of the Azores and, to a much lesser extent, the Rockall populations can be explained by the neritic habit of the species, as it does not extend below 1000 m depth or beyond open water off the shelf edge.

3.2.2.2 *Loligo vulgaris*

Very little genetic information is available on this species. Garoia *et al.* (2004), using five microsatellite loci, indicated that a single population is present within the Adriatic Sea. The limited data available suggest that the genetic population structure in *L. vulgaris* may be similar to that seen in *L. forbesii*, with genetically homogeneous populations over large geographical scales. However, more work is needed using additional genetic markers developed specifically for this species.

3.2.2.3 *Illex coindetii*

Unpublished results from the FAIR-CT96-1520 project (Boyle, 2000), based on five microsatellite loci developed for *Illex argentinus* (Adcock *et al.*, 1999), indicated that samples spanning the species' range in European waters from west of Ireland to the eastern Mediterranean demonstrate no significant heterogeneity, although a sample from Mauritania was genetically differentiated from the European samples. Martinez *et al.* (2005), screening 33 allozyme loci in samples from northwest Spain and Italy, found no evidence for genetic differentiation, although they suggested that there was some evidence for genetic differences among temporally separated samples from the same locations, potentially indicating differentiated spawning stocks. The data from both studies present a pattern of wide-scale genetic homogeneity of the European population of this species (i.e. a single genetic stock), which is consistent with predictions from the life history of highly mobile and migratory adults producing a pelagic, dispersing larval stage.

3.2.2.4 *Todaropsis eblanae*

Dillane *et al.* (2005), using four microsatellite loci and one minisatellite locus, found no significant genetic heterogeneity among samples from throughout the species range in the Northeast Atlantic (western Ireland, English Channel, northwest Spain, southern Portugal), slight (but not significant) differentiation between Atlantic and western Mediterranean samples, and significant differentiation between European samples and samples from West (Mauritania) and South Africa. The pattern of genetic panmixia throughout the species range in European waters (i.e. a single genetic stock) is consistent with predictions from the life history of the species of highly mobile and migratory adults producing a dispersing larval stage.

3.2.2.5 *Octopus vulgaris*

Maltagliati *et al.* (2002), using 20 allozyme loci, demonstrated genetic homogeneity (no significant allele frequency differences) over large geographic scales (hundreds of kilometres) within the Mediterranean Sea, but did find evidence for significant differentiation between western and eastern Mediterranean samples. Murphy *et al.* (2002), using three microsatellite loci, demonstrated significant allele frequency differences between fishery samples from western Saharan and Mauritanian waters, and between northern and southern Saharan Bank sites. Unpublished FAIR-CT96-1520 project data (Boyle, 2000), also using three microsatellite loci, indicate significant differentiation between single samples from the eastern Mediterranean, western Mediterranean, northwest Spain, and the Saharan Bank. Casu *et al.* (2002), using one microsatellite locus, found highly significant differences among samples from northwest Spain to Crete (mostly around Italy). Recently, Cabranes *et al.* (2008), using five microsatellite loci, found significant genetic differentiation among samples around the Atlantic coasts of Spain and Portugal (and similarly for one sample in the Mediterranean), which fits an isolation-by-distance (IBD) pattern, but with samples within 200 km demonstrating no significant differences.

Most of the genetic studies of *Octopus vulgaris* to date used a small number of samples spread over a wide geographical area, so they can suggest only broad geographical patterns. The available data suggest some genetic homogeneity within localized areas (at least several hundreds of kilometres), but there is also evidence of significant genetic structuring at the scale of identifiable basins in the Mediterranean, between Mediterranean and Atlantic areas, and associated with discontinuities in population distributions. The more detailed study of Cabranes *et al.* (2008) indicates that genetic mixing may be limited at distances over 200 km, at least along Atlantic coasts. These studies indicate that the position for *O. vulgaris* may lie somewhere between *Sepia officinalis* (see Section 3.2.2.6) and *Loligo forbesii* (see Section 3.2.2.2). It is probably more similar to *Sepia*, with a breakdown of genetic exchange over large distances (isolation by distance, but on a larger scale than seen in *S. officinalis*) and possibly associated with distinct hydrographical regimes (such as those associated with separate basins of the Mediterranean).

A pattern in *O. vulgaris* of gene flow limited by distance and/or oceanographic features is counter to predictions from life-history parameters of this species. A long-lived pelagic larval stage would suggest genetic exchange over great distances, maintaining genetic homogeneity throughout European waters. If gene flow is generated only by the larval stage, it is feasible that oceanographic features would be more important as barriers to exchange. Further study of this species is required, focusing on identification of the potential barriers to gene flow (oceanographic fronts, current systems associated with basins, etc.), in order to identify clearly the distribution of different stocks in European waters.

3.2.2.6 *Sepia officinalis*

Both allozymes (Pérez-Losada *et al.*, 1999) and microsatellites (Pérez-Losada *et al.*, 2002) indicate significant genetic structuring over relatively small geographical scales (down to ~300 km at least) for populations around the Iberian Peninsula. Microsatellite data also indicate a genetic breakpoint associated with the Almeria–Oran hydrographic feature. The scale of genetic structuring indicates that little gene flow is occurring among local populations. Limited exchange among populations could result from the life-history characteristics of *S. officinalis* (see Section 3.1.11), although a breakdown of gene flow at such spatial scales in a highly mobile marine species is surprising and may suggest the action of other factors, such as migration back to geographically restricted natal spawning sites. A broader-scale microsatellite study (Boyle, 2000) also indicated significant genetic stock structuring throughout the range of *S. officinalis* in European waters, and the presence of distinct English Channel, Northeast Atlantic, western Mediterranean, and eastern Mediterranean stocks.

Both allozyme and microsatellite data displayed clinal changes in gene frequencies around the Iberian Peninsula, suggesting either secondary introgression between ancestral Mediterranean and Atlantic populations that were isolated by low sea-level events during Pleistocene glaciations or IBD effects owing to restricted gene flow along a string of coastal populations. Garoia *et al.* (2004) also found significant differences among *S. officinalis* samples at scales of hundreds of kilometres within the Adriatic, although they did not find any evidence for an IBD pattern. A recent phylogeographic study using mitochondrial cytochrome oxidase I (COI) gene sequences (Pérez-Losada *et al.*, 2007) has not only confirmed the widespread action of IBD processes in *S. officinalis* population dynamics, but also the presence of several major genetic clades, indicating distinct ancestral Atlantic, western Mediterranean, and Aegean populations.

Together, the genetic results to date for *S. officinalis* indicate the presence of localized genetic subpopulations at intranational scales (hundreds–thousands of kilometres), and genetically distinct Atlantic, western Mediterranean, eastern Mediterranean, and Aegean populations. Allozyme and morphological data on samples of *Sepia* from the Canary Islands and the Iberian Peninsula indicate that the described subspecies of *S. officinalis* (*S. o. officinalis* and *S. o. hierredda*) are, in fact, distinct species (Guerra *et al.*, 2001).

3.2.3 Gaps in genetic knowledge of commercially important European cephalopods

To date, no population genetic information is available for *Todarodes*, *Alloteuthis*, *Eledone*, or other *Sepia* species. In addition, there is still insufficient data or sampling coverage to allow confident detailed statements about stock structuring of European populations of *S. officinalis*, *O. vulgaris*, and *L. vulgaris*. For both *S. officinalis* and *O. vulgaris*, the genetic data indicate the presence of significant stock structuring throughout European waters.

In *S. officinalis*, the observed genetic structuring around the Iberian peninsula is consistent with an IBD model, suggesting low levels of interbreeding among very local populations (across hundreds–thousands of kilometres), but no substantial genetic exchange above this scale, resulting in a series of distinct localized stocks. There is also evidence for *S. officinalis* of the action of local oceanographic features presenting a barrier to migration/genetic exchange between populations. This may explain, and result in, distinct regional populations, such as Adriatic, eastern Mediterranean, western Mediterranean, English Channel, European Atlantic, North African Atlantic, Canary Islands, etc. With the present data, however, it is impossible to determine whether or not regional populations genetically intergrade into each other through local gene flow, at what scale localized gene flow occurs, and what are the important determinants of limitation to localized genetic exchange (such as the presence of isolated breeding sites or the action of hydrographic features).

In *O. vulgaris*, there is genetic evidence for distinct regional stocks/populations. However, there are no data on the geographical scale of localized interbreeding populations and, therefore, on the critical factors in determining levels of migration/gene flow. As *O. vulgaris* possesses a pelagic larval stage, it has been assumed previously that it will exhibit wide geographical dispersal and interbreeding, and, therefore, single genetic stocks over large geographical distances. The genetic data indicate that this assumption cannot be supported. However, owing to the pelagic larval stage, *O. vulgaris* may display a different localized population structure to that suggested above for *S. officinalis.* Rather than a continuous, local-scale, IBD pattern of interlinked populations, *O. vulgaris* may exhibit genetically homogeneous populations over local scales (hundreds of kilometres), with gene flow effected by larval dispersal, but regionally distinct populations where hydrographic barriers prevent larval exchange. For example, we might expect genetically distinct regional populations in the Adriatic, Aegean, eastern Mediterranean, western Mediterranean, European Atlantic, North African Atlantic, and Canary Islands.

For *L. vulgaris*, the available genetic data are very limited and suggest that definable oceanographic regions contain single populations with high migration/gene flow within them (e.g. the Adriatic; Garoia *et al.*, 2004). Species life-history and genetic-structuring patterns observed for other loliginid squid species elsewhere (Shaw *et al.*, 1999, 2004; Reichow and Smith, 2001) lead to predictions of high genetic exchange among areas and effective panmixia across its entire range in European waters (as in *L. forbesii*).

3.2.4 Recommendations for future genetic studies of European cephalopod species

We recommend that genetic studies of population/stock structuring be carried out for *Todarodes*, *Alloteuthis*, *Eledone*, and *Sepia* species of commercial or biodiversity importance. Microsatellite DNA markers would be the most appropriate system, preferably coupled with examination of a variable mtDNA region.

We also recommend that further population genetic studies, using microsatellite DNA and mtDNA markers, of *S. officinalis*, *O. vulgaris*, and *L. vulgaris*, be conducted in European, especially 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 relationship of such structuring to geographical distance (i.e. IBD determinants of species dispersal) and/or to oceanographic features (i.e. distinct physical barriers to dispersal). Further genetic studies of *L. forbesii*, *T. eblanae*, and *I. coindetii* are not considered a priority at present.

3.3 Habitat use

Graham Pierce, Ángel González, and Ana Moreno

3.3.1 Brief overview of environmental effects on cephalopods

The concept of the niche and the idea that species have preferred and tolerated zones along each axis of a multidimensional "niche space" has long provided a focus for research on interspecific competition and competitive exclusion. Increasingly now, it is also seen as a tool for fishery and conservation management through the concepts of environmental envelopes and essential fish habitat, which are readily applied to cephalopods. Our ability to derive empirical models of the preferred habitat of marine organisms has been facilitated in the last two decades by developments in remote sensing, GIS, and statistical modelling (e.g. Eastwood *et al.*, 2001; Pierce *et al.*, 2001, 2002; Redfern *et al.*, 2006; Valavanis, 2008; Valavanis *et al.*, 2008, and references therein).

Cephalopods are widely recognized as being highly sensitive to environmental conditions and changes, and at a range of spatial and temporal scales, because of their short life cycles and rapid growth. For most European cephalopods, information is available on broad distribution and depth preferences of juveniles and adults, whether these are primarily benthic, demersal, or pelagic. Most larval forms ("paralarvae") are planktonic. Various observational and experimental data point to limits to tolerance, e.g. in relation to water temperature, oxygen concentration, and salinity (few species tolerate low-salinity coastal waters).

As relationships between cephalopods and their environment, specifically effects on distribution, abundance, and life cycle, have recently been reviewed by Pierce *et al.* (2008b), only a brief overview and update is provided here. The majority of studies cited refer to post-recruit stages.

Relationships documented between cephalopod stock dynamics and environmental conditions are of two main types: (i) those concerning the geographic distribution of abundance, for which the mechanism is often unknown; and (ii) those relating to biological processes, such as egg survival, growth, recruitment, and migration, where mechanisms are sometimes known – and, in a very few cases, supported by experimental evidence. Of particular interest are recent experimental studies, such as Rosa and Seibel (2008) and Kikkawa *et al.* (2008), which examine effects of elevated CO_2 levels on cephalopods, and a recent study by André *et al.* (2009), which uses captive-rearing data to model the effect of temperature on individual growth curves.

Cephalopods seem to respond to environmental variation both actively (e.g. by migrating to areas with more favourable environmental conditions for feeding or spawning) and passively (e.g. by variations in growth and survival according to conditions experienced, and by passive migration with prevailing currents). Environmental effects on early life stages can affect post-recruit, life-history characteristics (growth and maturation rates) as well as adult distribution and abundance.

Both large-scale atmospheric and oceanic processes and local environmental variation appear to play important roles in species–environment interactions. Although oceanographic conditions are of particular significance for mobile pelagic species, such as the ommastrephid squid, the less widely ranging demersal and benthic species may depend more on other physical habitat characteristics (e.g. substrata and bathymetry). Coastal species may be affected by variations in water quality and salinity (related to rainfall and river flow).

Key research goals include linking distribution and abundance to environmental effects on biological processes, finding ways of incorporating information on the role of currents in passive transport, and using such knowledge to provide environmental indicators and underpin fishery management. Above all, there is a need to focus on the effects of environmental conditions on the early life stages, namely eggs and paralarvae.

3.3.2 Habitats of paralarvae

The hatchlings (paralarvae) of many cephalopods, including both neritic and oceanic species, are planktonic. The paralarvae tend to occur in association with the biologically productive continental shelves or close to islands or seamounts. Oceanographic mesoscale features thus play an important role in modulating their distribution, as they do for other plankton communities (e.g. Bakun, 1996; Dos Santos *et al.*, 2007; Santos, A. M. P., *et al.*, 2007). However, little is still known about the influences of hydrographic and water-quality variables on the distribution and survival of planktonic paralarvae in the field, particularly in the Northeast Atlantic and Mediterranean (Piatkowski, 1998).

A major constraint for research on cephalopod paralarvae is that they appear in small numbers in standard plankton hauls. This may be related, at least in part, to their vertical movements. Few studies have recorded the daily vertical movement cycles of paralarvae. *Loligo vulgaris* paralarvae seem to spend most of the time close to the seabed, undergoing a vertical migration to subsurface waters at night (Moreno *et al.*, 2009). Paralarvae of *Octopus vulgaris* are also nearly absent from surface waters during the day and occur from the seabed to the surface at night (Takeda, 1990; Sakaguchi *et al.*, 1999; Otero, 2006). Development of new plankton sampling devices (e.g. benthic devices and modified opening/closing nets) specifically targeted at cephalopods would be recommended for future work.

Another key issue to be solved in future is the ageing of paralarvae in order to estimate the duration of the planktonic phase, especially of commercially important species. To date, there has been only one study of the age of wild paralarvae: by González *et al.* (in press) on the common squid (*L. vulgaris*). Age determination for paralarvae should be implemented in future in order to understand the dispersal capacities during the planktonic phase. As the increments deposited in the statoliths during paralarval life are hard to discern in the statoliths of older squid, such data can also provide an improved understanding of the lifespan.

The first study of the relationship between upwelling and paralarval presence was made in Galician waters (northwest Spain) by Rocha *et al.* (1999). Subsequent work on the abundance and distribution of paralarvae of commercially important cephalopod species in relation to the physical environment was undertaken in 2000 and 2001 in Galicia (González *et al.*, 2005) and later in Portuguese waters (Moreno *et al.*, 2009). The west Iberian coast from Galicia to southwest Portugal (44–37°N) constitutes the northern boundary of the Iberian–Canary Current upwelling system. In this area, the presence/absence of upwelling has a strong influence on the annual cycles of primary and secondary production, modulating the abundance and spatial distribution of the planktonic cephalopod paralarvae (González *et al.*, 2005; Otero, 2006; Moreno *et al.*, 2009).

Studies in Galicia demonstrated that windstress propagates its effects upwards through the trophic web, inducing changes in the abundance of *O. vulgaris*. The structure of windstress in both spring–summer (previous to the hatching peak) and autumn–winter affects the planktonic stage of this species and subsequent recruitment, explaining up to 90% of the interannual variability of catches of adult octopus in the region (Otero *et al.*, 2008).

Studies on the Portuguese shelf highlighted the role of temperature and upwelling in modulating seasonality and distribution of *L. vulgaris* and *O. vulgaris* paralarvae. The influence of the physical environment was especially pronounced for *O. vulgaris*, which demonstrated significant differences in distribution related to the oceanography of the western Iberia vs. the Gulf of Cadiz systems (Moreno *et al.*, 2009).

The relationship between the dynamics of coastal upwelling areas and planktonic paralarval distribution and abundance is complex. A model has recently been developed to test the effect of rapid variability of upwelling chemistry on *O. vulgaris* paralarval abundance and biomass in the Ría de Vigo (Galicia, Northeast Atlantic) and the adjacent shelf (Otero *et al.*, 2009). Model results indicate that decreases in nitrate, ammonium, and chlorophyll concentrations explain up to 88% of the increase in common octopus paralarval abundance in years of weak upwelling. These conditions occur during the relaxation of upwelling events, when the biogenic matter produced from the consumption of nutrient salts is retained in the system and transferred through the foodweb.

3.4 Diseases, parasites, and contaminants

Shelagh Malham, Paco Bustamante, Santiago Pascual, and Sonia Seixas

3.4.1 Introduction

Recorded incidences of disease and mass mortality events in marine organisms are increasing, a trend thought to be linked to climate-mediated change and anthropogenic inputs. The marine environment is a microbial soup that contains an abundance of potentially pathogenic organisms and parasites, and the spread of disease in the ocean is extremely rapid. Given the various marine habitats occupied by cephalopods during their life cycle, contact with disease-causing organisms is inevitable. However, there are only a few reports of viral, bacterial, or fungal diseases affecting wild stocks of cephalopods.

An understanding of disease dynamics is vital for conserving marine ecosystems. However, compared with terrestrial systems, the role of diseases in most marine ecosystems is relatively poorly known. How diseases affect organisms depends on a range of interacting factors, including whether the disease is specific or non-specific and the effects of other environmental stressors on individuals and populations (e.g. pollution, fishing, and climatic variation). Interactions between hosts and pathogens, such as viruses or bacteria, will alter with changes in climatic features (e.g. temperature), thus affecting the severity of disease outbreaks (Harvell *et al.*, 2002). Results from simulation models of the effects of stress on the population dynamics of infectious diseases suggests that the impact of specific diseases on hosts declines with increasing stress, while that of non-specific diseases increases with stress (Lafferty and Holt, 2003). Effects of diseases on individuals potentially have consequences at population and ecosystem levels. Thus, some diseases have “positive” effects at the ecosystem level by promoting biodiversity.

Importantly, diseases can be pelagic as well as benthic. Suspended sediments can provide food and/or shelter and transport for pathogenic organisms. Water column turbidity can promote waterborne disease outbreaks, with the bottom sediment acting as a reservoir for pathogens. Disturbance, such as dredging or boating activity, can cause resuspension of sediment and release of pathogens. In addition, electrostatic forces that bind viruses/microbes to sediment particles or particulate organic matter can be overcome by hydrological changes that influence the pH, salinity, and temperature of the water column.

The emergence of infectious diseases in coastal and ocean ecosystems is often a result of human-induced environmental change. The underlying causes of emerging infectious diseases range from human encroachment and population increase to climate change, agriculture, increased interaction between humans, domestic animals and wildlife, and immunosuppression in the host owing to environmental stressors or infection by immunosuppressive viruses such as the morbilliviruses (Daszak *et al.*, 2001).

Whether or not the reported increases in diseases and mass mortality events in the ocean are symptomatic of larger problems is unknown. Various factors have been blamed, including climatic change, pollution (see Section 3.5.2), eutrophication, overfishing, and habitat destruction, although obviously not all mass mortality events can be attributed to these factors. Such stressors can increase susceptibility to disease or toxin accumulation in individual cephalopods, with potential consequences at population and community levels. Indeed, where environmental impacts persist over an extended period (e.g. after an oil spill), more than one generation of cephalopods may be affected. The issue of climate change and its effects on cephalopods is examined in more detail in Section 6.

Cephalopods are known to carry a diverse assemblage of parasites and symbionts, and apparently "healthy" individuals in the wild appear able to survive trauma without suffering major infections (Boyle, 1991). Potentially pathogenic organisms found associated with cephalopods include viruses, bacteria, fungi, protozoans, nematodes, monogeans, digeneans, cestodes, acanthocephalans, polychaetes, hirudineans, crustaceans, copepods, and isopods (Hochberg, 1983; Forsythe *et al.*, 1991).

3.4.2 Viruses

Oceans teem with viruses typically numbering tens of billions litre^{-1} (Fuhrman, 1999). Viruses infect most marine organisms from bacteria to invertebrates and vertebrates. Importantly, viruses appear to play a major role in regulating population density and diversity in their bacterial and phytoplankton hosts, significantly affecting primary production in the world's oceans (Fuhrman, 1999; Wommack and Colwell, 2000).

Recent research has demonstrated that the Earth's oceans are a primary reservoir of emerging infectious diseases caused by RNA viruses (the Caliciviridae), which are capable of causing a whole suite of diseases in marine and terrestrial organisms (Smith, 2002). Additionally, viruses are transferring from the land to the sea. Thus, the canine distemper morbillivirus is thought to have been responsible for deaths in pinnipeds, although other reported mass mortalities in marine mammals appear to be caused by different (related) morbilliviruses (De Guardo *et al.*, 2005).

Cephalopods such as *Octopus vulgaris* have been demonstrated to contain virus-like particles associated with tumours (Rungger *et al.*, 1971; Hanlon and Forsythe 1990a, 1990b). In addition, squid axoplasm has been demonstrated to transport neurotropic viruses such as *Herpes simplex* virus type 1 (Bearer *et al.*, 1999), suggesting that these viral particles could survive in cephalopods.

3.4.3 Bacteria

Bacteria are essential to the ocean's biogeochemistry and for their role in the decomposition of organic matter necessary for marine foodwebs. However, oceans are also the conduits for various bacterial diseases affecting humans (usually through contact with contaminated seawater or shellfish), including typhoid fever, meningo-encephalitis, and gastroenteritis. Bacterial organisms that occur naturally in the ocean, and can be pathogenic, include *Aeromonas*, *Clostridium*, *Klebsiella*, *Rickettsia*, *Legionella*, *Listeria*, *Pseudomonas*, and *Vibrio*. Bacterial diseases in the ocean have resulted in large-scale epidemics in marine organisms, ranging from seagrasses to oysters and fish.

A number of bacterial diseases of cultured cephalopods were described by Hanlon and Forsythe (1990a) in their review of cephalopod diseases. These appear to be linked to several bacterial groups including representatives from *Vibrio*, *Aeromonas*, *Pseudomonas*, and *Flavobacterium* sp. Infections often follow injury and result in skin lesions (Hanlon and Forsythe, 1990a; Ford, 1992), with *Vibrio* sp. bacterial infections being the main problem for captive cephalopods (Scimeca, 2006). Additionally, in cuttlefish, fracture of the cuttlebone often causes infections that lead to mortality. A few studies have been undertaken on diseases in wild cephalopods. In wild *Octopus vulgaris*, researchers demonstrated that signs of disease, such as lesions on the arm and mantle, were associated with the bacterium *Vibrio lentus* (Farto *et al.*, 2003). Quantifying the incidence of diseases in cephalopod populations may be difficult because diseased and dead animals (especially as they are soft-bodied) are likely to be rapidly removed by predators or scavengers.

3.4.4 Parasites

Parasites are found in almost all taxa of eukaryotes. Parasite hosts are more susceptible to disease when they contain the added burden of parasites. In turn, reduced fitness and mortality of hosts can affect host population dynamics and community composition. Invasion of parasites into naïve areas is a major cause of biodiversity loss (Lafferty, 1997; Hoberg and Klassen, 2002; Rohde, 2002).

Almost all wild and laboratory-cultured cephalopods contain parasites, which, apart from viruses and bacteria, include polychaetes, copepods, and metazoans. A number of these parasites use cephalopods as a reservoir or second or third intermediate host. Generally, cephalopod parasites are mainly found on the skin and gills and in the digestive gland, digestive tract, and kidneys (Hochberg, 1990; Pascual *et al.*, 1996; Gestal *et al.*, 1999), although parasites have been associated with most organs. The most frequently encountered cephalopod parasites are the ciliates, which mainly infect pelagic cephalopods, and the dicyemids, present in the renal appendages, digestive glands, and digestive tract. Dicyemids eliminate the ciliate parasites when juvenile benthic cephalopods settle after their initial pelagic stage and are the most common and characteristic parasites of cephalopod renal appendages. Dicyemids have been found in benthic and epibenthic cephalopods, including cuttlefish, octopus, and loliginid squid (Hochberg, 1990; Furuya *et al.*, 2003, 2004) and may have a detrimental effect. Recent studies have demonstrated that parasites (both micro and macro) affect cephalopods by diminishing their nutrient absorption capabilities (Pascual *et al.*, 2007a). These authors demonstrate that the parasites lyse large areas of functional tissue within the animal, deplete energy stores, and affect the host's immune defence mechanisms. Cephalopods have also been described as harbouring parasitic platyhelminths, including monogeneans, digeneans, and cestodes, probably acquired through eating infected invertebrates and fish (Hochberg, 1990).

Various studies indicate that the ecological niche of a cephalopod species is more important than its phylogeny in determining its risk of parasitic infection (González *et al.*, 2003). However, various biotic and abiotic environmental drivers will determine the extent of the infection. Stressed laboratory animals demonstrate increased parasitic burdens (Forsythe *et al.*, 1990; S. Malham, pers. comm.). Pollution may also make marine animals more susceptible to infections and lead to changes in parasite loads. Parasites will themselves be affected by pollution and may be useful in monitoring environmental conditions (Rohde, 2002). Parasites, including those found in cephalopods, have been used as biological tags (Rohde, 2002).

3.4.5 Cephalopod immune system

The immune system of an animal is its defence against invading pathogenic organisms and reflects its state of health. However, the use of the status of the immune system as an indicator of ecosystem health or pollution stress is complicated by the range of different factors involved in any immune response. Sublethal exposure to environmental contaminants can have measurable effects on many physiological processes, but different degrees of exposure to a stressor can elicit different types of immune system response. The ability of animals and plants to protect themselves from infection relies mainly on the detection of non-self and the capacity of the immune system to mount a response. The ability of animals or plants to defend themselves against disease can be linked directly to the "quality" of the surrounding environment (Oliver and Fisher, 1999; Nürnberger and Brunner, 2002). Animals are likely to be at risk of disease and/or mortality if the normal functioning of the immune system is disrupted.

Immune systems in invertebrates involve complex combinations of cellular and humoral components, including external barriers, which act to prevent invasion by pathogens. Invertebrate immunity tends to be thought of as innate, non-adaptive, and non-specific. However, recent research has revealed similarities and conserved mechanisms, at the cellular and molecular levels, between vertebrates and invertebrates, such as the complement pathway (Cooper, 2002).

The cephalopod immune system is capable of recognition of non-self and appears, at present, to be innate. Cephalopods, unlike other molluscs, have a closed circulatory system with a central systemic heart and two branchial hearts (Wells, 1978, 1983; Wells and Smith, 1987). In addition, the arterial, venous, and capillary bed circulatory system of cephalopods is similar to that of vertebrates (Browning, 1979; Wells, 1983; Shadwick and Nilsson, 1990). The blood consists of haemolymph (plasma), haemocyanin (respiratory pigment), and haemocytes (blood cells). Little detailed information is available on cephalopod immunology (Ford, 1992; Malham and Runham, 1998). Changes linked to climate-mediated or anthropogenic impacts (e.g. in relation to water quality, temperature, pollution, or fishing) will affect the immune system of cephalopods (Lacoue-Labarthe *et al.*, 2009a) and their parasites, and potentially lead to mortality. Immune-compromised animals tend to have higher infection rates, although, as noted above, this may not be noticeable in soft-bodied cephalopods because diseased animals would quickly be picked off and eaten, leaving very little trace.

3.4.6 Contaminants

Anthropogenic inputs to the marine environment, such as excess nutrients and pollutants, including heavy metals and persistent organic pollutants (POPs), all have numerous, usually negative, effects on marine organisms and the animals that eat them. Anthropogenic inputs can directly or indirectly affect a whole marine community or ecosystem.

The release of a large quantity of pollutants can cause immediate mortality, whereas lower levels of pollutant discharge may lead to accumulation of the pollutant within animals, with consequences such as immunosuppression and reproductive failure. Once in the ocean, pollutants can be distributed over wide areas through physical processes (e.g. currents and gyres). Generally, movement of contaminants from organism to organism is through trophic links (i.e. by direct assimilation following ingestion of the prey). Bioaccumulation is basically an equilibrium phenomenon. A contaminated environment leads to contaminated animals, and certain compounds (e.g. lipophilic POPs) have a greater affinity for animal tissues than for seawater, so that concentrations in animals can greatly exceed those in their surroundings. Heavy metals can accumulate in specific tissues, depending on the detoxification mechanisms that an animal possesses. In addition, concentrations of persistent organic pollutants (POPs), and also of some heavy metals, typically increase through food-chain transfers (biomagnification). Thus, cephalopods are responsible for transfer of cadmium to top marine predators (Bustamante *et al.*, 1998a).

There is considerable evidence that marine animals may be more susceptible to disease if they are contaminated with pollutants. Harvell *et al*. (1999) state that mass mortality of marine mammals appears to be associated with heavily polluted coastal areas of the North Atlantic. Other areas "identified" by these authors as being "hot spots" for disease include the Caribbean basin and the Indo–Pacific, although, in practice, the problem appears to be worldwide. Sources of anthropogenic pollutants entering coastal and ocean ecosystems range from atmospheric deposition to industrial and agricultural run-off involving both point sources (such as rivers and dumping) and diffuse sources (such as atmospheric deposition and groundwater). All of these sources have the potential to disturb ecosystems and increase the risk of disease, harmful algal blooms, and viral epidemics.

Generally, chemical pollution (e.g. from metals or organic compounds), has been linked to various disease problems worldwide and is suggested to be a potential cause of mass mortalities and changes in biodiversity. Chemicals such as polycyclic aromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs) have been linked with deformities, cancer, compromised immune systems, and increased susceptibility to parasitic infection and disease. Environmental pollution can alter the host–pathogen relationship, thus increasing the probability of disease and significantly affecting the host population (Arkoosh *et al.*, 1998). In addition, some chemicals, such as the PAHs, can serve as growth-stimulating nutrients for pathogenic bacteria, such as some species of *Vibrio*.

Pollutants may have impacts on areas far removed from their point of discharge. Oceans transport substances and organisms over very long distances; for example, the Arctic is polluted with PCBs and pesticides that originated mainly at lower latitudes. Migratory and planktonic marine organisms, including cephalopods and their paralarvae, which swim or drift over long distances, may be exposed to a variety of environmental hazards. Impacts of pollution at some intermediate location may seriously affect the population at the end of the migration or drift route. There is also often a significant time-lag between the release of the pollutant and the manifestation of its impact on the marine environment. Thus, dichlorodiphenyltrichloroethane (DDT) accumulated in the marine environment from the mid-1940s to the mid-1970s and, even 20 years later, was still found in high levels in species such as dolphins and birds (Addison, 1989; Fry, 1995). The timing of a pollution event is also important, because even a small release at the wrong time or season in a sensitive environment can cause considerable harm and leave organisms susceptible to disease.

Cephalopods are arguably very suitable biological indicators of ecosystem health. They are short-lived, fast-growing animals in which individual and population parameters, such as growth and recruitment, are known to depend strongly on environmental conditions. Importantly, many cephalopod species (e.g. octopus) inhabit coastal waters or come to mate and spawn close to the coast (e.g. cuttlefish). Therefore, they are more subject to direct contamination with high concentrations of pollutants released by industrial, domestic, and agricultural run-off than species, which live their entire lives away from the coast (e.g. some squid). The effects of these pollutants are many and varied, ranging from the molecular level, through individual organisms, to the level of communities and ecosystems. Chemicals may affect the physiology and immune responses of individuals, as well as reproductive success and sex ratios within populations. Biological effects may include direct toxicity, stress, disease, and reproductive failure. Invertebrate embryos and the first stages of development are particularly sensitive to pollutants (e.g. Calabrese *et al.*, 1984), which may be particularly critical for the success of population recruitment of cephalopods.

Several studies have revealed that cephalopods have the capacity to accumulate heavy metals at high levels in their tissues (e.g. Miramand and Bentley, 1992; Rossi *et al.*, 1993; Bustamante *et al.*, 1998a, 1998b, 2000, 2002a, 2002b; Storelli and Marcotrigiano, 1999; Seixas and Pierce, 2005a, 2005b; Seixas *et al.*, 2005a, 2005b; Pierce *et al.*, 2008a). Heavy metals include both toxic elements (e.g. mercury, cadmium, lead, silver) and numerous trace elements that are essential to biota (e.g. copper, cobalt, or zinc), but may be toxic in high concentrations. These elements accumulate in the sediment, and can be re-mobilized after natural events (e.g. storms) or anthropogenic modification (e.g. dredging). Of the cephalopod tissues, the digestive gland and branchial hearts appear to play a major role in the bioaccumulation of toxic elements, such as cadmium and silver, which are detoxified and sequestrated, sometimes over a very long time-scale (Beuerlein *et al.*, 2002; Bustamante *et al.*, 2002a, 2004).

Metals such as cadmium can have direct effects on embryogenesis in squid (e.g. Şen and Sunlu, 2007). Recent experimental studies have demonstrated that some heavy metals reduce the survival and growth of both eggs and juveniles of the cuttlefish *Sepia officinalis* (E. Le Bihan, pers. comm.). Nonetheless, the eggshell limits the incorporation of cadmium, lead, and mercury during embryogenesis in cuttlefish, but silver is strongly accumulated and can affect survival (Lacoue-Labarthe *et al.*, 2008a). Furthermore, there is evidence that maternal transfer of metals occurs in cuttlefish (Lacoue-Labarthe *et al.*, 2008b). Indeed, invertebrate embryos and the first stages of development are particularly sensitive to pollutants, which may be critical for the success of population recruitment of cephalopods.

Heavy metals can also be a concern for human health. For example, some concentrations of cadmium and lead, determined in edible tissues of octopus in Portugal, exceeded the legal limits set by the European Community for those metals (Seixas, 2004). Moreover, over 75% of the mercury accumulated in cephalopod muscle is in the organic form, which is the most toxic chemical species of this metal (Bustamante *et al.*, 2006).

Other chemicals, mainly anthropogenic in origin, can also have profound effects on marine systems. Examples include POPs, such as PCBs, pesticides, PAHs, and radioactive compounds. Compared with heavy metals, fewer studies have focused on the metabolism of POPs in cephalopods, most of them investigating baseline levels in the flesh (e.g. Goerke *et al.*, 2004; Perugini *et al.*, 2004; Storelli *et al.*, 2006). In general, relatively low POP levels have been reported for cephalopod flesh. Nonetheless, both field and experimental analysis of POPs in cephalopod tissues revealed that they are accumulated at high concentrations in the digestive gland (e.g. Ueno *et al.*, 2003; Danis *et al.*, 2005). Recent work has identified POPs in nine species of deep-sea cephalopods, demonstrating persistence of these chemicals at oceanic depths to 2000 m; the physiological effects on these animals are unknown (Unger *et al.*, 2008). In general, very little is known about toxic effects of POPs on cephalopods.

In countries where humans consume the digestive gland and other viscera (e.g. Japan), exposure to bioaccumulated pollutants could be much higher than if only the muscular mantle and arms were eaten. For example, the toxic equivalent (TEQ) concentrations of dioxins in gut samples of the Japanese common squid were 50-fold larger than those in muscle tissues; indeed the gut contained ca. 95% of the total dioxin load of the squid (Tsutsumi *et al.*, 2007).

Overall, there is a need to collect further information on the effects of pollutants on cephalopods, especially those living in the coastal zone, which form part of the human food chain. This issue is of special concern in the context of ocean acidification and ocean warming, which increase the metal uptake of the early life stage (Lacoue-Labarthe *et al.*, 2009b).

4 European cephalopod fisheries and aquaculture

Eugenia Lefkaditou, Nick Bailey, Isabel Bruno, Ángel Guerra, Lee C. Hastie, Patrizia Jereb, Noussithé Koueta, João Pereira, Graham J. Pierce, Jean-Paul Robin, Pilar Sánchez, Ignacio Sobrino, Roger Villanueva, and Iain G. Young

4.1 Overview of 1950–2006 cephalopod landings statistics for Europe

Fishery statistics on cephalopod landings from the Northeast Atlantic by European nations are available from the ICES website in a form compatible with the FAO′s Fishstat Plus software. There are minor discrepancies between the two sources, but the same broad patterns can be extracted. The FAO data also afford a broader view of cephalopod fisheries in "European" waters. Total cephalopod landings from the Northeast Atlantic and Mediterranean (including landings by non-European countries) have increased from ca. 30 000 t annually in 1950 to a present-day total of ca. 120 000 t. However, there was a steady decrease in landings from 1965 to 1979, associated with substantial contraction of the Spanish Atlantic octopus and cuttlefish fisheries. The three fisheries that were most important in the 1950s and 1960s, for octopus and cuttlefish in Italy and for octopus in the Spanish Atlantic, all remain important, but the post-1980 rise is mainly the result of increases in other fisheries, including the emergence of the French Atlantic cuttlefish fishery (Figure 4.1.1). The most important non-European fishing nation in the region, with catches of almost 10 000 t of cephalopods from the Mediterranean in 2006, is Tunisia.

In the Northeast Atlantic, annual cephalopod landings increased steadily from 1950 to the mid-1960s, when they first exceeded 50 000 t. Levels declined again after 1972, falling to mid-1950s levels (under 20 000 t) in 1980. This initial rise was caused by an increase in octopus landings and, to a lesser extent, in cuttlefish landings. Since then, landings have generally increased again, with a major surge in short-finned squid landings in the early to mid-1980s being responsible for most of the initial rise, caused by the short-lived fishery for *Todarodes sagittatus* in Norway. The general rising trend since 1980 is almost entirely the result of increased cuttlefish landings (Figure 4.1.2).

With the exception of the Norwegian *Todarodes* fishery in the 1980s, four countries (France, Portugal, Spain, and the UK) have been responsible for the majority of landings. Spain had the highest landings until around 1970 (ca. 18 000 t of octopus annually in 1967–1971), after which the octopus fishery crashed dramatically to under 10 000 t annually, where it has remained ever since. France has become the leading fisher of cephalopods, as reflected by high landings of cuttlefish and, to a lesser extent, short-finned squid (Figure 4.1.3).

In the Mediterranean, octopus and cuttlefish dominate the landings. The overall landings trend was upwards from 1950 to 1966 and then remained fairly stable until around 1982, although octopus increased in importance relative to cuttlefish over this period. Thereafter, landings again increased, reaching an all-time high in 1988. Over the following 12 years, landings decreased to the 1970s level, but have increased again since 2003 (Figure 4.1.4).

By far the most important contributor to total cephalopod landings from the Mediterranean is Italy. Indeed, the decline in total landings since 1988 is almost entirely the result of declining landings in Italy. Initially, this was caused mainly by a decline in cuttlefish catches, but there have been subsequent declines in Italian landings of all cephalopod categories. Similarly, the recovery since 2003 is largely restricted to Italian cuttlefish catches. Spain, Tunisia, and Greece are the other important contributors to Mediterranean cephalopod catches (Figure 4.1.5).

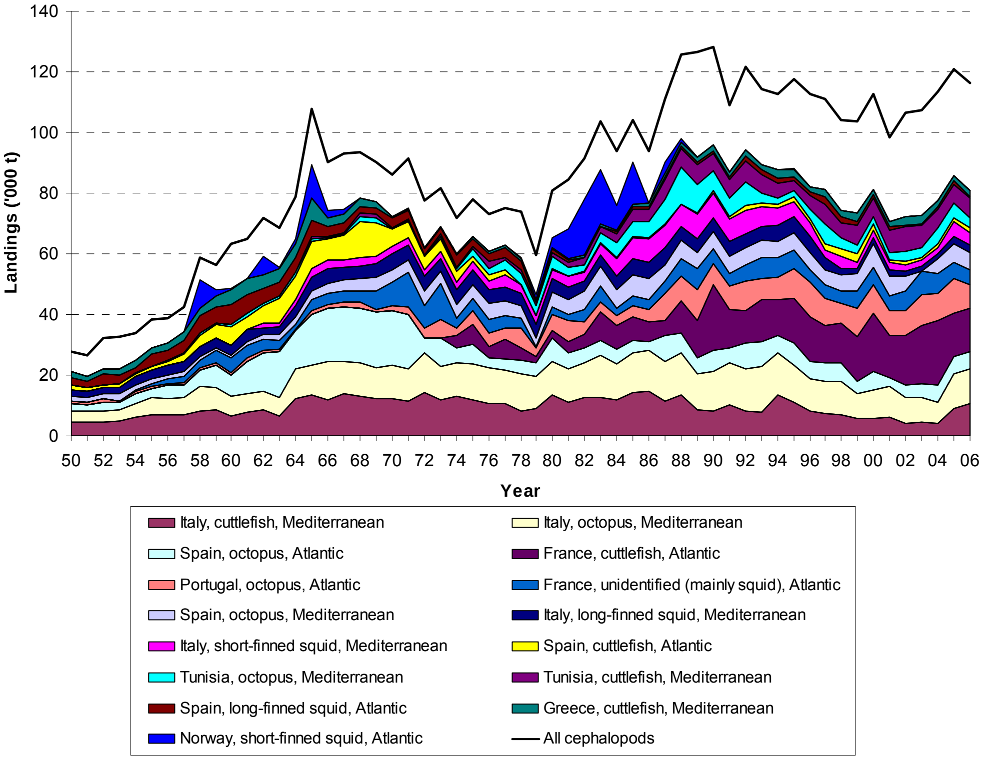


Figure 4.1.1. Total cephalopod landings from the Northeast Atlantic and Mediterranean, 1950–2006.

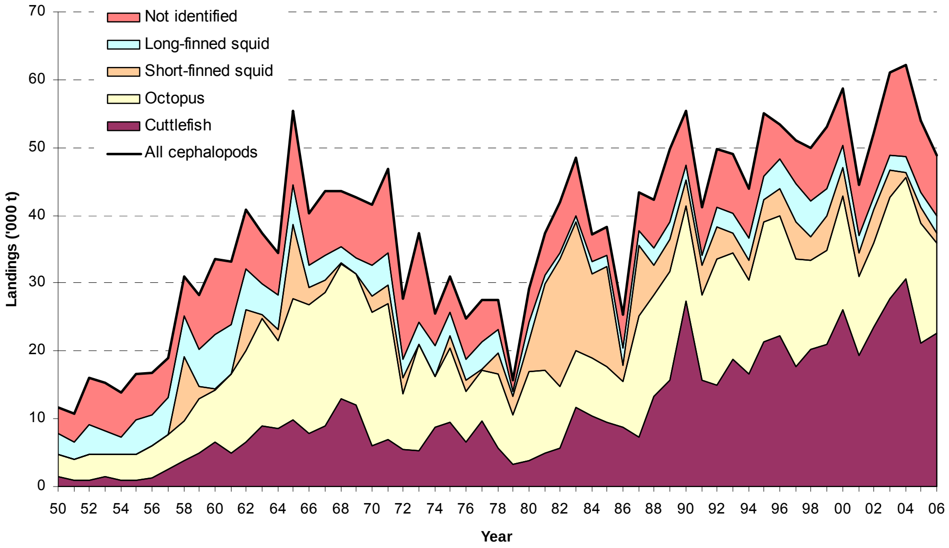


Figure 4.1.2. Annual cephalopod landings into Europe from the Northeast Atlantic by taxon, 1950–2006.

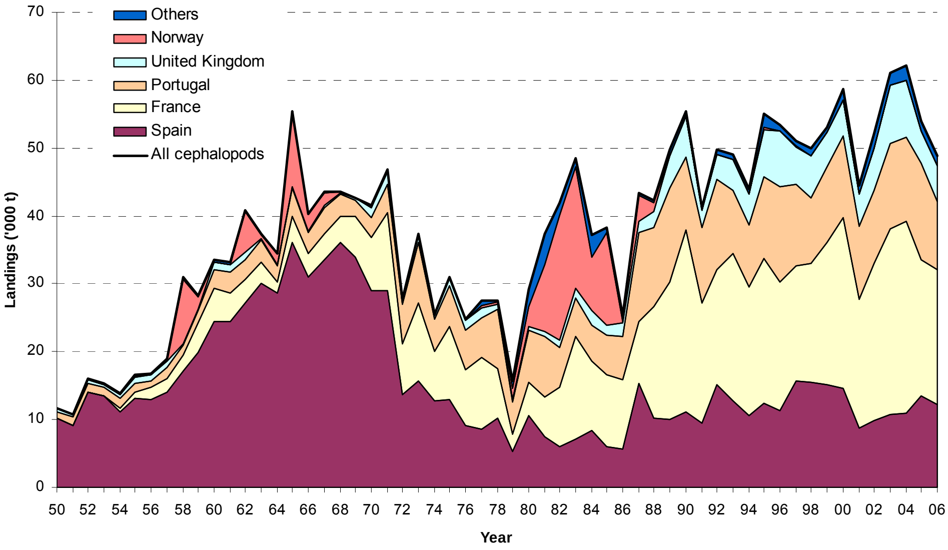


Figure 4.1.3. Annual cephalopod landings into Europe from the Northeast Atlantic by country, 1950–2006.

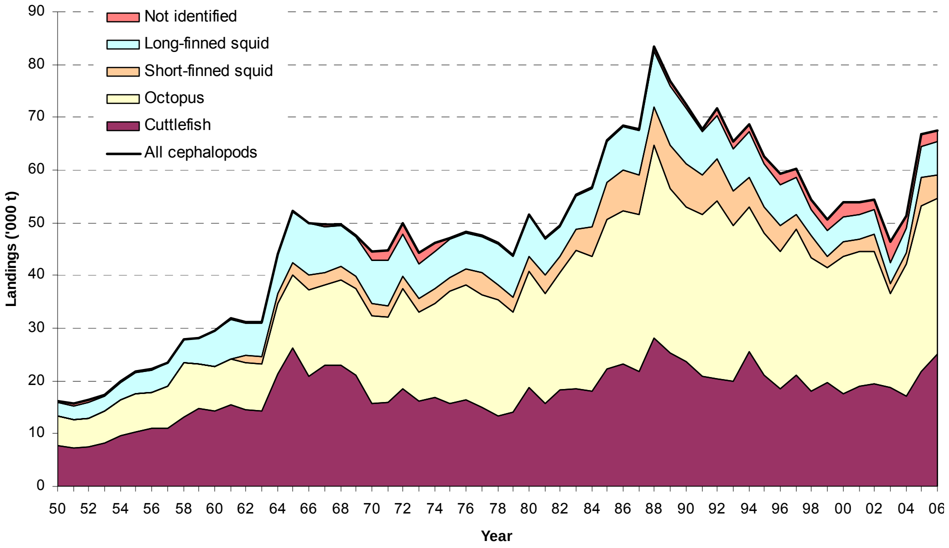


Figure 4.1.4. Annual cephalopod landings from the Mediterranean by taxon, 1950–2006.

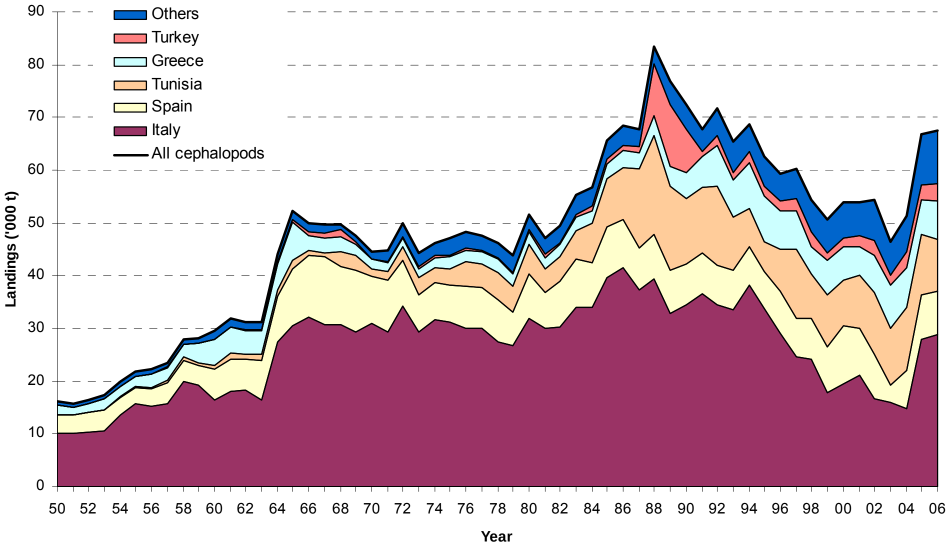


Figure 4.1.5. Annual cephalopod landings from the Mediterranean by country, 1950–2006.

4.2 European cephalopod fisheries: a detailed snapshot, 1998–2002

Cephalopod landings in Europe are usually grouped into four broad commercial categories.

1) Cuttlefish, mainly *Sepia officinalis*, but also some quantities of *S. orbignyana* and *S. elegans*

2) Octopods, mainly *Octopus vulgaris*, *Eledone cirrhosa*, and *E. moschata*

3) Long-finned squid, mainly *Loligo vulgaris* and *L. forbesii*, but also *Alloteuthis media* and *A. subulata*

4) Short-finned squid, *Illex coindetii, Todaropsis eblanae*, and *Todarodes sagittatus*

Landings are, in some cases, classified into narrower categories (e.g. common octopus, common cuttlefish, although it is not clear whether or not the classification is always accurate), but are also sometimes grouped into broader categories (e.g. "squid" or simply "cephalopods"). The most important fishing gears for catching cephalopods are trawl, purse-seine, and "other gears" (mainly gear carried by traditional multipurpose fishing boats, e.g. traps, setnets, and jigs).

Data on cephalopod landings from fishing areas in the Northeast Atlantic were grouped according to ICES divisions where possible. The Spanish Atlantic coast was divided into two regions: northern Spain (ICES Divisions VIIIc and IXa-North) and Gulf of Cádiz (ICES Division IXa-South). For the Mediterranean, data are presented for the Spanish Mediterranean coast (General Fisheries Commission for the Mediterranean (GFCM) Geographical Sub-Areas GSA01, 05, and 06, excluding Balearic Islands ports), Italy, and Greece.

4.2.1 Gear category contribution by species and general trends in landings

The two most important gear types for the capture of cephalopods are trawl gears and "other gears". Purse-seine captures, in comparison, are minimal. Trawling is responsible for the highest landings in European waters of cephalopod species, except octopods, which are landed in equal quantities by trawling and by inshore "métiers" grouped within "other gears" (Figure 4.2.1). However, the importance of "other gears", especially the various inshore "artisanal" métiers used to catch squid, cuttlefish, and octopus in southern Europe, is likely to be underestimated in official statistics. This is because not all catches pass through monitored markets, and they are also of considerable socio-economic importance in terms of providing employment and income in coastal fishing communities (Shaw, 1994; Pierce, 1999).

Total reported annual landings of cephalopods in Europe increased from 46 801 t in 1998 to 97 184 t in 2000, and decreased to 82 534 t in 2002, with cuttlefish and octopods being the dominant groups landed. Long-finned and short-finned squid represented a smaller fraction of the total landings. Landings of both cuttlefish and octopods also increased from 1999 to 2000 (from 37 531 to 41 159 t, and from 37 974 to 42 342 t, respectively) and decreased from 2000 to 2002 (to 35 297 t and 32 672 t, respectively). Total landings of long-finned and short-finned squid peaked in 1999 at 12 160 t and 7061 t, respectively, decreased until 2001, and increased slightly in 2002 (Figure 4.2.2).

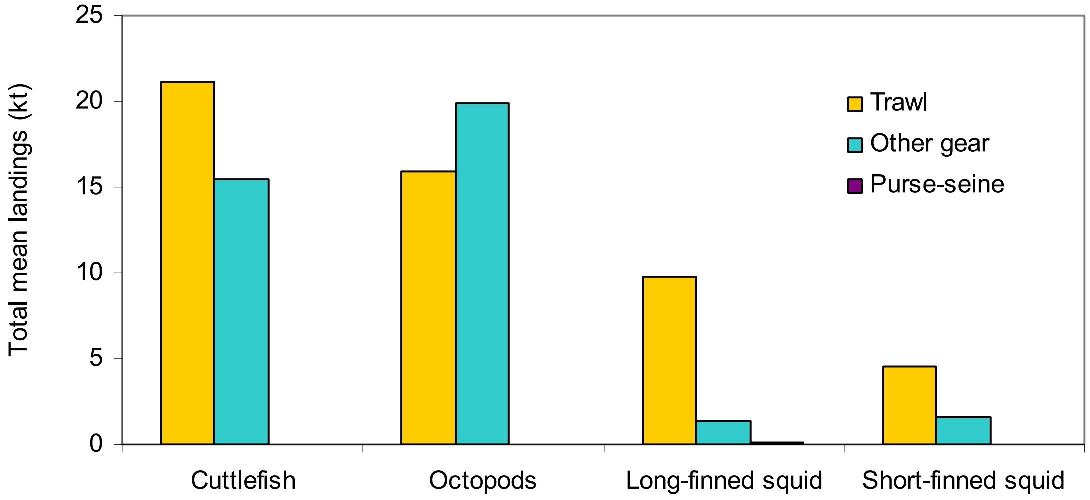


Figure 4.2.1. Average annual landings of cuttlefish, octopods, long-finned squid, and short-finned squid in Europe by gear type, 1998–2002.

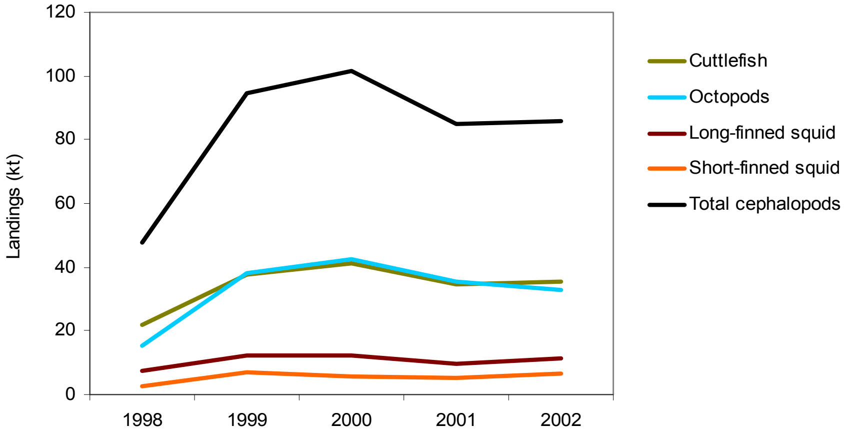
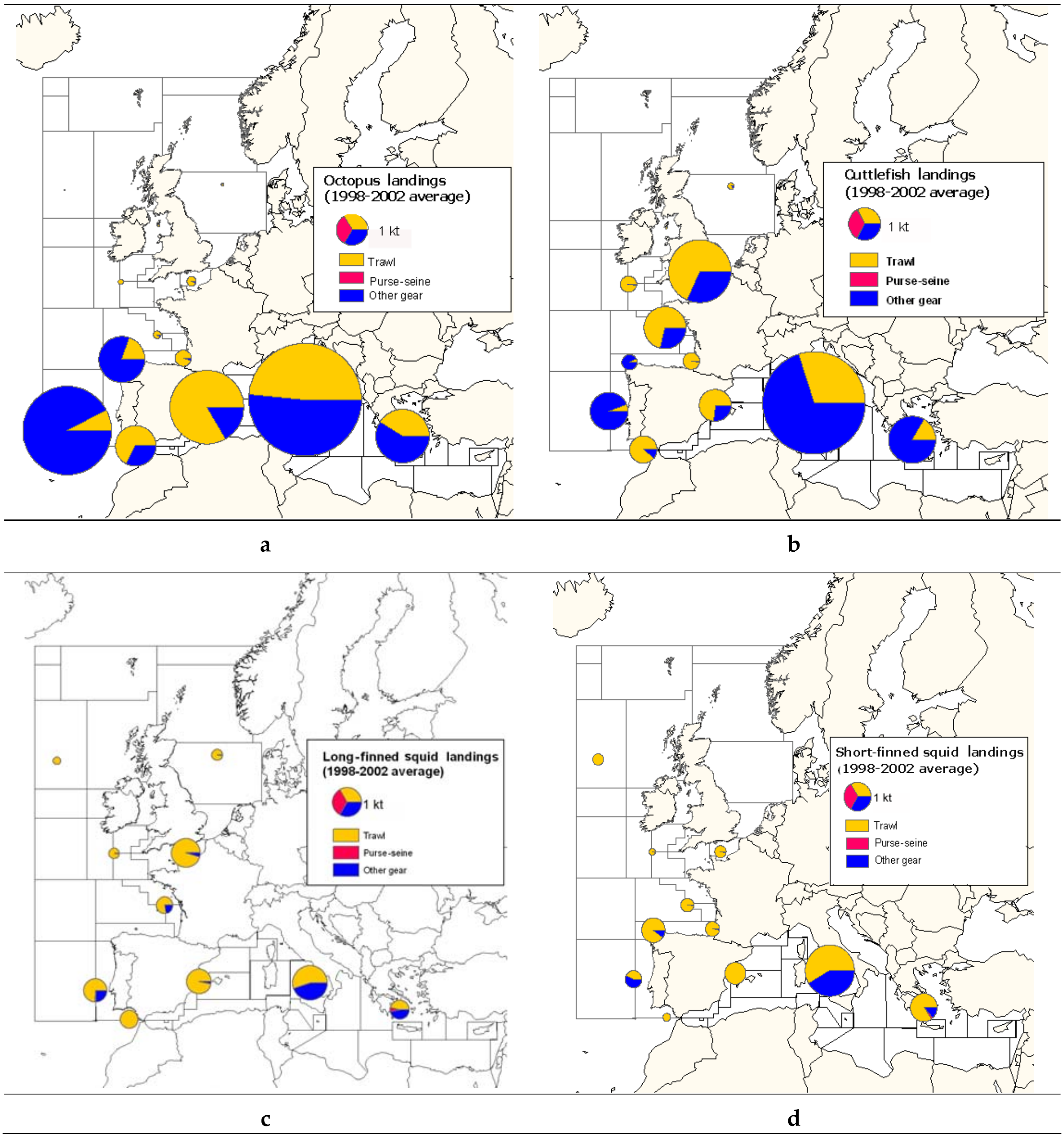


Figure 4.2.2. Total landings of cephalopods in Europe, 1998–2002.

4.2.2 Geographical variation in species landings and shares by fishing gear categories

The main areas of capture for cuttlefish and long-finned common squid during 1998–2002 were the English Channel, Bay of Biscay, and Italian waters, where French and Italian fisheries yielded the highest landings (Figures 4.2.3a and c). For octopods, the highest landings were registered by Portuguese and Italian fisheries along the western shelf of the Iberian Peninsula and in the central Mediterranean, respectively (Figure 4.2.3b). For short-finned squid, the main areas of capture were located in the Mediterranean Sea, with highest quantities landed by Italian and Greek fishing fleets. The Italian fleet's average landings, amounting to 3501 t, were approximately tenfold greater than those of other European fleets in the Northeast Atlantic (Figure 4.2.3d).

Long-finned and short-finned squid are taken either exclusively or mainly by trawling, although other gears contribute substantial proportions of landings in Portuguese (ICES Division IXa), Italian, and Greek waters (Figure 4.2.3c and d). Inshore fishing fleets, using mainly specific trammelnets, traps, and pots, land the majority of cuttlefish and octopod catches off the north and west coasts of the Iberian Peninsula (ICES Divisions VIIIc and IXa), as well as in the central and eastern Mediterranean Sea (Figure 4.2.3a and b). In the other parts of Europe, trawling contributes more than 60% of the landings of these species.



a b

c d

Figure 4.2.3. Averaged landings of (a) cuttlefish, (b) octopods, (c) long-finned squid, and (d) short-finned squid in European waters by geographic region, 1998–2002.

4.3 Fishing methods

The most commercially important cephalopod species inhabiting the neritic zones of European countries are targeted by inshore fishing fleets using a variety of fishing gears (Table 4.3.1), which are generally grouped, for fisheries statistics purposes, under the category "other gears". Passive selective gears, including static nets, traps, and pots, are used in directed fisheries for cuttlefish and octopus, whereas multispecies gears, including different kinds of seinenets and inshore trawlnets, are used for seasonally targeting squid and cuttlefish. Brief descriptions of the most important "métiers" targeting cephalopods are presented below, by species, mentioning their particular characteristics and relative importance by geographic area.

4.3.1 Cuttlefish métiers

Trammelnets are widely used in most southern European countries for the exploitation of common cuttlefish (Table 4.3.1). These nets are typically 1.5–2.5 m high and 50–100 m long (per piece of net), with a mesh size of 300–460 mm for the outer panels and 54–80 mm (stretched mesh) for the inner net. These traditional fisheries are seasonal and are related to the massive inshore spawning migration of *Sepia officinalis*. The operation of these nets to catch cuttlefish usually extends from late winter to early autumn, depending on the availability of the resource as well as the seasonal abundance of other commercial species (e.g. shrimp, sole) that are also targeted on inshore fishing grounds (Arnáiz *et al.*, 2001; Lefkaditou *et al.*, 2004). These fisheries are of primary importance for inshore fishing fleets, particularly in areas like Galicia (ICES Division IXa-North), where cuttlefish catches represent ca. 70% of total catches in the multispecies gillnet fishery (Rocha *et al.*, 2006). Short-term studies of cephalopod fisheries in the Mediterranean Sea have also demonstrated that medium-mesh trammelnets contribute the major part of cuttlefish catches by small-scale fishing fleets operating in the northeastern Mediterranean and the Ligurian Sea, whereas in the Catalan Sea, they share equal importance in landings with traps (Belcari *et al.*, 2002b).

Traps are the dominant gear for the capture of cuttlefish in the Algarve (south Portugal; Carneiro *et al.*, 2006) and also contribute almost half of cuttlefish landings from inshore fisheries in the coastal zones of Basse Normandy (ICES Division VIId, France) and Catalonia (northwestern Mediterranean, Spain), where their importance has increased in recent years (Belcari *et al.*, 2002b; Denis and Robin, 2002). Traps ("nasa de choco") are also used to catch cuttlefish in the interior waters of the Galician rías (northwest Spain).

Traps are round or rectangular, comprising an iron or wooden frame lined with nylon net, with one to four openings (Figure 4.3.1); they can be set individually or in groups of 5–30 roped together. In Normandy, each trap is weighted with cement, to ensure that it remains on the bottom, and baited with one or several live cuttlefish, which attract others into the trap (Madelaine and Aquab, 1991). Traps used in Portugal are weighted and can be baited or unbaited. They are mainly operated near or within the major river and lagoon systems, most of which are located in the area influenced by the Tagus and Sado rivers (Lisbon and the Tagus) and in the Algarve. Traps operate mainly in spring (March–June) when mature adult cuttlefish concentrate inshore to spawn. During the breeding season, it is also common to insert branches of *Cytisus* sp. (broom) into the traps to attract spawning females.

Table 4.3.1. Landed cephalopod species by region (including ICES divisions) and specific fishing gears used in inshore fisheries, in rank of regional importance. Fishing gears by region are in red when the importance of their contribution is confirmed by official fisheries statistics (continued).

	France	United Kingdom		Portugal	Greece
	VIId–e, VIIf–k, VIIIa--b, VIIId	Scotland (IVa,VIa)	England and Wales (VIId–k)	(IXa)	Eastern Mediterranean (GSA20, 22, 23)
Sepia officinalis	Traps Inshore trawlnets		Gillnets Trammelnets (VIId–e) Pots Dredges	Traps Trammelnets Gillnets	Trammelnets Boat-seine with bag
Octopus vulgaris *Eledone cirrhosa* *Eledone moschata**	Trammelnets		Dredges Devon spinners Pots	Traps Clay pots Plastic pots Trawlnets	Fykenets Pots Trammelnets Devon spinners Boat-seine with bag
Loligo vulgaris *Loligo forbesi*		Inshore trawlnets (IVa)	Scottish fly-seine Dredges Hand-jigs Pots Driftnets	Trawlnets Hand-jigs	Boat-seine with bag Trammelnets Hand-jigs Purse-seine
Illex coindetii *Todaropsis eblanae* *Todarodes sagittatus*	Gillnets (VIIId)		Purse-seine Scottish fly-seine	Trawlnets Trammelnets Gill-nets	Trammelnets Purse-seine Hand-jigs

* only in IXa-South and the Mediterranean

Table 4.3.1. (continued)

	Spain				**Italy**
	Basque Country (VI, VII, VIIIa–d)	Galicia, Asturias and Cantabria (VIIIc, IXa-North)	Gulf of Cádiz (IXa-South)	Western Mediterranean (GSA01, 05, 06)	Central Mediterranean (GSA09–11, 15, 17–19)
Sepia officinalis *Sepia orbignyana* *Sepia elegans*		Trammelnets Gillnets Traps	Trammelnets Hand-jigs	Traps Trammelnets	Trammelnets Gillnets Traps Pots Fykenets
Octopus vulgaris *Eledone cirrhosa* *Eledone moschata**		Traps (IXa-North)	Traps Clay pots Devon spinners	Clay pots Traps Devon spinners	Trammelnets Combined gillnet-trammelnets Pots Devon spinners
Loligo vulgaris *Loligo forbesi* *Alloteuthis media* *Alloteuthis subulata*		Boat-seine with bag Hand-jigs		Hand-jigs Trammelnets Purse-seine	Hand-jigs Combined gillnet–trammelnets
Illex coindetii *Todaropsis eblanae* *Todarodes sagittatus*	Gillnets (VIIId)				Hand-jigs (for *T. sagittatus*)

* only in IXa-South and the Mediterranean

a

b

c

d

Figure 4.3.1. Cuttlefish traps: (a) rectangular and (b) round traps used in Basse Normandie (Bay of Seine and West Cotentin); traps made from (c) iron ("covo") and (d) wire ("murejona"), used in the octopus and cuttlefish fisheries in the Algarve.

Trawlnets constitute one of the two main gears used in the coastal zone of Basse Normandie (ICES Division VIId) for the capture of cuttlefish. During spring, inshore bottom trawlers represent 48% of the fishing fleet, the remainder being vessels using traps. Trawlers use nets with a diamond-shaped mesh of 80 mm (Council Regulation (EC) No. 850/98). Inshore bottom trawling occurs mainly in spring (March–June), when mature adults concentrate inshore to spawn, but continues into August–September as trawlers are able to catch 1-year-old immature animals in summer and juveniles from the 0-group recruited to the fishery in autumn before their offshore migration in winter (Boucaud-Camou and Boismery, 1991).

Fykenets consist of an external net and two internal cone-shaped bags supported by plastic rings (Ferretti *et al.*, 2002) and are becoming popular in Italy for the capture of cuttlefish. However, it is not yet possible to evaluate this fishery´s contribution to total Italian cuttlefish landings. These nets are usually placed on the seabed, with the opening oriented against the current, and tied to each other by a rope (Figure 4.3.2).

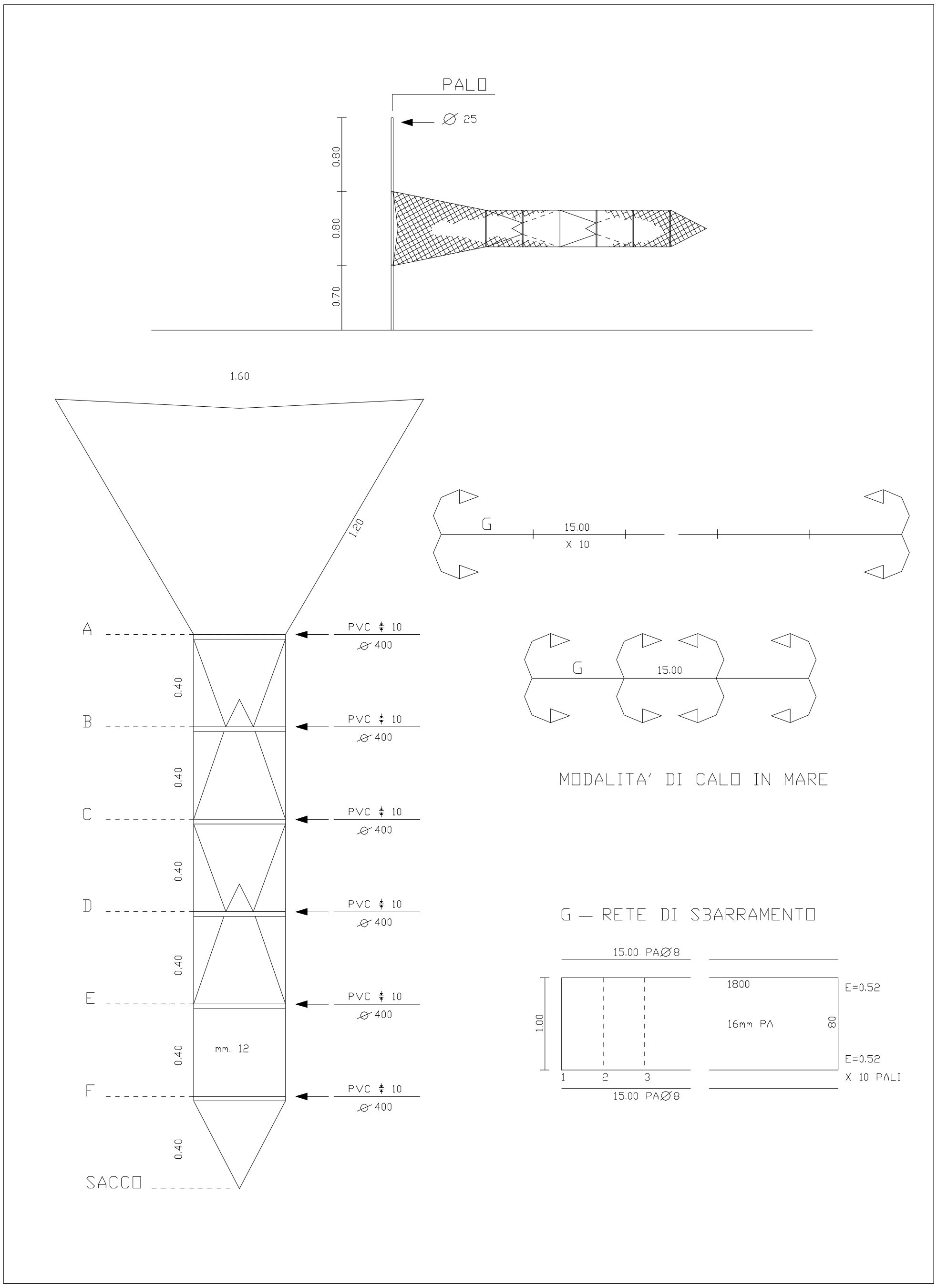


Figure 4.3.2. Italian fykenets ("cogolli"), used for the capture of cuttlefish (from Ferretti *et al.*, 2002).

Jigs and Devon spinners are also important in nearshore cuttlefish catches in the Algarve (southern Portugal), although the former is predominantly a squid-catching gear, and the latter an octopus-catching gear (Carneiro *et al.*, 2006).

4.3.2 Octopus métiers

Pots made of clay or PVC/plastic in different shapes and sizes (Figure 4.3.3) are typically used for the octopus (*Octopus vulgaris*) fishery along south European coasts. This fishing method is based on knowledge of octopus behaviour. The species is very territorial and "hermit-like", constantly looking for shelter to use for its "home/nest". Clay pots have been deployed in the Iberian Peninsula since at least the 15th century

(Godinho, 1985), being one of the main gears used for octopus capture particularly along the west and southeast coasts (Sánchez and Obarti, 1993; Pereira *et al.*, 1997; Tsangridis *et al.*, 2002). Recently, plastic pots with different shapes have been introduced with great success along the Portuguese and northeast Greek coasts. They have also been introduced into Galicia (northwest Spain), although their use is not authorized.

Pots are used in sets (longline type; Figure 4.3.4). The sets of clay pots used in the Algarve, Gulf of Cádiz, and Mediterranean coast of Spain comprise 100–200 pots, and the length of the mainline is between 1400 and 2000 m. Each clay pot has a rope around its neck, with a slipping knot, and the pots are connected to the mainline at intervals of 10–15 m. At each end of the mainline is a cable that connects the anchor to the buoy on the surface. The gear is set in areas of sandy bottoms at depths of no more than 100 m. The pots used in shallower waters are 21 cm in height, with a 10 cm diameter opening. Bigger pots are used for medium depths (27 cm height, 10 cm diameter opening) and deeper waters (32 cm height, 13 m diameter opening). Every pot has to be identified with the name of the boat, the name of the port where the boat is registered, and the type of fishery for which they are registered ("local" or "coastal"). Pot longlines can be deployed in various ways, e.g. forming a labyrinth of lines containing 50–70 clay pots or placed in lines parallel with the coastline.

The sets of plastic pots used in the Thracian Sea (northeastern Mediterranean) since 1992 consist of a mainline, 4–6 km long, and 500–600 pots (Lefkaditou *et al.*, 2007). The pots usually consist of PVC cylinders 30 cm high and 14 cm in diameter, closed at one end with cement, which also serves as a weight to keep the pot on the seabed. The pots are attached to the mainline either directly or by short lines of 0.5–1 m, which facilitates their lifting. Floating buoys are placed every 50 pots to demonstrate the direction of the "longline". Fishing depth is 10–70 m and soaking time is 5–10 days (Adamidou, 2007). Pots remain in the sea during the entire fishery season, being pulled up by fishers periodically to collect the catch. To take the octopus from the pot, fishers spray bleach into the pot through a small hole in the bottom, or place the pot in a pail of freshwater.

Pot métiers operate year-round, except during periods of fishery closure that have been implemented for these gears by regional fishery regulations. Seasonal peaks of catches vary between different regions, depending on the availability of the resource and the fishing fleet strategy (Pereira *et al.*, 1997; Lefkaditou *et al.*, 2004). The seasonal increase observed in clay pot catcher per unit of effort (cpue) in the southeast Spanish fishery coincides with a seasonal peak in the incidence of mature individuals (Sánchez and Obarti, 1993). The exploitation pattern can vary spatially and temporally, depending on the biology of the species (spawning season, recruitment, feeding grounds, etc.) and the predominant environmental conditions (mainly related to the meteorological situation).

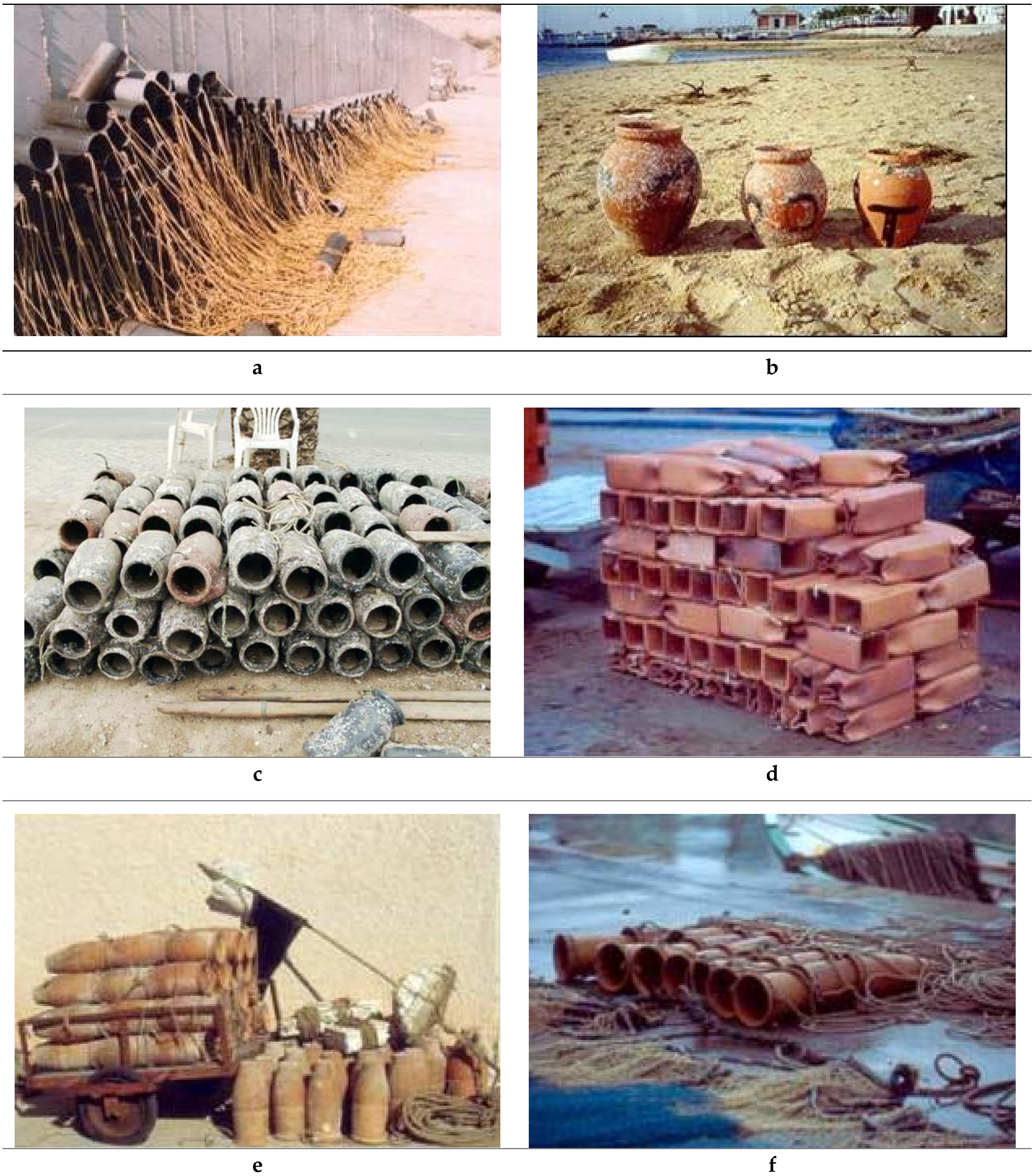


Figure 4.3.3. Octopus pots: (a) PVC pots used in Greece; (b) three sizes of clay pots ("alcatruzes") from Portugal; (c) plastic pots from Portugal; (d, e, f) various types of pots used along the Catalan coast in the common octopus fishery.

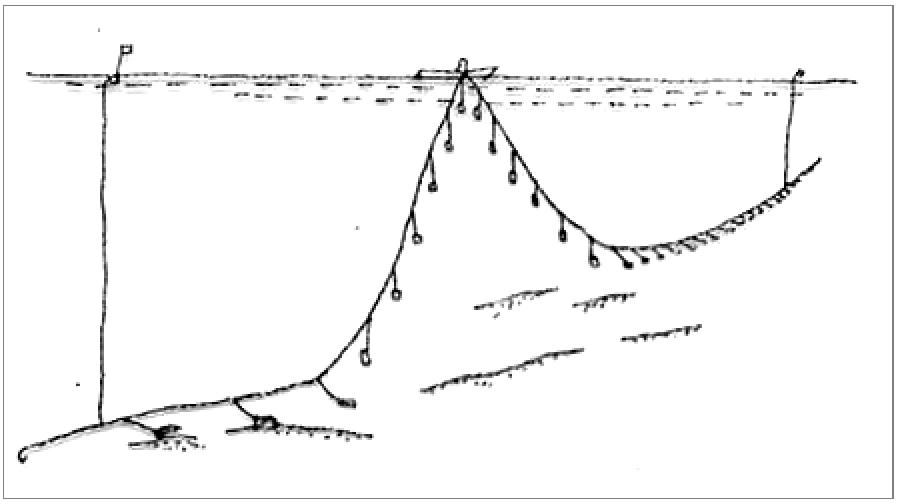


Figure 4.3.4. Schematic diagram of the setting of clay pots ("alcatruzes") and iron traps ("covos").

A problem associated with many fishing gears is their ability to continue to capture animals after the gears have been lost, a process called "ghost fishing" (Hubert, 1996). When traditional clay pots are lost, they not only become a refuge for the octopus but also provide a substrate for a variety of other organisms. Thus, they are one of the most "environmentally friendly" fishing gears. Even broken, they continue to serve as substrata for the establishment of a variety of organisms, thus playing an important role in the local trophic chain, especially in an area such as the eastern Algarve, which lacks natural hard bottoms. More recently, however, the traditional clay pot has been replaced by plastic pots of different forms. Studies are being carried out to determine the environmental effects of plastic pots, as well as their economic feasibility.

Traps of different designs (see Figure 4.3.1c and d) constitute the dominant gear for the octopus fishery in Portugal and northwest Spain. This métier operates in depths of less than 50 m. A seasonal trend has been observed in effort, yield, and median depth of fishing — all of which decrease in summer and increase in winter (Bañón *et al.*, 2007). Along the Galician coast, where an inshore fishing fleet of 1561 vessels operates (data from 2004), 89% of common octopus landings derive from octopus traps, whereas 4% comes from traps for small edible crab, 4% from gillnets, and 1% from hook gears. In Portugal, until the 1970s, catches of octopus were traditionally concentrated in the Algarve region, which yielded 70–80% of the total national octopus landings. In recent years, the Algarve region has contributed no more than 40% of the national octopus landings, reflecting changes in the distribution of catches along the Portuguese coast.

Fykenets of two or three chambers, made of netting with hoops, have been used in Greece for fishing octopus since 1982. The catching system (Figure 4.3.5) consists of two fykenets connected by a 4 m leader net. The hoop diameter ranges between 38 and 60 cm, and the mesh size is 20–22 mm from knot to knot (Adamidou, 2007). One or two fishers with a boat of 22 t or less can operate 200–2000 pairs of fykenets (Figure 4.3.6). Lines of 50–100 pairs of fykenets are set parallel with the coastline. Soaking time is 10–15 days. This method is mainly used in shallow water, ca. 8–30 m in depth, on bottoms covered by seagrass. *S. officinalis* and *Eledone moschata* are bycatches in this fishery. The fykenet métier operates for nine months of the year, the fishery being closed during July–September. Maximum cpue values have been observed for fykenets operating in the western Thracian Sea during late spring–early summer, similar to the increase in cpue seen for octopus traps in the Canary Islands (Hernández-García *et al.*, 1998b), and in both cases coinciding with the season of maximum incidence of mature individuals.

Recent investigations, carried out as part of EU-funded study projects (96/54, 97/54) have confirmed that this gear contributes the major part of octopus landings by the small-scale fishing fleet in the Thracian Sea (northeastern Aegean Sea). This is where the most intensive exploitation of octopus occurs, yielding ca. 60% of the total national octopus landings (Lefkaditou *et al.*, 2001, 2007).

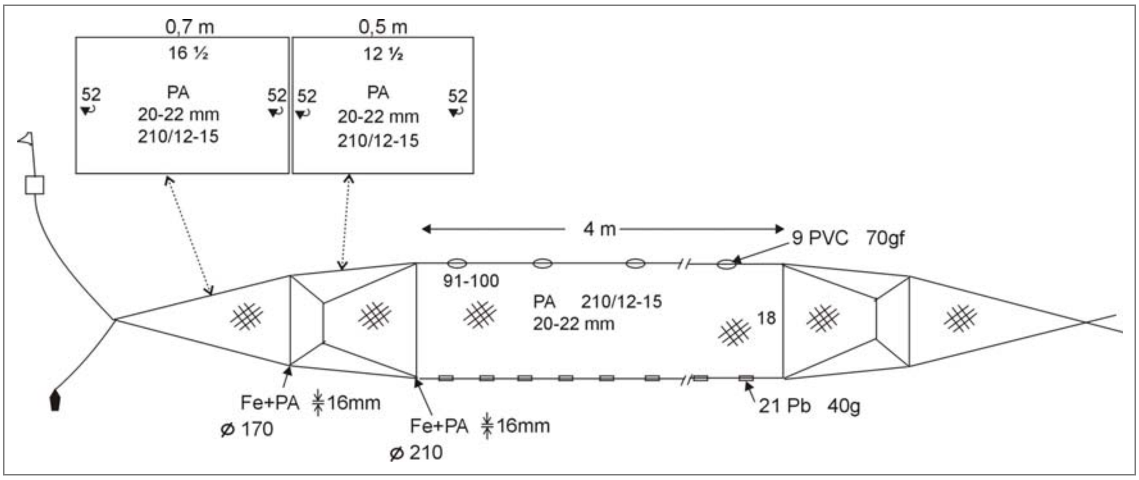


Figure 4.3.5. Diagrammatic representation of the fykenets used for the octopus fishery in the northern Aegean Sea (from Lefkaditou *et al.*, 2003b).

Figure 4.3.6. Winches, (left) mechanical and (right) hydraulic, specially designed for hauling fykenets by small-scale fishing vessels from Thasos Island (Greece).

Devon spinners of very diverse types, called “salagia” (Greek), “polpaia” (Italian), “zagaia” or “piteira” (Portuguese), "chivo" or "pulpera" (Spanish), are used to fish for octopus. They consist of a wooden or metal pole, with between one and four crowns of hooks either welded or tied to one end (Figure 4.3.7), and a ring at the other end, joined to a handline, permitting fishing manoeuvres. This fishing gear is used with bait, a weight made of lead (lead sinker), and a lure, which can be variously shaped and made of aluminium foil, to attract octopus. When used from an anchored boat, the fisher allows the Devon spinner to reach the bottom and then pulls the handline repeatedly to drag it along the bottom. In a moving boat, the fisher only has to hold the handline because the device will be dragged along the bottom. Each fisher usually uses more than one of these devices. The fishing strategy is mainly determined by the type of bottom substratum and by the predominant currents in the area. Each fishing trip requires searching for areas of high concentrations of octopus and, because the fishing manoeuvres require drifting with the currents, the vessels can sail for several miles. In practice, the vessels fish on rising and ebb tides, and never in still tide, because the baited hand-jig must move over the bottom to attract the octopus. The importance of these gears has not been generally assessed, but certainly depends on local fishing traditions.

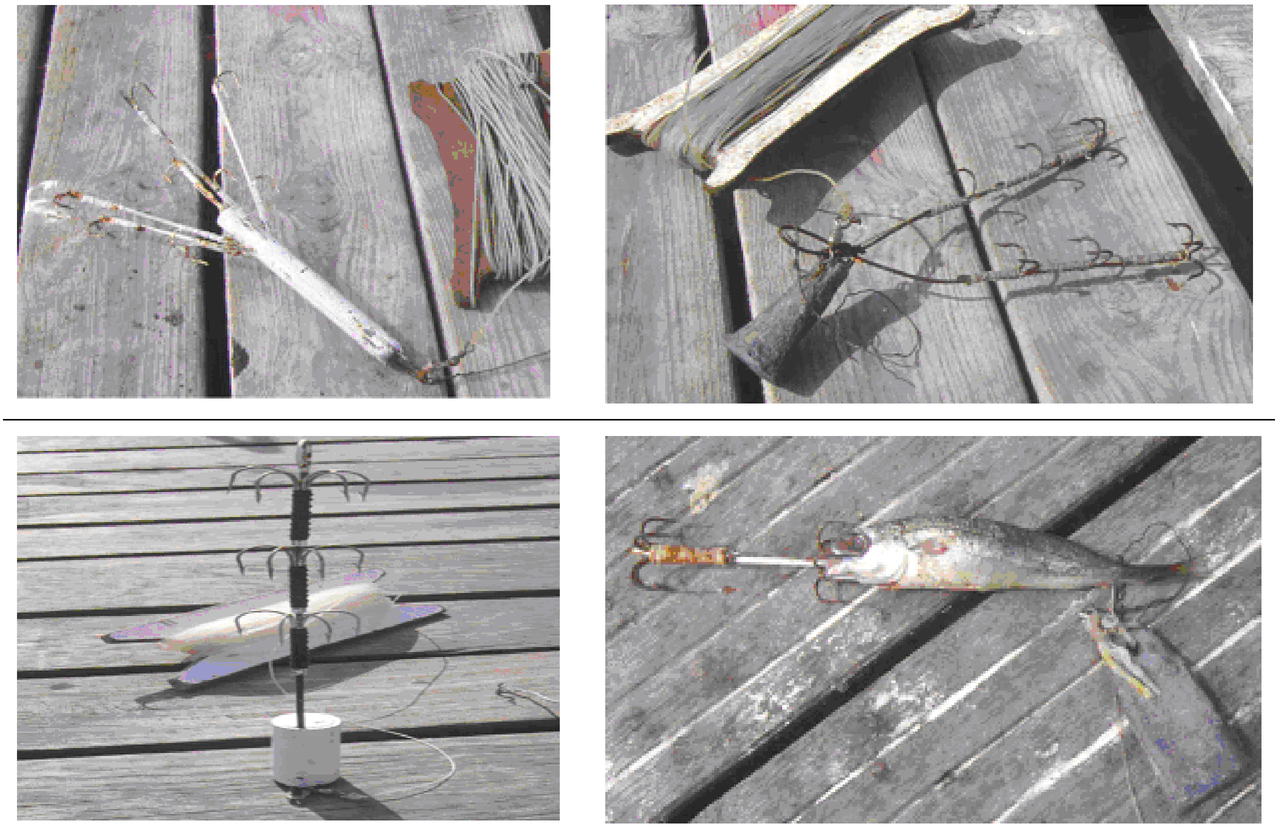


Figure 4.3.7. Different types of Devon spinners used for octopus fishing by artisanal vessels in the Gulf of Cadiz.

In the Gulf of Cadiz, the "chivo" fishery is quite important; it begins in autumn, the season in which octopus usually become sufficiently available to make it commercially exploitable. During this season, octopus attain a mean weight of 1.5 kg. If these conditions are not met, and fishing for other species is more commercially profitable, there is no "chivo" fishery. Once the octopus fishery starts to obtain good yields, this fishing method continues until the resource begins to decrease, which is ca. May and June, after the peak spawning of the species.

At the mouth of the Tagus estuary in Lisbon, a bimonthly fishery occurring on spring tides attracts a multitude of small vessels. These vessels, manned by one or two persons, conduct a non-professional fishery. This is a very significant fishery locally, which can produce in excess of 30 kg person^{-1} d^{-1}. Thus, it is so profitable that many people will take one or two days a month off work to go fishing. Overall, the fishery can yield ca. 10 t d^{-1} on each tide.

4.3.3 Squid-targeting métiers

Inshore trawlnets, lightly constructed with 200–300 mm mesh near the fishing line, tapering to 80 mm in the bag and with a 35–40 mm codend, are used to catch *Loligo forbesii* in Scotland. Although squid is mostly a bycatch in UK waters, over the last decade, a directed trawl fishery for *L. forbesii* has been developed in the Moray Firth (ICES Division IVa), yielding a substantial proportion of the Scottish squid landings. *Loligo forbesii* is the most important fished cephalopod in Scottish (UK) waters and the only cephalopod for which there is a reliable market (see Young *et al.*, 2006a).

Various modifications of demersal trawling gears for squid fishing have been tried. One aim is to keep the net just off the seabed, which is achieved by the use of several 30 cm chains hung at equal distances from the groundrope and enough floats on the headline to give the net neutral buoyancy. The net is considered to be fishing correctly if just the lower few centimetres of the chains are polished – indicating contact with the seabed. The main Scottish fishery for *L. forbesii* occurs in coastal waters. It commences around the middle of September and continues for around eight or nine weeks, with a marked seasonal peak around October–November, corresponding to the occurrence of prebreeding squid (Howard, 1979; Howard *et al.*, 1987; Pierce *et al.*, 1994a, 1994b). The directed fishery tends to start in July or August (Young *et al.*, 2006a). Spawning grounds have not yet been documented, although eggs are often reported from inshore creel lines, and almost all records of eggs arise from coastal waters (see Lum-Kong *et al.*, 1992; Viana *et al.*, 2009). Previous analysis of spatial patterns in fishery data suggested that *L. forbesii* move from the west coast of Scotland into the North Sea to spawn (Waluda and Pierce, 1998; Pierce *et al.*, 2001). However, more recent and extensive analysis by Viana *et al.* (2009) casts doubt on this being a general pattern in all years, pointing to a more usual pattern of expansion from a core area along the north coast of Scotland. Nevertheless, it is very likely that the Moray Firth includes spawning grounds for this species.

At the beginning of the season, catches are best in shallow water over hard (even rocky) ground close inshore at ca. 10 m depth. As the season progresses, the fishery gradually moves farther offshore to a sandy/muddy bottom in waters of ca. 55 m depth. Better catches have been reported in areas that experience stronger tidal currents. Large vessels with lengths of 14–21 m and 200–500 horsepower (hp; 373 kW), with crews of three to five men, as well as small vessels less than 10 m in length with ca. 100 hp (75 kW) and operated usually by one person, are involved in this fishery. Larger vessels tend to carry two sets of gear and fish at night for *Nephrops norvegicus*, changing to squid gear during the day, whereas smaller vessels exclusively target squid during the season. At the peak of the fishery, squid catches for a 1-day trip average ca. 24 and 9 boxes (a box typically weighs ca. 40 kg) for the large and small vessels, respectively. The resulting catch in the 2000 fishery was usually 100 % squid and free of sediments and, therefore, did not require washing, which could devalue the catch because of the loss of ink. In autumn 2003, this fishery produced exceptionally high landings, to the extent that squid was one of the most important species in the Fraserburgh and Peterhead fish markets, with up to 65 trawlers involved in the fishery at its peak.

Although commonly catching squid as a bycatch in the 1980s and 1990s, the Scottish fly-seine is now less popular in Scotland, with most boats having switched to trawling.

Boat-seines with bag are commonly used along the Spanish and Greek coasts, seasonally targeting *L. vulgaris* in certain regions where it is concentrated in coastal fishing grounds. The boat-seine with bag (EC, 1987) consists of a codend, bag, shoulders, wings, and gussets (Figure 4.3.8). The “boliche” or “chinchorro” used in Spain has two wings, each 75 m long, and the codend is 10 m long with a mesh size of 18–60 mm (the minimum legal mesh size is 17 mm). More than 200 vessels were authorized to fish with "boliche" along the Galician coast from 1988 to 2003. *Loligo vulgaris* was the most important catch (45.5%) for "boliche" gear during 1999–2003. *Alloteuthis* spp. (*A. media* and *A. subulata*) constituted 2.3% of the catches. A recent study of this gear has confirmed its low selectivity (nearly 80% of squid catches are between 4 and 10 cm in length), mainly the result of incorrect assembly of the gear, but also because of its use in inappropriate places and periods (UTPB, 2005).

The Greek "pezotrata" or "vintzotrata" is operated very close to shore, the boats anchoring within 70 m of the coast, as specified by Greek regulations. Regulations also state that the hauling ropes cannot be longer than 700 m (Regulation of 2007) and the stretched mesh size cannnot be smaller than 16 mm. Since 2005, no fishing has been allowed from 1 April to 30 September. The fishery currently numbers some 360 vessels, employing ca. 1500 persons. Its technical characteristics vary considerably by geographic region (Adamidou, 2007). The length of the net ranges from 200 to 440 m and the perimeter of the mouth opening from 58 to 135 m. Stretched mesh sizes range from the legal minimum of 16 mm at the codend to 1000 mm at the wings. Two to ten hauling ropes, each 100 m long, are used on each side of the net. Geomorphology of the fishing area and target species are the main factors that fishers take into consideration for efficient and profitable operation of the gear. Adjustment of the gear in different conditions is achieved by changes in the number of hauling ropes and in rigging (Adamidou, 2007). This métier is separately registered in Greek fisheries statistics and yields 25–30% of the total national catches of *L. vulgaris*. Although it is a multispecies gear, it could be considered to undertake specific hauls targeting *L. vulgaris,* especially in certain fishing areas such as the Thracian Sea, where *L. vulgaris* is the second most important species in terms of sales for this gear (Lefkaditou and Adamidou, 1997).

Analyses of monthly variation in cpue demonstrate a peak during early autumn–winter that is related to the prespawning and spawning aggregation of *L. vulgaris* on inshore fishing grounds. The gradual decline of *L. vulgaris* catches during spring is most probably the result of the high level of post-spawning mortality (Lefkaditou *et al*., 1998b; Tsangridis *et al*., 1998). Other cephalopod species caught by beach-seine are *S. officinalis, O. vulgaris*, *E. moschata,* and *Alloteuthis media* (e.g. Sánchez *et al*., 1995).

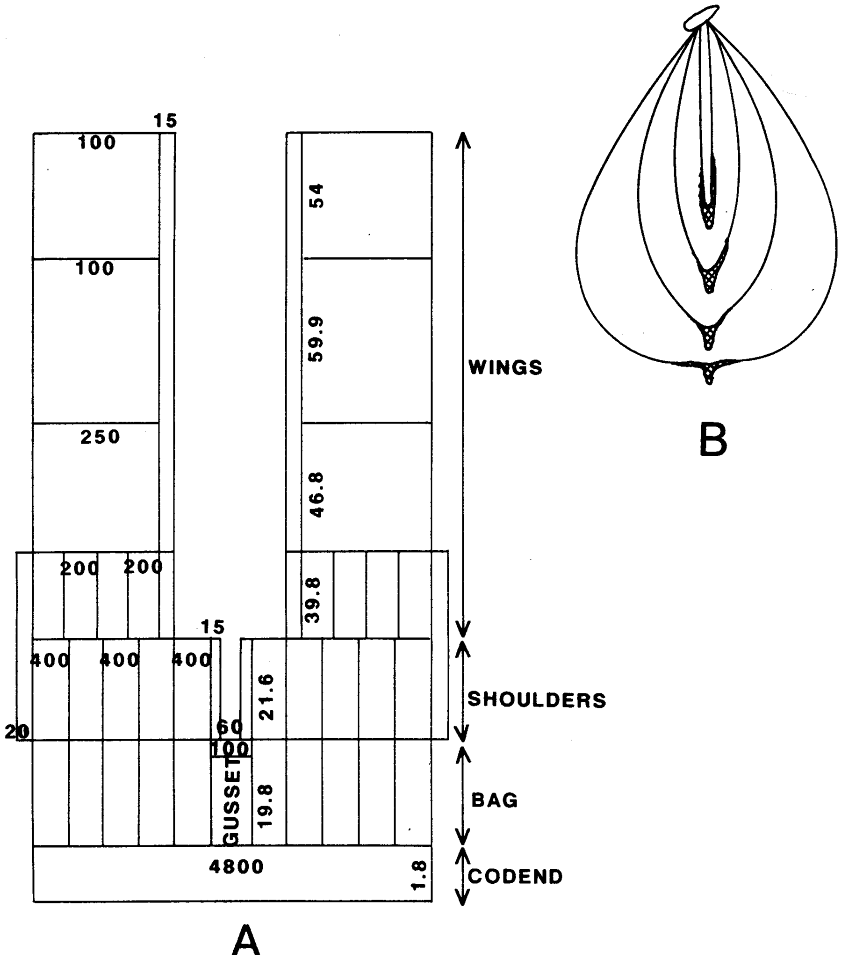


Figure 4.3.8. (A) Scheme of the boat-seine with bag and (B) the fishing operation (from Adamidou, 2007).

Hand-jigs of various types (Figure 4.3.9), named "calamarieres" (Greek), "totanare" (Italian), "palhacinhos" or "toneiras" (Portuguese), and "poteras" (Spanish), are used by artisanal and sport-fishery vessels to catch *L. vulgaris* and *T. sagitattus* (Biagi, 1997; Santulli and Bertolino, 1997). Jigs are not baited and are usually made of lead, painted a light colour, with one to two crowns of metal hooks at one end, and a metal ring on the other end, to which the fishing line is tied. The fisher holds the fishing line, making "jigging" movements to attract the animal. Jig fishing is mostly carried out before sunset or during the night using some kind of light attraction.

Jigs have been used in Scotland to a limited extent in directed squid fishing by small vessels in the Moray Firth and some west coast areas (although currently all directed fishing on squid in these areas is by demersal trawlers; Young *et al.*, 2006a), and also on the south coast of England (Shaw, 1994). In the 1980s, interest in squid jigging was sufficiently high in the UK that a guide to jigging was published (Hamabe *et al.*, 1982) and various trials of mechanized jigging machines for catching *Loligo* spp. were carried out by the Sea Fish Industry Authority and its predecessor, the White Fish Authority (reviewed in Pierce *et al.*, 1994b). Most of these trials met with very little success. For example, in one trial, the few squid taken were all *Todarodes sagittatus*. However, scrutiny of the original reports of these trials raises doubts as to whether the right kind of jig was used for catching *Loligo*, whether the gear was always properly deployed, and whether it was used in areas and at times when sufficient concentrations of squid would have been present to make the method worthwhile.

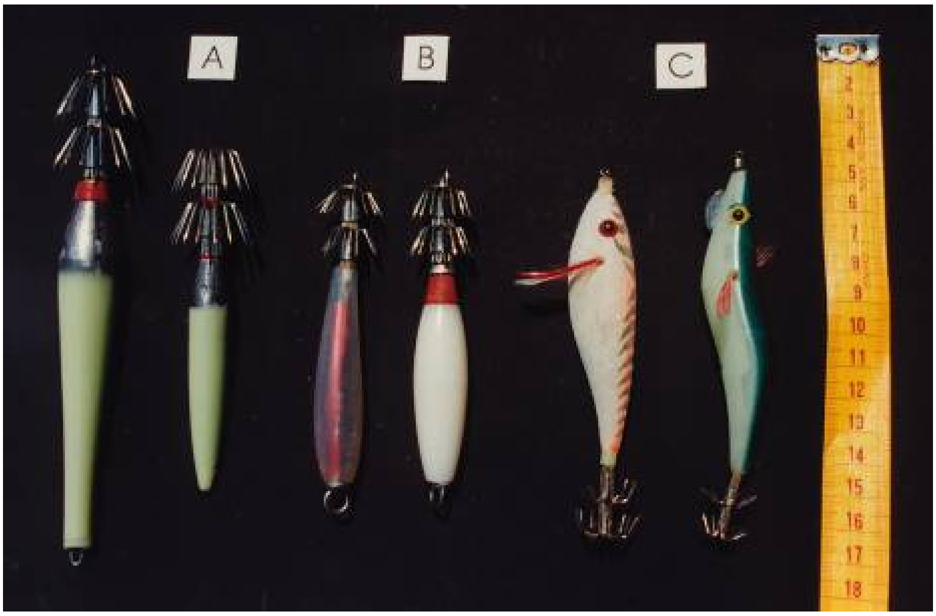


Figure 4.3.9. Jigs of different types used for fishing of *T. sagitattus* (mainly type A) and *L. vulgaris* (mainly types B and C).

4.4 Cephalopod discarding in European waters

Most available information on discards of cephalopods in European waters derives from opportunistic data collection within the framework of studies on general discarding practices of finfish fisheries, covering limited areas (see Figure 4.4.1). Discarding of cephalopods is mainly for economic reasons. However, although there are no landings quotas, some European countries have set minimum landing sizes for commercial species. In practice, sizes are checked at auction sites (and at retail outlets), and it is likely that undersized animals are often used for consumption by the fishers and/or sold directly to restaurants rather than being discarded at sea. Some cuttlefish (*Sepia orbignyana, S. elegans*) and smaller long-finned squid species (*Alloteuthis media, A. subulata*), although constituting important bycatches of trawl fisheries, are usually discarded apart in certain regions in Portugal, Spain, Italy, and Greece. However, they may be landed when the number of specimens justifies their sale and/or they can be mixed with commercial species of the same group (Sartor *et al.*, 1998; Machias *et al.*, 2001; Sendao *et al.*, 2002; Young *et al.*, 2004).

Catches of short-finned squid and *Eledone* spp. are routinely discarded in some regions, such as Normandy, north Spain, and Scotland, because of low abundance or low market demand (Denis *et al.*, 2002; Santurtun *et al.*, 2004; Young *et al.*, 2004).

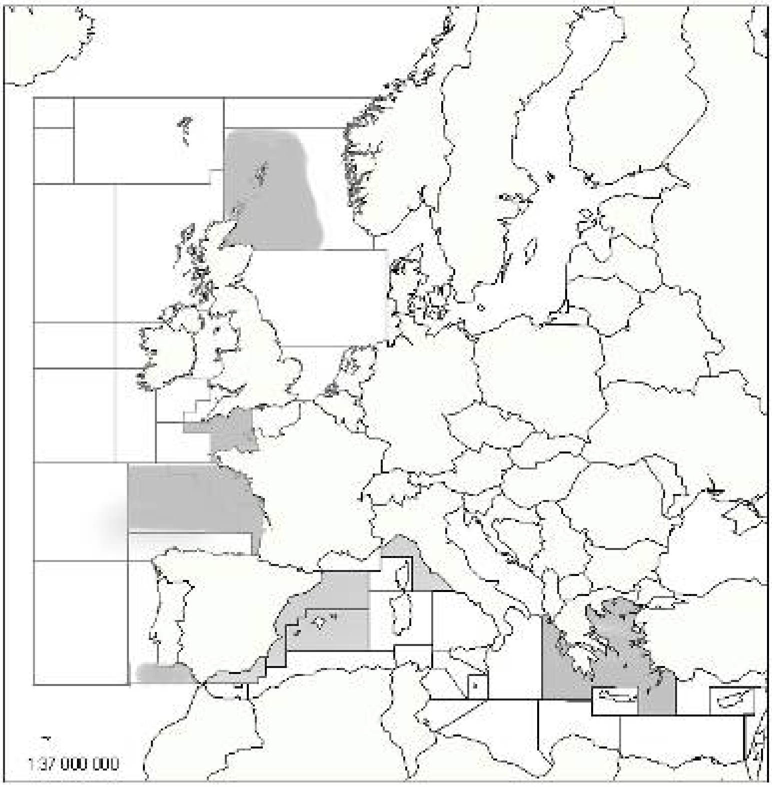


Figure 4.4.1. The geographic areas (shaded) where studies on cephalopod discards have been carried out.

4.5 Socio-economic importance of cephalopod fisheries

For countries such as the UK, France, Spain, Portugal, Italy, and Greece, cephalopods are important fishery resources not only in terms of quantities landed, but also in terms of trade. In addition to fishing and landing cephalopods, these countries deal in cephalopods as import and export products, and three of them land catches of fishing fleets operating outside their European territorial waters. Of the countries involved, Spain is the most active in all aspects of the trade (ranked 12th among the producers of cephalopods in the world), Germany is the smallest producer, and the UK is the least significant consumer, but all of these are net consumers.

Cephalopod imports are largest in countries that also display the highest production. The European market is the most important market in the world for this resource (FAO, 2004).

Cost–benefit analysis for these fisheries is difficult because (according to official statistics) they are mainly bycatch species. In some fisheries, cephalopods are taken as bycatch for part of the year and targeted during the remainder of the year. Some fisheries are totally directed. To compound the problem, many fisheries are very small-scale enterprises, which keep only the most basic forms of accounts and often do not correctly report costs and benefits. Indeed, as much as 50% of the cephalopod landings in some EU countries may never be recorded through official channels (see EC Directorate General for Fisheries, Study Reports: Pierce, 1999; Guerra *et al.*, 2000; Pereira, 2001).

In Portugal, the economic importance of cephalopods is relatively high. In fact, over the years, the landings and their economic value have maintained a significant growth in importance in relation to those of other marine catches, indicating an increasing dependence of the fisheries economy on cephalopod landings.

As cephalopod catches are mainly a result of mixed fisheries, the cost of fishing for cephalopods does not appear to be any different from those of fishing for other resources. In each case, the same means are employed, with only very few exceptions, such as jigs and pots that overall (at least according to official statistics) have little importance. The increased proportion of cephalopods in total landings may be the result of increased relative abundance, and not the result of either an active fishing strategy or increased absolute abundance.

In Portugal and Greece, although the landings of other resources decreased significantly between 1997 and 2003, those of cephalopods demonstrate a slight increase. However, trends in prices of first sale suggest that the importance of cephalopods in relation to other resources did not change.

According to data supplied to ICES, landings in Galician waters (Spain) of octopus species (*Octopus vulgaris*, *Eledone cirrhosa*) and cuttlefish (*Sepia officinalis*) declined between 1998 and 2003, (especially for *Eledone*), but their total value remained fairly stable. The sepiolids, a minor component of landings, declined by ca. 50% during that period. Long-finned squid (*Loligo vulgaris*) demonstrated a clear decline in 2003, also noted in *Alloteuthis subulata*, a species of minor importance but landed in larger amounts than *Loligo vulgaris*. The short-finned squid (*Todaropsis eblanae*) is the only species for which landings remained relatively stable over the period in question, their value increasing slightly. *Illex coindetii*, already a very minor component of landings in 1998, had virtually disappeared in 2003.

A second dataseries for Galicia, based on sales at fish markets (1997–2007), can be obtained from the Department of Fishing and Maritime Matters, Galician Autonomous Community (Consellería de Pesca e Asuntos Marítimos da Xunta de Galicia; available online at http://www.pescadegalicia.com; see also Figure 4.5.1). Amounts estimated from sales were higher than those from landings, but trends were very similar for most cephalopod groups and years. However, some differences were observed. According to the Xunta de Galicia, landings of *O. vulgaris* declined from 1997 to 2000, then increased slightly between 2001 and 2004. Sales of *E. cirrhosa* demonstrated a clear increase over the whole period, opposite to the trend identified from landings data. Sales of *S. officinalis* declined by ca. 50% between 1997 and 2001 but subsequently increased to near the 1997 value in 2007. Differences between the two sources of data could arise because sales data include some cephalopods caught outside Galician waters (e.g. from ICES Subarea VII and Division IXa-Centre. The most important differences were observed in data for *E. cirrhosa*, which is caught mainly in ICES Subarea VII.

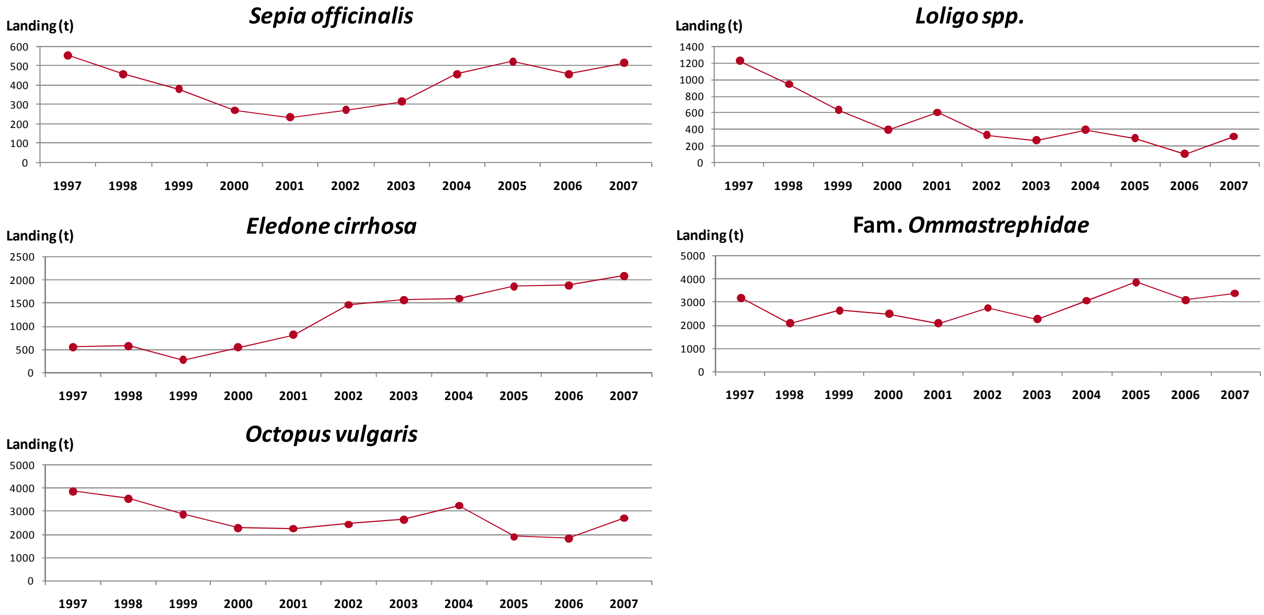


Figure 4.5.1. Trends in cephalopod landings in Galicia based on sales data.

The cephalopod trade is very important in Italy, which is the third major importer of cephalopods in 2002, after Spain and China. Cephalopods accounted for 22% of the imports of fishery commodities in Italy, with a monetary value corresponding to 18% of the total national expenditure on fishery products. This constant increase in imports of cephalopod products into Italy has taken place against a background of steadily decreasing capture production during the last 15 years, whereas, apparently, national consumption of cephalopods continues to increase. The major component of national landings, ca. 54% in 2002 (P. Jereb, pers. comm.), comes from bottom trawlers, but a substantial fraction still depends on small-scale and mixed fisheries, despite the reduced capacity of these fishing categories in recent years. Both activities employ an important number of local fishers in the many small landing places scattered along the Italian coast. In spite of the undoubtedly important social and economic roles of these fisheries, very poor quantitative information exists on them.

In the UK, the most important commercial cephalopod is the cuttlefish (*S. officinalis*), most catches of which are taken in the English Channel. The cuttlefish fishery is based on a combination of trawling and artisanal fishing, the latter exclusively directed at cuttlefish. Long-finned squid are the second-most important category, being landed from most waters around the UK. Most landings of long-finned squid are bycatches, but there is increased targeting, notably by a small-scale directed fishery for *L. forbesii* in the Moray Firth, of new recruits as they appear close inshore in autumn (Young *et al.*, 2006a). Several other cephalopods of potential value are routinely caught by UK fishing vessels, especially the short-finned squid (*T. eblanae*, *T. sagittatus*, and *I. coindetii*) and the octopus (*E. cirrhosa*), but these are often discarded.

4.6 Aquaculture of European cephalopods

The high commercial value of cephalopods and their rapid growth makes the aquaculture of this group of molluscs an area of increasing interest, particularly in Mediterranean markets. The study of cephalopod culture has recently increased significantly in Europe, especially in Spain, Italy, Portugal, and Greece (Vaz-Pires *et al.*, 2004). The need to diversify the available number of farmable marine species, taking into consideration biological and economic aspects, make cephalopods in general, and octopus in particular, potential candidates for industrial-scale culture. For cuttlefish, there is potential for further exploitation, particularly with regard to the ongrowth of undersized individuals, which are considered a delicacy and have the highest commercial value in Portugal and Spain. Such a practice might reduce the impact of illegal catches of this species from the natural environment.

The main features of cephalopods that enhance their potential for culture are as follows.

- **High food conversion rate**. 30–60% of the ingested food is incorporated (Mangold and Boletzky, 1973; Wells, 1978; Mangold, 1983; Cerezo Valverde *et al.*, 2008);
- **Fast growth**. ca. 3% daily growth rate, depending on the developmental stage (Mangold and Boletzky, 1973; Mangold, 1983; Forsythe and van Heukelem, 1987);
- **High protein content**. 70–90% by dry weight of the edible parts is mantle and arms (O'Dor and Wells, 1987; Lee, 1994);
- **High fecundity**. Wells (1978); Mangold (1983); Iglesias *et al.* (1996, 1997).

In addition, cephalopods remain an important and highly appreciated food resource in Europe (especially southern countries) and many other parts of the world.

Boletzky (2004), in a brief survey of cephalopod culture techniques, suggested that four conditions must be fulfilled in culture experiments or advanced routine applications: (i) viable hatchlings, (ii) good water quality, (iii) appropriate food, and (iv) suitable living space. The nature of cephalopod protein metabolism means that their requirement for proteins and amino acids is high (Lee, 1994). Appropriate and inexpensive diets are a basic requirement for the success of commercial aquaculture (Chen and Long, 1991). A major obstacle to the establishment of large-scale culture has been the dependence on natural prey and the scarcity of suitable alternative diets (O'Dor and Wells, 1987; De Rusha *et al.*, 1989; Lee *et al.*, 1991; Di Marco *et al.* 1993; Lee, 1994; Domingues, 1999; Domingues *et al.*, 2005, 2008). The use of prepared diets, as a replacement for natural diets, can reduce production costs by 40% initially, and further reductions can be obtained later (Lee, 1994). Two species in European waters have been identified as candidates for aquaculture in the near future: *Sepia officinalis* and *Octopus vulgaris*. Until now, only a modest production of ongrown, wild-collected *O. vulgaris* has been obtained in Galicia, northwest Spain.

4.6.1 *Sepia officinalis*

Richard (1971) and Pascual (1978) were among the first researchers to culture European cuttlefish (*Sepia officinalis*) successfully in the laboratory. Hanlon *et al.* (1991) obtained daily growth rates of 3–4% body weight d^{-1} over 10 months, with a weight increase of 500–1400 g, at temperatures that varied between 20°C and 24°C. Domingues *et al.* (2001a, 2001b) cultured *S. officinalis* at 24–30°C and obtained a growth rate of 11.8% body weight d^{-1} for hatchlings and mean growth of 2.5–8.5% body weight d^{-1} over the course of the life cycle. As problems with water quality have been minimized during the past few years, the main problem that has kept this species out of the commercial aquaculture business is adequate food supply and associated costs. Many different diets have been tested, but only live food has produced good results for growth, condition, and survival (Toll and Strain, 1988; De Rusha *et al.*, 1989; Lee *et al.*, 1991; Castro *et al.*, 1993; Domingues, 1999; Koueta and Boucaud-Camou, 1999; Domingues *et al.*, 2001a, 2008). Koueta *et al.* (2002)

demonstrated that enrichment of the natural diet with polyunsaturated fatty acids resulted in faster growth in juvenile cuttlefish. There is also an interaction between feeding regime and photoperiod, with slower growth observed in cuttlefish when the light period was shorter (Koueta and Bouacaud-Camou, 2003).

The development of artificial diets for *S. officinalis* started in the early 1990s (Castro, 1991; Lee *et al.*, 1991; Domingues, 1999; Domingues *et al.*, 2005), but its success has been limited. Early feeding experiments with *S. officinalis* used either moist or dry pellets (Castro, 1991; Lee *et al.*, 1991; Castro *et al.*, 1993) or surimi (fish myofibrillar protein concentrate; Castro *et al.*, 1993; Castro and Lee, 1994; Domingues, 1999; Domingues *et al.*, 2005) and demonstrated that subadults and adults readily accepted prepared diets. Feeding rates for *S. officinalis* fed prepared diets were always considerably lower than those fed a normal laboratory maintenance diet of crustaceans (Richard, 1971, 1976; Pascual, 1978; Boletzky, 1979b; Lee *et al.*, 1991; Castro *et al.*, 1993; Castro and Lee, 1994; Forsythe *et al.*, 1994; Domingues *et al.*, 2001a, 2002, 2003a, 2003b, 2004, 2006, 2008; Koueta and Boucaud-Camou, 1999, 2001; Perrin *et al.*, 2004). Adequate food supply also remains a key problem for rearing hatchlings and juveniles of cuttlefish (Almansa *et al.*, 2006). The youngest animals need live prey (mysids, shrimps) during the first 15 days of their life, but it is very costly to rear grass shrimp or to trawl for this prey in the field. For large-scale production, it appears necessary to develop a surimi-based artificial food that is accepted by young cuttlefish at the earliest possible age. Recent studies by Perrin (2004) and Perrin *et al.* (2004) have demonstrated that juvenile cuttlefish (*S. officinalis*) can eat surimi during the first days of their life if this artificial diet is visually attractive, will adhere to the tentacles, and is suitable for the animals′ chemoreceptors. The surimi that were accepted were cylindrical in shape and had to be gently shaken.

Sykes *et al.* (2006) summarized current research on *S. officinalis* culture and identified the main biological characteristics that represent bottlenecks for the development of aquaculture of the species and need urgent research. These included:

- lower fertility and fecundity under culture conditions;
- semelparous life history, so that a new group of breeders is required for each cycle;
- hatchlings require live food, and juveniles and adult stages refuse dry pellets;
- the species is cannibalistic;
- production of the live food required is not yet developed, so the cost of food supply is high;
- the presence of a basic immunological system (Forsythe *et al.*, 1987, 1990), which may generate problems in intensive culture.

In Portugal, the University of the Algarve, in cooperation with a private company, "Necton – Companhia Portuguesa de Culturas Marinhas, S.A.", began to lay the foundations for the socio-economically viable production of *S. officinalis,* with the prospect of introducing this species to the market for human consumption.

4.6.2 *Octopus vulgaris*

The common octopus (*Octopus vulgaris*) has been identified as an important potential candidate for mariculture (Iglesias *et al.*, 1996) because subadults and adults have suitable characteristics for rearing (Mangold and Boletzky, 1973; Boletzky and Hanlon, 1983; García and Aguado, 2002). It represents one of the most interesting new species for the aquaculture sector, and there have been rearing experiments in Spain (see below) and Italy (Lenzi *et al.*, 2002; Mattei *et al.*, 2002). Research conducted on subadults of this species in Spain has demonstrated that season and diet seem to be the most important factors influencing the success of commercial culture (Iglesias *et al.*, 2000, 2004; Giménez and García, 2002; UTPB, 2005; Rodríguez *et al.*, 2006).

In Galicia, northwest Spain, the minimum legal weight of landed common octopus is 1 kg (increased from 750 g in 2008). Therefore, the ongrowing of these subadult animals would increase their market value and help to regulate the supply of large animals. Some limited ongrowing trials have been conducted in Galicia since 1995 by growing these subadult octopuses for 4 months on a diet of commercially discarded fish and crustaceans to obtain individual weights of 3–4 kg. Some trials were undertaken using tanks (Iglesias *et al.*, 1997; Sánchez, F. J., *et al.*, 1998; Otero *et al.*, 2001), whereas others used various types of cages (Rama-Villar and Rey-Mendez, 1997; Luaces and Rey-Mendez, 2001; Chapela *et al.*, 2006).

Rafts currently in use for mussel culture may also be suitable for ongrowing experiments with cephalopods. The success of experiments from rafts will depend on several factors, including environmental conditions, diet, design of cages, and density of animals.

In 2005, five Galician companies were licensed to undertake trials, but after the oil spill resulting from the wreckage of the tanker "Prestige" and/or other difficulties, only two remain in operation, "Arrecifes del Atlántico" and "Samertolameu, S. C. L.". In the same year, in Valencia, on the Spanish Mediterranean coast, a new company applied for a licence to produce octopus kept under the same conditions as in Galicia.

Table 4.6.1. Production (t) of *Octopus vulgaris* during recent years in Galicia, northwest Spain, by ongrowing wild-collected subadults in floating cages. Source: FAO (2007).

Year	1998	1999	2000	2001	2002	2003	2004	2005
Production	32	32	28	15	14	8	12	16

Although no compound feed formulations are available for octopus, recent studies on subadult growth performance using artificial wet diets agglutinated with gelatin or alginate for *O. vulgaris* (Cerezo Valverde *et al.*, 2008; Quintana *et al.*, 2008) and *O. maya* (Aguila *et al.*, 2007; Rosas *et al.*, 2008) identified the future research needs in this field. These authors concluded that the type of binder affects octopus growth. They also signalled the importance of including taste enhancers, and the necessary improvement of the stability of these diets in water, their texture, nutritive composition, and manufacture.

At present, the main problem to overcome for the commercial culture of common octopus is related to the low survival of the paralarvae of this species. This planktonic phase lasts nearly two months before the animals become benthic. At present, larval rearing techniques remain under development despite recent progress (see reviews by Iglesias *et al.*, 2007; Villanueva and Norman, 2008). To improve paralarval survival, recent research has focused on the nutritional requirements of the paralarvae. It is generally recognized that diets must be rich in protein and essential amino acids, particularly lysine, leucine, and arginine (Villanueva *et al.*, 2004), phospholipids, cholesterol, and particularly in the highly unsaturated fatty acids (HUFAs) 22:6n−3 and 20:5n−3 (Navarro and Villanueva, 2000, 2003; Moxica *et al.*, 2002; Okumura *et al.*, 2005; Seixas *et al.*, 2008), copper (Villanueva and Bustamante, 2006), and vitamin E (Villanueva *et al.*, 2009).

In future, large-scale culture of the paralarvae should probably use *Artemia*, and it is known that *O. vulgaris* hatchlings select juvenile *Artemia* of 1.4 mm length as suitable prey (Iglesias *et al.*, 2006). Future research is needed to obtain suitable enrichment of juvenile *Artemia* by the use of different algal sources, such as *Rhodomonas lens* (Seixas *et al.*, 2008) and to design new co-feeding techniques using micropellets. Compound millicapsules made by a process of gelification and composed of squid powder and crab meal have been used as supplementary food, in addition to *Artemia*, and were ingested by the paralarvae from the age of 5 days. However, results did not lead to a significant increase in octopus weight compared with control cultures fed only with *Artemia* (Villanueva *et al.*, 2002a).

4.6.3 Sustainability

Cephalopods are carnivorous, their body is rich in protein, and shallow-water species, such as *S. officinalis* and *O. vulgaris*, are characterized by vigorous protein metabolism (Lee, 1994). This suggests that artificial diets need to be rich in protein. At present, the use of fish powder, obtained mainly from pelagic fish, in the manufacture of most marine aquaculture foods, is a serious environmental problem because of its tremendous impact on fish stocks and ocean ecosystems (Pauly *et al.*, 2002).

For future cephalopod aquaculture, finding an appropriate protein source will be a major problem. Alternative sources of vegetal protein should be tested in order to support the development of sustainable and environmentally friendly cephalopod culture in future. Mazon *et al.* (2007) evaluated the possible environmental impact arising from the intensive ongrowing of common octopus in sea cages by estimating the waste generated during one growth cycle (starting with a mean individual weight of 750 g and ending with 3500 g) in octopus fed with crab (*Carcinus mediterraneus*) or fish (*Boops boops*). These authors found that the percentage of total nitrogen excreted by octopus differs little from that observed for teleost species, such as sea bream (*Dentex dentex*) and sea bass (*Dicentrarchus labrax*). However, the low percentage of nitrogen in particulate waste from octopus, compared with that from sea bream, sea bass, and tuna (*Thunnus* spp.), reflects the high digestibility of protein in octopus. The authors concluded that the main environmental impact would come from the non-edible fraction of the food provided (50% crab and 23.3% fish) and from particulate wastes. This is because the production of 1000 kg of octopus from a crab diet would generate 110.6 kg of nitrogen and 37.9 kg of phosphorus, whereas the corresponding figures for a fish diet would be 71.7 kg of nitrogen and 16.8 kg of phosphorus.

5 Assessment and management

Graham J. Pierce, Manuel Garcia Tasende, Ane Iriondo, Eugenia Lefkaditou, Véronique Legrand, Pia Orr, Adam Payne, João Pereira, Jean-Paul Robin, Pilar Sánchez, Marina Santurtún, and Ignacio Sobrino

5.1 Data collection

Traditional methods of fish stock assessment have generally been thought unsuitable for assessing cephalopods. Reasons given include various aspects of the particular biology and dynamics of these species. They are short-lived and semelparous, with only one or two generations present in the fishery at any time, although within generations there may be multiple "microcohorts" (i.e. groups defined according to hatching date) and/or alternative maturation strategies, leading to the simultaneous presence of animals of different sizes and ages, and with different growth trajectories. They also have apparently complex (or poorly defined) stock–recruitment relationships, strongly related to environmental factors, and demonstrate wide interannual fluctuations in abundance. In addition, there are difficulties in age determination: although recording structures have been identified in most groups (e.g. the statoliths of squid), reading of growth increments is time-consuming and, for most species, daily increment deposition is assumed rather than fully validated. However, similar problems are common in many finfish species for which regular assessments are carried out annually under the ICES framework. Furthermore, many traditional approaches to stock assessment have been applied to cephalopod stocks in various parts of the world (Pierce and Guerra, 1994). Pauly (1998), among others, has argued that the differences between squid and fish have been overstated and that efforts should be made to apply the approaches developed for fish to cephalopods.

The implementation of stock-assessment models relies on appropriate stock identification and consistent data-collection programmes. Perhaps the most important impediment to routine assessment for European cephalopods is that, to date, few European countries have collected detailed data on cephalopod fisheries (e.g. ICES, 2000, 2004a, 2008, 2009). Commercial landings from larger vessels are relatively well recorded, but catches and fishing effort of the very important artisanal fisheries are not so well known. Until 2002, much of the limited market and discard cephalopod sampling was carried out under the auspices of EC-funded projects. From 2002 onwards, cephalopod sampling became part of regular official data collection under the national sampling programmes at a basic level (minimum sampling). The fishery and biological data thus obtained from national fisheries can be used for some basic assessment. However, this sampling did not include all the commercially important species in each area and, because of the short life cycles and non-overlapping generations of these species, biological data are of limited value unless collected on a monthly basis (see ICES, 2008). Monthly (or more frequent) sampling for biological data allows the possibility of applying DeLury depletion methods which, for many years, has been the approach of choice in squid fisheries around the Falkland Islands (e.g. Beddington *et al.*, 1990; Rosenberg *et al.*, 1990; Agnew *et al.*, 1998).

Nevertheless, lack of detailed information should not prevent countries from starting to assess cephalopod stocks. Where cephalopod fishery and biology data are incomplete, simple assessment models should be chosen rather than more complex models (i.e. those that require more and higher quality data). Where there are insufficient data to define stocks, *ad hoc* definitions can be used in the first instance.

All European countries should be able to start assessing cephalopod stocks individually and/or cooperatively in order to identify population sizes, trends in abundance, and projections of future trends.

Probably the simplest approach to assessment, the application of production models, is at first sight unsuitable for short-lived species for which environmental carrying capacity is unlikely to be consistent between years. However, such an approach, which requires only catch and effort data, has been applied with some success to fisheries in the Saharan Bank (Bravo de Laguna, 1989).

As of 2009, under the new European Community's Data Collection Regulation (DCR; Commission Decision 2008/949/EC), the sampling unit for fishery data has changed from the species or stock to the métier. A métier is defined in the new DCR as a group of fishing operations targeting a similar (assemblage of) species, using similar gear, during the same period of the year and/or within the same area, and which are characterized by a similar exploitation pattern. The new DCR sampling system offers a greater opportunity for sampling of cephalopods in countries where these species are frequent in catches, but may not be economically important overall.

Basic fisheries data required for any assessment of cephalopod species, whether simple or more complex, can be summarized as follows.

- **Total nominal catches**. By country, by species and species groups, and by statistical divisions. To link these data to effort data in order to create abundance indices, it is also necessary to have landings data available by fleet or métier and to have information on discards.
- **Fishing effort and catch per unit of effort (cpue)**. By fleet or métier.
- **Biological data**. Sampling and measurements of commercial landings at an appropriate frequency (e.g. length frequency for squid and cuttlefish, weight frequency for octopus). Data on weight, sex, maturity, and fecundity are also desirable.

Currently used assessment models, such as DeLury depletion analysis, cohort analysis, and biomass models, require much more detailed information than is available from the current basic fishery data collection. Under the new DCR, sampling intensity is proportional to the relative effort and variability of the catches of a particular métier. The minimum number of fishing trips to be sampled is not less than one fishing trip per month during the fishing season for trips of less than 2 weeks and one fishing trip per quarter otherwise. For short-lived species, such as cephalopods, quarterly sampling is of little value, and for certain kinds of assessment (e.g. depletion methods), weekly data may be needed.

In many national statistical schemes, substantial improvement in sampling is feasible, very often without entailing a comparable rise in cost. National sampling schemes could be refined so that better estimates of catches, cpue, and size composition of landings can be obtained. Progress could also be made by integration with programmes of work carried out by research institutions in each country (e.g. regular trawl surveys) and fostering exchange of information between the fishing industry and such agencies.

Routine trawling surveys, such as the ICES International Bottom Trawl Survey (IBTS) in the North Sea, could collect data on the most important cephalopod species. The German RV "Walther Herwig" has been doing this for many years using a simple identification key for North Sea cephalopods. Cephalopod data from the IBTS could give an excellent indication of trends in stock size of various species from year to year, because the effort is the same each year. One important caveat, however, relates to estimation of recruitment. The timing of life-cycle events in cephalopods seems to be very labile, and apparent year-to-year differences in recruitment strength, at least in part, may reflect different timing of recruitment.

Another useful additional type of data collection would be a dedicated set of cephalopod plankton stations within existing plankton surveys to collect data on the planktonic paralarvae. Such stations should be sampled taking into account the epibenthic location of paralarvae. Such data could be invaluable for cephalopod assessment and management purposes.

5.2 Assessment in practice

Very little, if any, information is available on recruitment and stock biomass for most octopus, cuttlefish, and squid stocks in European waters, a situation that has remained relatively unchanged since the publication of a review of cephalopod assessment methods by Pierce and Guerra (1994) ca. 15 years ago. In order to redress this situation, the CEPHSTOCK project convened two stock-assessment workshops, in London in 2004 and Tenerife in 2005, with the objective of providing the opportunity for European and invited non-European scientists to discuss assessment issues and methodologies. A selection of papers presented at these workshops was published in a special issue of *Fisheries Research* (Payne *et al.*, 2006), and many of these are referred to in the following section.

In general, European cephalopod stocks are not currently valued sufficiently highly to warrant routine, full-scale assessments. Few of these stocks have been subjected to any type of rigorous stock assessments, with the notable exceptions of English Channel populations of *Loligo forbesii* and *L. vulgaris* (Royer *et al.*, 2002) and cuttlefish (*Sepia officinalis*; Royer *et al.*, 2006) and *L. forbesii* in Scottish waters (Young *et al.*, 2004). All these assessments were retrospective, using historical data, but effective management of fishing on annual species, for example, to ensure escapement of a sufficient number of spawners, arguably requires real-time assessment (see e.g., Beddington *et al.*, 1990; Rosenberg *et al.*, 1990). However, not all cephalopods are annual; some species live for two or three years.

The analysis of catch and/or effort data has been used in place of formal assessments to provide information on abundance trends, for example, *L. forbesii* in Scottish waters (Zuur and Pierce, 2004; Chen *et al.*, 2006; Young *et al.*, 2006b), *S. officinalis* in the English Channel (Dunn, 1999; Denis and Robin, 2002), *Octopus vulgaris* in Portugal (Lourenço and Pereira, 2006), loliginid and ommastrephid squid from the northern Aegean Sea (Georgakarakos *et al.*, 2006), and *Eledone cirrhosa* in the Ligurian Sea (Orsi-Relini *et al.*, 2006). Recent studies have also focused on the use of environmental information (such as sea surface temperature) or biological parameters to examine trends in abundance (Waluda and Pierce, 1998; Sobrino *et al.*, 2002; Pierce and Boyle, 2003; Wang *et al.*, 2003; Challier *et al.*, 2005b; Chen *et al.*, 2006; Orsi-Relini *et al.*, 2006; Ceriola *et al.*, 2007).

As the exploitation of European cephalopod populations increases and their commercial value becomes increasingly significant, it is expected that routine rigorous assessments will become necessary to maintain sustainable fisheries. Current practice for assessment of cephalopods outside Europe suggests various approaches.

Major non-European cephalopod stocks, such as Falkland Island *Loligo gahi* and *Illex argentinus* (Agnew *et al.*, 2005), South African *L. vulgaris reynaudi* (Roel and

Butterworth, 2000), and Japanese *Todarodes pacificus* (Suzuki, 1990) are all economically important stocks that are assessed regularly. Assessment methods can be classified in three categories, depending on whether they are used before, during, or after the fishing season (Pierce and Guerra, 1994).

Preseason assessments generally assume the form of a stock survey prior to recruitment at the start of the season, as is the case for the biomass projection estimate of *L. gahi* (Roa-Ureta and Arkhipkin, 2007). In-season and post-season assessments commonly involve the application of the Leslie–Delury depletion model to cpue data, as is the case for the *I. argentinus* and *L. gahi* fisheries in Falkland waters (Agnew *et al.*, 2002, 2005; Roa-Ureta and Arkhipkin, 2007). Other post-season assessments have been performed using cohort analysis for *Illex illecebrosus* (Hendrickson and Hart, 2006), the swept-area survey method for *Ommastrephes bartramii* (Ichii *et al.*, 2006), a combination of swept-area and hydroacoustic surveys for *L. reynaudii* (Lipinski and Soule, 2007), and a Bayesian approach to the Leslie–Delury model for *L. gahi* (McAllister *et al.*, 2004). Other recent developments have focused on the relationships between environmental parameters (such as sea surface temperature) and stock size, and their possible use for fishery forecasting (e.g. Waluda *et al.*, 1999, 2001a, 2001b; Dawe *et al.*, 2000, 2007; Agnew *et al.*, 2002, 2005).

5.3 Management of cephalopod fisheries

5.3.1 Introduction

Management of cephalopod stocks in European waters remains limited, and there is currently no quota-managed cephalopod fishery in Europe. Nevertheless, examples of both input controls (e.g. restrictions on the characteristics of the gear and the number of licences) and output controls (e.g. limits on the length or weight of the specimens landed) exist, and cephalopod fishing is, of course, also subject to a range of general fishery legislation.

Southern European countries appear to manage their cephalopod fisheries more actively than northern European countries. This may be a reflection of the long history of these fisheries and the local importance of the species. These are the countries where the internal consumption of the resources and the relative economic and/or social value of the fisheries are the greatest.

The present analysis was made on a country-by-country basis, because relevant national legislation is significantly different between countries, even in relation to the adoption of general legislation issued by the EU and subsequently transcribed to national legislation. Legislation directly related to regulation of cephalopod fishing in Europe is summarized in Table 5.3.1, and minimum landing sizes are summarized in Table 5.3.2. In general, the information presented concerns regulations introduced up to 2005. However, information on legislation in Galicia (northwest Spain) related to fishing for *O. vulgaris, L. vulgaris*, and *S. officinalis* was current in 2008.

Table 5.3.1. Synoptic overview of legislative regulations concerning specific fisheries targeting cephalopods in European waters (GRT = gross registered tonnes, OL = overall length).

Species	***Octopus vulgaris***			
Country	Greece		Spain	
Region			Mediterranean	
Fishing gear	Plastic cylindrical pots	Fykenets	Clay pots	Traps
Size/technical characteristics of fishing gear	<1500/vessel	<1000 pairs/vessel	<1000/vessel (Andalucia), <800/vessel (Valencia, Catalonia)	<200/vessel
Fishing bans	01/07 – 30/09		01/04 – 30/05 and 01/09 – 31/10 (Andalusia), 01/07 – 30/09 (Valencia), 010/9 – 31/05 (Taragona), 15/09 – 31/04 (Barcelona), 1/10 – 28/02 (Gerona)	
Fishing depth	>10 m		<50 m (Almeria, Granada), 11 – 35 m (Malaga, Cádiz), 25 – 50 m (Murcia), 5 – 40 m (Catalonia)	
Other limitations				
No./year of fishing regulation	Presidential Decree 157/2004		Order APA/973/2002 (Andalusia), Order of 19 Sep. 2002 (Murcia), Decree 263/97 (Valencia), Order ARP/182/2002 (Catalonia)	

Species	***Octopus vulgaris***		
Country	Spain		
Region	Gulf of Cádiz		Galicia
Fishing gear	Clay pots	Traps	Traps
Size/technical characteristics of fishing gear	<1000/vessel, <2000 m length of pot line	<250/vessel, <2000 m length of trap line	20 mm (square shape) Length <5000 m Number traps <350: a) vessels <2.5 GRT; 50 traps/vessel + 50 trap/each sailor b) vessels 2.5-5 GRT; 100 traps/vessel + 50 trap/each sailor c) vessels >5 GRT; 200 traps/vessel + 50 trap/each sailor (in any case, never more than 350 traps)
Fishing bans	01/05 – 30/06		2 months (from first week of May to first week of July)
Fishing depth			
Other limitations	<6 nautical miles from the coast		<40 kg/day/fisher + 40 kg/vessel/40 kg fisher^{-1} day^{-1} 40kg vessel^{-1}
No./year of fishing regulation	Order of 11 Nov. 1996 Order of 20 Jul. 2005		Regional Decree 424/1993 Regional Decree 348/2002 Regional Order of 23 May 2008 Regional Resolution of 13 Aug. 2008 (Consellería de Pesca y Asuntos Marítimos)

Species	*Octopus vulgaris*		*Loligo vulgaris*	
Country	Portugal		Spain	
Region			Gulf of Cádiz	Galicia
Fishing gear	Pots	Traps	Nets	Boat-seine with bag
Size/technical characteristics of fishing gear	<3000/vessel	<500/vessel OL <9 m), <750/vessel (OL 9–12 m), <1000/vessel (OL >12 m)	>60 mm mesh size, <4500 m length, <4 m height	>17 mm mesh size Wings <75 m, codend <10 m
Fishing bans				Weekends
Fishing depth				
Other limitations		>0.5 nautical miles distance from the coast		Fishing season during July–September (October)
No./year of fishing regulation	Order of 23 May 2005		Royal Decree 1428/1997	Regional Decree 424/1993

Species	*Sepia officinalis*			
Country	Spain		France	
Region	Gulf of Cádiz	Galicia	Normandy	
Fishing gear	Nets	Gillnets	Traps	Inshore trawl
Size/technical characteristics of fishing gear	>50 mm mesh size, <4500 m length, <4 m height	"Trasmallos": >70/400 mm mesh size, <2 m height "Miños": >90/500 mm mesh size, <3 m height, <4000 m length	250/vessel (1000 pots/vessel)	80 mm mesh size (Council Regulation (EC) No. 850/98)
Fishing bans		Weekends		Allowed 2 months per year in spring (April–June), and 10 days in summer in the West Cotentin area only
Fishing depth				
Other limitations		2 fishers/vessel	OL of vessel <12 m	OL of vessel <16 m
No./year of fishing regulation	Royal Decree 1428/1997	Regional Decree 424/1993		

Table 5.3.2. Legislative regulations concerning minimum landing size of cephalopod species in European countries.

Species	Country/region	Minimum landing size	Regulation
Octopus vulgaris	Greece	500 g (weight)	Presidential Decree 144/1986
	Spain (Mediterranean, Gulf of Cádiz, and Galicia)	1000 g (weight)	Regional Orders: APA/973/2002 (Andalusia), ARP/182/2002 (Catalonia) Order of 22 Nov. 1996 (Gulf of Cádiz) Regional Order of FMAC/28 Jul. 2008 (Galicia)
	Portugal	750 g (weight)	Portaria 27/2001
Sepia officinalis	Spain (Galicia)	80 mm (ML)	Regional Order of FMAC/28 Jul. 2008 (Galicia)
	France (Normandie)	100 g (weight)	Council Regulation (EC) No. 2406/96 (26/11/1996).
	Portugal	100 mm (ML)	Portaria 27/2001
Loligo vulgaris	Portugal	100 mm (ML)	Portaria 27/2001
	Spain (Galicia)	100 mm (ML)	Regional Order of FMAC/28 Jul. 2008 (Galicia)

5.3.2 Management of cuttlefish fishing in France

5.3.2.1 History of regulation

In the 1960s, cuttlefish fishing was not common in Lower Normandy. Most catches were taken by multispecies trawlers, and trapfishing was rare. A government order, signed in 1974, introduced some regulation of trawling for cuttlefish in the western English Channel. It permitted fishing within the 3-mile limit, while specifying the fishing period, a specific schedule for fishing, and permitted trawl mesh sizes. In the 1980s, scientific studies of cuttlefish biology and exploitation were instigated, the concept of sustainable management was launched, and some protection was introduced, taking into account the different "métiers" involved in cuttlefish exploitation and the spatial distribution of the resource.

Since the 1990s, the French regulatory framework has been changing. The state gives power to regional fishing committees, so that the state, the regional committee, and scientists share responsibility for the management of cuttlefish fishing. Usually, for trawling, the state takes decisions in consultation with the regional committee and after considering scientific advice from IFREMER. These decisions include those concerning the implementation of international, European, or national measures linked to the protection and sustainable management of resources.

Three administrative regions are involved in cuttlefish exploitation: Normandy and Brittany in the English Channel, and Brittany and the Pays de Loire in the Bay of Biscay. Each regional maritime affairs directorate (Direction Régionale des Affaires Maritimes (DRAM)) may issue regional orders (ROs) to establish compulsory impact mitigation measures for a specific period in a specific fishing area (e.g. limits to the number of licences issued, limited fishing seasons, and the definition of authorized fishing gear). These measures have the force of law. For example, along the west coast of Cotentin, where trawling and trapfishing are both used to catch cuttlefish in inshore waters, the following regulations have been implemented under ROs.

- 1993: new limit for trawling (within the 3-mile limit), identification and restriction of ships authorized to fish

- 1995: restriction of access authorization and new specifications for ship characteristics
- 1998: implementation of trapfishing licences, with restrictions placed on numbers of trapfishers and definition of numbers of authorized traps

There are no specific limits on cuttlefish fishing beyond the 3-mile limit, although EU regulations for multispecies bottom trawling apply. Fishing by trawlers in inshore waters is regulated under Decree 90/94 of 25 January 1990 (issued in accordance with the application of Article 3 of the Decree of 9 January 1852, imposing maritime fishing regulations). This decree allows, among other things, the possibility of trawling within three miles off the coast provided that an administrative authorization (AA) is obtained. This is issued by the state after consultation with the relevant professional organizations and is temporary, susceptible to suspension, and may be withdrawn at any time.

Trapfishing is covered under the Regulatory Framework for the Management of Regional Species through Fishing Licenses (except trawling).

- Law of 2 May 1991 regulates the delegation of regulatory power to the marine fisheries professional organizations to define technical measures needed to ensure sustainable management of marine resources and to regulate access under the principles of the precautionary approach.
- Decree of 30 March 1992, Article 22, defines the nature of regulations that may be introduced. Specifically, these may include limitation of fishing time, establishment of fishing seasons, establishment of rules of resource sharing among occupations, quotas of fishing licences, limitation of fishing vessel size and engine power, and definition of the characteristics of fishing gear.
- Fishing Law of November 1997, Articles 4 and 13, concern particular circumstances for the exercise of inshore fishing activities, particularly within territorial waters, for the protection of fragile habitats. The law aims to regulate the sharing of the resources among different occupations.

5.3.2.2 Management of cuttlefish fishing in Lower Normandy

Cuttlefish is one of the most significant marine resources in Lower Normandy. It is exploited mainly by three different "métiers", according to the season: offshore trawlers in wintering grounds in the central English Channel, inshore trawlers, and trapfishing in the western and eastern Channel. After a period of increasing pressure on the cuttlefish stock, licences are now limited to 180 trapfishing vessels and 140 coastal trawlers, which fish in spring and summer. Trawling for cuttlefish within the 3-mile limit requires an AA issued under the framework of the Normandy ROs. The state issues regulatory dispositions after consulting the Regional Fisheries Council (CRPM), taking research advice into consideration.

In spring, trawlers are allowed to fish within the 3-mile limit in three areas: (i) along the east coast of the English Channel, (ii) along 90 km of coastline in the Bay of Seine (since 1955), and (iii) north of the Cape of Antifer. Since 1993, trawlers have been able to fish within the 3-mile limit along almost 64 km of coast between Granville and Carteret in the West Cotentin sector. Trawling is restricted to two months each year, depending on the migratory movement of adult cuttlefish in spring, between April and June. This period is adjusted every year as a function of the probability of the arrival of cuttlefish, indicated by the volume of landings in the preceding autumn or the results of the trapfishery in the same season. Within this spring fishing season, since 1995, fishing for cuttlefish has been opened for 45 days, 5 days per week. Specific engine-power limits (331 kW) and overall boat length limits (16 m), established since 1995, serve as a basis for the issuing of licences. Between 1996 and 2002, the average engine power (AEP) among trawlers targeting cuttlefish in this region remained stable, indicating that the largest boats did not participate in this activity (Table 5.3.3). The number of boats that met these criteria and were allowed to enter the fishery declined from 156 to 98 between 1994 and 1999, and from ca. 90 to 70 between 2002 and 2008. Authorization to fish is revised annually. Mesh size is limited to a minimum of 80 mm in accordance with Council Regulation (EC) No. 850/98. Fishers contribute to the cost of delimiting the trawl-fishing area with floating devices. Each trawlerman has to pay €70, and this amount can rise to €150 to cover compensation payments for damage to other fishing activities, e.g. bivalve culture.

Table 5.3.3. Number (*n*) and average engine power (AEP, kW) of inshore trawlers operating in spring along Lower Normandy coasts, 1993–2002.

Year	1993	1994	1996	1997	1998	1999	2000	2001	2002
AEP	243	–	219	228	219	226	231	227	224
n	–	156	131	121	121	103	98	95	–

Spatial limits to the area of coastal waters within which trawling for cuttlefish can take place in summer were defined in 1993. The summer trawling period has been progressively reduced over the years, from three months between 1993 and 1998, to nine weeks in 2001, five weeks in 2008, and two weeks (ten days) in 2008. This reduction is designed to protect nursery areas of a multitude of species, particularly spider crabs (*Maja squinado*). As in spring, mesh size is limited to a minimum of 80 mm in accordance with Council Regulation (EC) No. 850/98. Although a minimum market size of 150 g has been proposed to protect juveniles, the only size limit at present is determined by the lower boundary of the smallest commercial category defined at the European level (i.e. 100 g; Council Regulation (EC) No. 2406/96).

Trapfishing is subject to issue of licences by the CRPM under a regional order. With state approval, the CRPM operates a co-management procedure. Co-management ensures limited, but shared, access to the resource and adequate spatial management, which may allow simultaneous exploitation by competing "métiers". There is a defined geographical area where inshore trapfishing is authorized. In the western sector, where the tidal zone is extensive, the area extends along 64 km of coastline. Access is limited by licence and according to vessel characteristics: only vessels <12 m in length may obtain a licence, and since 1998, the number of licensed boats has remained at 127. Since 1999, the average length of boat in the fishery has been 8 m and the AEP 85 kW. If the income from a boat depends almost exclusively on cuttlefish trapping, up to 500 traps can be carried (otherwise only 200). The total number of traps used in the fishery each year is currently ca. 34 000 and, although it is increasing, remains under the estimated total used before implementation of the regulation. The fishing season and number of fishing days are not limited. The status of the fishery and the resource are reviewed every year, but it has not been found necessary to amend the regulations since 2002.

5.3.2.3 Consensual conflict management for cuttlefish fishing in Lower Normandy

A consensual decision-making process is used to manage interactions between different fisheries and between fisheries and other marine-resource users. Although it has no legal force, it is generally accepted. Trapfishing for cuttlefish may interact with other métiers using traps for different species (e.g. crustaceans, whelks) in the same fishing grounds in different seasons. Relationships between trapfishers and trawlfishers are maintained by designating protected areas for traps and other areas for trawlers or dredgers. Problems are solved at the local level and on a case-by-case basis. The increase in recreational fishing is an issue because catches often exceed what would be consistent with individual consumption and because some activities (notably walking along the shore) can damage habitats.

Conflict between the cuttlefish fishery and shellfish farming along the coast of Normandy may occur where shellfish farming uses large portions of the shore. Again, problems are solved at the local level and on a case-by-case basis. Interactions with several other types of human activity in the marine environment are more problematic. Installation of submarine cables, or concrete foundations for equipment such as windmills, and extraction of aggregates and sediments, affect the cuttlefish by reducing the natural surface area available for egg-laying, and the amount of food.

5.3.2.4 Concluding remarks

Despite the lack of stock assessment, the English Channel cuttlefish fishery has been routinely monitored and regulated in order to limit the increase in fishing pressure. The management initiatives for the spring fishing period, which targets reproductive adults, seem to be effective. However, regulation of fishing on juvenile cuttlefish is still a work in progress. Trawlfishers and trapfishers share the resource in the coastal zone and together take 1500–2000 t of cuttlefish per year. For trapfishers, cuttlefish represents 20–60% of their annual income, whereas for trawlfishers, it represents 20–30%.

Local environmental conditions can be harmful for spring fishing on cuttlefish. In recent years, fishers have complained about the amount of drifting seaweed that reduces fishing gear efficiency (trapfishing or trawling) in the western part of the Channel. The impact of environmental factors is not negligible and can change the way the fishery develops, or even modify the biology of the species itself. In future, the monitoring and management of the exploitation of cuttlefish will have to include an evaluation of its environmental requirements and role in the ecosystem.

5.3.3 Spain

5.3.3.1 Gulf of Cádiz

Fishery management policies in Spanish waters of the Gulf of Cádiz are regulated by more than one public body. The management and conservation of resources policy is transcribed from EU regulations, thus establishing a series of technical measures. Bottom trawling and artisanal fisheries are regulated by different specific legislation.

Bottom trawling is only allowed with mesh sizes >40 mm (Council Regulation (EC) No. 215/1992). Technical protective measures (reflected in the Spanish Royal Decrees 632/1993 and 60/1994) regulate this fishing activity. The determination of closed or restricted areas, limitations to fishing effort, permitted bottom-trawling gear, and minimum sizes of mesh and species are regulated by the same decrees. The Order of 13 June 1996 established two trawling exclusion areas located near the mouths of the Piedras and Guadalquivir rivers. The enforcement of these regulations and the protection of the artisanal fisheries from conflicts with trawl fisheries were encouraged by the deployment of artificial reefs. Trawling is banned in some coastal areas reserved exclusively for military use. Fishing is banned on Saturday and Sunday. A minimum individual octopus (*O. vulgaris*) landing weight of 1 kg was established by the Order of 22 November 1996, which also bans sport fishing for the species. The Order of 23 October 2004 published new measures for trawl fisheries in the Gulf of Cádiz that include a closed season (15/10 to 30/11) and a night-fishing ban.

In accordance with Council Regulation (EC) No. 894/97, the Gulf of Cádiz artisanal fisheries are regulated by the national administration by Royal Decree 1428/1997, which covers the classification of fishing gear (nets, hooks, and traps) and the regulation of their technical characteristics, as well as fishing effort. Artisanal fishing in outer waters by boats with outboard engines is restricted to distances shorter than 2 nautical miles offshore. The maximum permitted horsepower and length for artisanal vessels are, respectively, 250 hp and 15 m for vessels with inboard engines, and 50 hp and 5 m for those with outboard engines. New vessels must be built with an inboard engine and a minimum length and GRT of 5 m and 2.5 t, respectively. Fishing gear must be lifted and stored in port for 48 hours a week. Although alternation of fishing gear is allowed, artisanal fishing activity with more than one gear type is banned during the same fishing trip. The seasonal use of a gear by a vessel licensed for another gear (either within an artisanal fishery or from an artisanal to non-artisanal fishery) is restricted to periods of no longer than 6 months a year and whenever conditions of the new targeted resource are deemed to allow the added effort. Nets (gillnets, trammelnets, mixed nets) may have a maximum length of 4500 m, a maximum height of 4 m, and a minimum mesh size of 60 mm for short-finned squid and 50 mm for cuttlefish. The maximum length of small-hook longlines is 2000 m, carrying up to 1000 hooks, but no regulations are established for hand-jig types ("chivo", "tablilla", "potera"). The maximum length of trap and clay-pot lines is 2000 m, and the maximum number per vessel is 250 traps and 1000 clay pots (details from the Spanish *Boletín Oficial del Estado* (www.boe.es), Royal Decree 1428/1997).

In addition to the measures above, the fishery for common octopus in "inner waters" is regulated by the Consejería (Order of 11 October 1996), which covers the same technical measures adopted later by the national fishing administration and extended to "outer waters". The Order of 20 July 2005 contains additional measures for *O. vulgaris* caught in the Gulf of Cádiz, including two closed seasons (1 May–30 June for artisanal fisheries and 15 September–31 October for all fisheries); the use of traps and clay pots is permitted between the coastal line and 6 nautical miles offshore; pots can only be made of clay (plastic is forbidden).

5.3.3.2 Mediterranean

In Spanish Mediterranean waters, fishery management policy is regulated by five public bodies. Bottom-trawl fishing is managed by EC regulations on technical measures for the Mediterranean (Council Regulation (EC) No. 1626/94), transcribed to Spanish Royal Decree 1440/1999, which regulates fishing activities. Regulations define the number of vessels licensed, fishing time per vessel (number of weekly fishing days cannot exceed five), length of the vessels (between 12 and 24 m), and horsepower (less than 500 hp). Trawling cannot be pursued inshore of the 50 m isobath, and the minimum mesh size is 40 mm. The same regulation establishes that trawling, seining, or similar activities are not allowed over *Posidonia* beds or over other marine phanerogams. Undersized molluscs cannot be retained on board, transhipped, landed, transferred, stored, sold, displayed, or offered for sale. Fishing in Andalusian waters is regulated by a management plan (Resolution of 18 February 2004, Regional Administration) which implemented a reduction in fishing effort by 25 %, limiting it to 160 fishing days per vessel per year, 60 h per week, and 12 h per day. Two closed seasons a year were established in May and October and, in order to protect nursery areas, some areas were delimited for closure to trawling.

Artisanal fisheries are regulated by the national administration by Royal Decree 1724/1990, the Order of 8 March 1999 and the Resolution of 18 October 1999 for longlines, and the Order of 22 October 1990 and Order of 12 June 1992 for nets. The main technical measures are a minimum length of 9 m for longline vessels and a minimum GRT of 2.5 t for net vessels. Nets must be lifted and stored in port for 24 h each week. Longlines must be lifted for 48 h each week, and their activity is restricted to distances of less than 60 nautical miles from the port. Fishing gear alternation is allowed, but the artisanal fishing vessels cannot operate more than one gear type during the same trip. Seasonal alternation of fishing gear is restricted to periods of no more than six months per gear, whenever the condition of the target resource permits. Nets (gillnets, trammelnets, and mixed nets) can be no longer than 4500 m and no higher than 4 m (gillnets and mixed nets) or 3 m (trammelnets), with a minimum mesh size of 40 mm. The maximum hook longline length is 7000 m, with up to 3000 hooks.

In addition to this national legislation, *O. vulgaris* fishing in inshore waters is regulated by the Spanish regional administrations. In Andalusia, the minimum weight was fixed at 1 kg, and sport fishing was prohibited by Order APA/973/2002 of 23 April 2002 (offshore waters) and by the Resolution of 18 February 2004 (inshore waters). The Order of 7 April 2004 restricted artisanal fishing to pots and traps, with a maximum number of 1000 pots and 200 traps per vessel. It is forbidden to catch octopus with pots or traps in April, May, September, and October. Vessels must remain in port throughout the weekend. Gear must be set between the coastline and a depth of 50 m in Almeria and Granada, and between 11 and 35 m depth in Malaga and Cádiz. In Murcia, the Order of 19 September 2002 regulates fishing with traps to a maximum number of 200 per vessel. Gear must be set between 25 and 50 m depth. Minimum landed weight must be 1 kg. In Valencia, Decree 263/1997 regulates fishing with pots, establishing a maximum number of 800 per vessel, forbidding fishing between 1 July and 30 September, and for 24 h per week. In Catalonia, Order ARP/182/2002 regulates fishing with pots and traps, establishing a minimum landing weight of 1 kg, limiting gear use to between 5 and 40 m depth, establishing a maximum number of 800 pots, and 200 traps per vessel, and instituting closed seasons between 1 September and 31 May in Tarragona, 15 September and 31 April in Barcelona, and 1 October and 28 February in Gerona.

5.3.3.3 Galicia

In Galicia (northwest Spain), fishing is regulated by Law 6/2009 of 11 December. The fishing ordinance (Regional Decree 424/1993) set limits on vessel size and engine power, established fishing seasons and times, and defined permitted fishing gear characteristics. In addition, the *O. vulgaris* fishery has been regulated under different orders over the years. Since 2005, fishing has been prohibited during 2 months (between May and July) of the year, depending on the timing of recruitment (i.e. fishing is banned when young specimens dominate).

Cuttlefish (*Sepia officinalis*) are mainly captured with two types of trammelnet, “trasmallos” (height ≤2 m) and “miños” (height ≤3 m). Maximum net length varies according to vessel size, from 1500 m (vessels <2.5 GRT) to 4000 m (vessels >5 GRT). Minimum mesh sizes for “trasmallos” are 70 mm for the inner sheet and 400 mm for the outer ones. For “miños”, minimum mesh sizes are 90 and 500 mm, respectively. From January to May (or June), during the main reproductive period of the species, small vessels (≤2.5 GRT) are authorized to work with "tramallos" nets in the interior waters of the rías, where cuttlefish concentrate to spawn. Maximum net length is 600 m. The minimum landing size (DML) for cuttlefish is 8 cm. Traditional trapfisheries employing egg-laying lures are still in use inside the rías. These cannot be operated over weekends, and there is a minimum mesh size. Eggs are returned to the sea.

The DML for squid (*L. vulgaris*) is 10 cm. Squid fishing is authorized year-round. However, a targeted squid fishery using a boat-seine with bag ("boliche") is authorized only from July to September (or October), when recruitment of squid takes place in the "Rías Baixas". The "boliche" has two wings, each 75 m long, and the codend is 10 m long with a minimum mesh size of 17 mm.

5.3.4 Portugal

In Portugal, the main responsibility for fishery policy and administration belongs to the Ministry of Agriculture, Fisheries and Rural Development through the Directorate General of Fisheries and Aquaculture. Different authorities under the Ministry of Defence are responsible for fishery control and regulation enforcement.

The main piece of fisheries legislation in Portugal is the Fisheries Act. Originally adopted in 1987 as Decree-Law 278/87, it has been amended several times; its present version dates from 1998 (amendment through Decree-Law 383/98). The Fisheries Act contains, in its Articles 15 and 15A, provisions concerning the competent authority in fishery matters. For the application of the Fisheries Act, secondary legislation has been adopted in the form of Decree-Regulation 43/87, as last amended by Decree-Regulation 7/2000, which contains general provisions concerning the exercise of fishing activities. It contains management and conservation rules, including technical rules, in accordance with EC legislation.

Legal gear descriptions and operating procedures for fishing on cephalopods were regulated by Portaria 1102-C/2000 of 22 November (linefishing), which specifies unbaited jig construction and their use for the catch of cuttlefish and squid, and baited jig construction and their use for the catch of octopus.

Portaria 1102-D/2000 of 22 November (trapfishing) specifies characteristics for artisanal fisheries with pots (maximum 3000 per vessel, set at a minimum of 0.8 km from the coast for vessels <9 m total length and 1.6 km for vessels >9 m total length) and with traps (maximum 500 for vessels <9 m long, 750 for vessels 9–12 m long, and 1000 for vessels >12 m long). Under this legislation, vessels may catch octopus with traps equipped with meshes of a variety of dimensions, but the mesh size used must relate to a specified minimum proportion of octopus in the total landings.

Portaria 1102-E/2000 of 22 November (trawlfishing) specifies characteristics of bottom trawls to two mesh-dimension classes (65–69 mm and >70 mm). For the smaller mesh size, catches must contain a minimum of 70 % of any target cephalopod species.

Portaria 1102-H/2000 of 22 November (gillnet fishing) specifies the characteristics of gillnets and trammelnets, determining that cuttlefish can only be caught by nets employing three mesh dimension classes (60–79, 80–99, and >100 mm).

The minimum landing sizes and weights of the several different cephalopod species caught by all applicable gear were regulated by Portaria 27/2001 of 15 January: 100-mm ML for the cuttlefish *Sepia officinalis* and the squid *Loligo vulgaris* and 750 g for the octopus *Octopus vulgaris*.

Portaria 635/2005 of 2 August (amended by Portaria 840/2005 of 19 September and valid until 31 July 2006) established an experimental fishing regime for *O. vulgaris,* aimed at enhancing the productivity of the species. This took place in the area bounded by the coastline to the north, the Portuguese EEZ to the east and south, and the line passing through the meridian of 8°59'8" to the west (part of the Algarve). The "local" category of fishing vessels could only set traps for octopus beyond 0.25 miles (0.4 km) from the coastline between 1 June and 31 October and beyond 0.5 miles (0.8 km) from the coastline between 1 November and 31 May, except between 1 and 30 September 2005, when it was forbidden to catch, keep on board, land, and market any specimen whatsoever. It was also forbidden to catch octopus with baited or unbaited jigs between 1 August and 30 October in the same year, or to catch, keep onboard, land, and market any specimen on any Sunday between 1 June and 31 October.

5.3.5 Greece

Fishery policy in Greek waters is regulated by the Hellenic Ministry of Rural Development and Food. The main body of fishery national regulations is included in Legislative Decree 420/1970 and subsequent presidential decrees. Additional technical measures for fisheries in the Mediterranean are implemented according to Council Regulation (EC) No. 1626/1994. A minimum landing weight is defined only for *Octopus vulgaris* (500 g), by Presidential Decree 144/1986.

Bottom trawls are the only kind of trawlnet used in Greek waters. In accordance with Council Regulation (EC) No. 1626/1994, trawlers operate at depths of >50 m or at a distance greater than 3 miles (4.8 km) from the coast, and the stretched mesh size in the codend is 40 mm. Additionally, in accordance with national regulation (Presidential Decree 817/1966), a ban on trawling extends from 1 June to 30 September, and more extensively in some gulfs or near estuaries. Beach-seines (a normal boat-seine hauled by a special winch) are used in Greece and regulated by Presidential Decree 817/1966, which states that the gear should be operated very close to shore, the boats anchoring within 70 m of the coast. Until 2002, the closed season for beach-seine operation extended from 1 June to 30 September, but according to Council Regulation (EC) No. 1626/1994, the use of this gear was supposed to have stopped in 2002. Ministerial Decree 292288/2001, however, permitted the use of this gear to continue, with a 6-month ban extending from 1 April to 30 September and a limit on the length of the hauling ropes (maximum 400 m). Fykenets and pots are regulated by Presidential Decree 157/2004 (in force from 10 January 2005), which implemented a ban on fishing with both gears from 1 July to 30 September, a maximum number of 1000 pairs of fykenets or 1500 cylindrical pots per vessel, and a limitation on fishing operations to depths greater than 10 m.

5.3.6 Conclusion

It is likely that the exclusion of cephalopods from quota regulations under the Common Fisheries Policy has been a good thing. The management regimes, which have evolved in the various small-scale fisheries described above, serve to regulate exploitation, although stock sizes are generally unknown. Thus, they effectively operate under a precautionary principle and, perhaps even more importantly, in relation to the CFP reforms ongoing in 2009, they are founded on local-scale management, participation of the fishers, and, in some cases, co-management.

The apparent success of these arrangements suggests that they can work for highly mobile species (such as cuttlefish and squid) that breed in coastal waters, and not only for species of shellfish that are essentially sedentary as adults. Applying this type of management to larger-scale fisheries, in which cephalopods are usually one of many species caught and may not be a target species, is clearly more difficult. In such multispecies fisheries, protection of the most vulnerable species almost invariably results in suboptimal exploitation of other species. The corollary of this is that optimal exploitation of the main target species is nearly always damaging to at least some species in the catches. Cephalopod populations are both theoretically vulnerable to overfishing (because of non-overlapping generations) and yet also apparently resilient to high fishing pressure. Thus, any measures designed to protect target finfish species should also be adequate to protect cephalopods.

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

Graham Pierce, Paola Belcari, Paco Bustamante, Laurence Challier, Yves Cherel, Ángel González, Ángel Guerra, Patrizia Jereb, Noussithé Koueta, Eugenia Lefkaditou, Ana Moreno, João Pereira, Uwe Piatkowski, Christina Pita, Jean-Paul Robin, Beatriz Roel, M. Begoña Santos, Marina Santurtun, Sonia Seixas, Paul Shaw, Jennifer Smith, Gabrielle Stowasser, Vasilis Valavanis, Roger Villanueva, Jianjun Wang, Sansanee Wangvoralak, Manuela Weis, and Karsten Zumholz

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.

7 References

Adam, W. 1952. Expédition océanographique belge dans les eaux côtiéres africaines de l'Atlantique sud. Céphalopodes (1948–1949). Résultats scientifiques. Institut Royal des Sciences Naturelles de Belgique, Bruxelles No. 3. 142 pp.

Adamidou, A. 2007. Commercial fishing gears and methods used in Hellas. *In* State of Hellenic Fisheries, pp. 118–131. Ed. by C. Papaconstantinou, A. Zenetos, C. Vassilopoulou, and G. Tserpes. SoHelFi, HCMR Publications, Athens. 466 pp.

Adcock, G. J., Shaw, P. W., Rodhouse, P. G., and Carvalho, G. R. 1999. Microsatellite analysis of genetic diversity in the squid *Illex argentinus* during a period of intensive fishing. Marine Ecology Progress Series, 187: 171–178.

Addison, R. F. 1989. Organochlorines and marine mammal reproduction. Canadian Journal of Fisheries and Aquatic Sciences, 46: 360–368.

Agnew, D. J., Baranowski, R., Beddington, J. R., des Clers, S., and Nolan, C. P. 1998. Approaches to assessing stocks of *Loligo gahi* around the Falkland Islands. Fisheries Research, 35: 155–169.

Agnew, D. J., Beddington, J. R., and Hill, S. L. 2002. The potential use of environmental information to manage squid stocks. Canadian Journal of Fisheries and Aquatic Sciences, 59: 1851–1857.

Agnew, D. J., Marlow, T. R., Lorenzen, K., Pompert, J., Wakeford, R. C., and Tingley, G. A. 2003. Influence of Drake Passage oceanography on the parasitic infection of individual year classes of southern blue whiting *Micromesistius australis*. Marine Ecology Progress Series, 254: 281–291.

Agnew, D. J., Hill, S. L., Beddington, J. R., Purchase, L. V., and Wakeford, R. C. 2005. Sustainability and management of southwest Atlantic squid fisheries. Bulletin of Marine Science, 76: 579–594.

Aguila, J., Cuzon, G., Pascual, C., Domingues, P. M., Gaxiola, G., Sanchez, A., Maldonado, T., *et al.* 2007. The effects of fish hydrolysate (CPSP) level on *Octopus maya* (Voss and Solis) diet: digestive enzyme activity, blood metabolites, and energy balance. Aquaculture, 273: 641–655.

Alexeyev, D. O. 1989. Advantages and limitations of using the gladius in diagnosis of species and genera of the family Loliginidae (Cephalopoda). Zoologicheskii Zhurnal, 68: 36–42 (in Russian).

Alexeyev, D. O. 1991. Taxonomical system, phylogeny, distribution, biology and prospects for fishery of squids of the suborder Myopsida. PhD thesis, Shirshov, Moscow (in Russian).

Alexeyev, D. O. 1992. The systematic position of bioluminescent squids of the family Loliginidae (Cephalopoda, Myopsida). Zoologicheskii Zhurnal, 71: 12–23 (in Russian).

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

Alidromiti, C. 2007. Study of age and growth of *Alloteuthis media* (Cephalopoda: Loliginidae). Investigation of geographical and gender differences in the statolith morphology and the mantle growth. MSc thesis, University of Athens, Greece. 68 pp. (in Greek, with English abstract).

Allcock, A. L., Strugnell, J. M., Ruggiero, H., and Collins, M. A. 2006. Redescription of the deep-sea octopod *Benthoctopus normani* (Massy, 1907) and a description of a new species from the Northeast Atlantic. Marine Biology Research, 2: 372–387.

Almansa, E., Domingues, P., Sykes, A., Tejera, N., Lorenzo, A., and Andrade, J. P. 2006. The effects of feeding with shrimp or fish fry on growth and mantle lipid composition of juvenile and adult cuttlefish (*Sepia officinalis*). Aquaculture, 256: 403–413.

Anderson, C. I. H., and Rodhouse, P. G. 2001. Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. Fisheries Research, 54: 133–143.

Anderson, F. E. 2000a. Phylogeny and historical biogeography of the loliginid squids (Mollusca: Cephalopoda) based on mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution, 15: 191–214.

Anderson, F. E. 2000b. Phylogenetic relationships among loliginid squids (Cephalopoda: Myopsida) based on analyses of multiple data sets. Zoological Journal of the Linnean Society, 130: 603–633.

Anderson, F. E., Pilsits, A., Clutts, S., Laptikhovsky, V., Bello, G., Balguerías, E., Lipinski, M., *et al.* 2008. Systematics of *Alloteuthis* (Cephalopoda: Loliginidae) based on molecular and morphometric data. Journal of Experimental Marine Biology and Ecology, 364: 99–109.

André, J., Grist, E. P. M., Semmens, J. M., Pecl, G. T., and Segawa, S. 2009. Effects of temperature on energetics and the growth pattern of benthic octopuses. Marine Ecology Progress Series, 374: 167–179.

Arkhipkin, A. I. 2005. Statoliths as "black boxes" (life recorders) in squid. Marine and Freshwater Research, 56: 573–583.

Arkhipkin, A. I., and Roa-Ureta, R. 2005. Identification of ontogenetic growth models for squid. Marine and Freshwater Research, 56: 371–386.

Arkhipkin, A. I., Jereb, P., and Ragonese, S. 1998. Age determination of *Illex coindetii* from the Strait of Sicily by statolith increments analysis. South African Journal of Marine Science, 20: 233–240.

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

Arkhipkin, A. I., Jereb, P., and Ragonese, S. 2000. Growth and maturation in two successive seasonal groups of the short-finned squid, *Illex coindetii* from the Strait of Sicily (central Mediterranean). ICES Journal of Marine Science, 57: 31–41.

Arkhipkin, A. I., Grzebielec, R., Sirota, A. M., Remeslo, A. V., Polishchuk, I. A., and Middleton, D. A. J. 2004a. The influence of seasonal environmental changes on ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf. Fisheries Oceanography, 13: 1–9.

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

Arkoosh, M. R., Casillas, E., Clemons, E., Kagley, A. N., Olson, R., Reno, P., and Stein, J. E. 1998. Effect of pollution on fish diseases: potential impacts on salmonid populations. Journal of Aquatic Animal Health, 10: 182–190.

Arnáiz, R., Rodríguez, E., Quintero, F., Bañón, R., Campelos, J. M., Gancedo, A., Tasende, M., *et al.* 2001. La pesquería de sepia (*Sepia officinalis*) con trasmallos en la enseñada de San Simón (1999–2000). *In* Los Recursos Marinos de Galicia. Serie Técnica No. 2, Consellería de Pesca e Asuntos Marítimimos, Xunta de Galicia, Dirección Xeral de Recursos Mariños, Santiago de Compostela, Spain. 54 pp.

Arnold, G. P. 1979. Squid. A Review of Their Biology and Fisheries. Laboratory Leaflet No. 48, Directorate of Fisheries Research, Ministry of Agriculture, Fisheries and Food, Lowestoft, UK. 38 pp.

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

Augustyn, C. J., and Grant, W. S. 1988. Biochemical and morphological systematics of *Loligo vulgaris vulgaris* Lamarck and *Loligo vulgaris reynaudii* D'Orbigny nov. comb. (Cephalopoda: Myopsida). Malacologia, 29: 215–233.

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

Baddyr, M. 1988. The biology of the squid *Loligo vulgaris* in relation to the artisanal fishing site of Tifnit, Morocco. PhD thesis, Institut Agronomique et Vètèrinaire Hassan II, Rabat, Morocco. 93 pp.

Bakun, A. 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. California Sea Grant College System, University of California, La Jolla. 339 pp.

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

Balguerías, E., Hernández-González, C., and Perales-Raya, C. 2002. On the identity of *Octopus vulgaris* Cuvier, 1797 stocks in the Saharian bank (Northwest Africa) and their spatio-temporal variations in abundance in relation to some environmental factors. Bulletin of Marine Science, 71: 147–163.

Bañón, R., Campelos, J. M., Tasende, M., Quintero, F., Ribó, J., Lamas, F., Gancedo, A., *et al.* 2007. La pesca de pulpo común con nasas en la costa gallega. *In* Los Recursos Marinos de Galicia. Serie Técnica No. 6, Consellería de Pesca e Asuntos Marítimimos, Xunta de Galicia, Dirección Xeral de Recursos Mariños, Santiago de Compostela, Spain. 193 pp.

Barber, M. C. (Ed). 1994. Environmental Monitoring and Assessment Program Indicator Development Strategy. EPA/620/R-94/022, US Environmental Protection Agency, Office of Research and Development, Washington, DC.

Barghigiani, G., and De Ranieri, S. 1992. Mercury content in different size classes of important edible species of the northern Tyrrhenian Sea. Marine Pollution Bulletin, 24: 114–116.

Beare, D. J., Batten, S., Edwards, M., and Reid, D. G. 2002. Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. Journal of Sea Research, 48: 29–49.

Bearer, E. L., Schlief, M. L., Breakefield, X. O., Schuback, D. E., Reese, T. S., and LaVail, J. H. 1999. Squid axoplasm supports the retrograde axonal transport of *Herpes simplex* virus. Biological Bulletin, 197: 257–258.

Beaugrand, G., and Ibanez, F. 2004. Monitoring marine plankton ecosystems. 2: Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. Marine Ecology Progress Series, 284: 35–47.

Beaugrand, G., and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology, 9: 801–817.

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. Nature, 426: 661–664.

Beddington, J. R., Rosenberg, A. A., Crombie, J. A., and Kirkwood, G. P. 1990. Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. Fisheries Research, 8: 351–365.

Belcari, P. 1996. Length–weight relationship in relation to sexual maturation of *Illex coindetii* (Cephalopoda: Ommastrephidae) in the northern Tyrrhenian Sea (western Mediterranean). Scientia Marina, 60: 379–384.

Belcari, P. 1999. *Sepia elegans* Blainville, 1827. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 675–679. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999a. *Loligo vulgaris*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 710–714. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999b. *Loligo forbesi*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 706–709. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999c. *Alloteuthis subulata*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 703–705. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999d. *Alloteuthis media*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 699–702. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999e. *Illex coindetii*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 715–720. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999f. *Todarodes sagittatus*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 725–728. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999g. *Todaropsis eblanae*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 729–732. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999h. *Sepia officinalis*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 680–686. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999i. *Sepia elegans*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 675–679. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P. 1999j. *Sepia orbignyana*. *In* "Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica)", pp 687–690. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P., Fedi, E., and Sartor, P. 1990. Analysis of the sexual development of *Eledone cirrhosa* (Cephalopoda, Octopoda) in the northern Tyrrhenian Sea through two maturity indices. Rapports de la Commission Internationale de la Mer Méditerranée, 32: 241.

Belcari, P., and Sartor, P. 1993. Bottom trawling teuthofauna of the Northern Tyrrhenian Sea. Scientia Marina, 57: 145–152.

Belcari, P., and Sartor, P. 1999a. *Eledone cirrhosa*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 737–746. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P., and Sartor, P. 1999b. *Octopus vulgaris*. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 757–766. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P., Sartor, P., and De Ranieri, S. 1998. I cefalopodi nello sbarcato commerciale con reti a strascico del Mar Tirreno Settentrionale. Biologia Marina Mediterranea, 5(2): 318–326.

Belcari, P., Sartor, P., Nannini, N., and De Ranieri, S. 1999. Length-weight relationship of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) of the northern Tyrrhenian Sea in relation to sexual maturation. *In* Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica), pp. 524–528. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P., and Sbrana, M. 1999. *Eledone moschata*. *In* Synthesis of the knowledge on bottom fishery resources in central Mediterranean (Italy and Corsica), pp. 747–752. Ed. by G. Relini, J. Bertrand, and A. Zamboni. Biologia Marina Mediterranea, 6(Suppl. 1). 868 pp.

Belcari, P., Tserpes, G., González, M., Lefkaditou, E., Marceta, B., Piccinetti, G., and Souplet, A. 2002a. Distribution and abundance of *Eledone cirrhosa* (Lamark, 1798) and *E. moschata* (Lamark, 1798; Cephalopoda: Octopoda) in the Mediterranean Sea. Scientia Marina, 66: 143–155.

Belcari, P., Cuccu, D., Gonzalez, M., Srairi, A., and Vidoris, P. 2002b. Distribution and abundance of *Octopus vulgaris* Cuvier, 1797 (Cephalopoda: Octopoda) in the Mediterranean sea. Scientia Marina, 66(Suppl. 2): 157–166.

Belcari, P., Sartor, P., Sánchez, P., Demestre, M., Tsangridis, A., Leondarakis, P., Lefkaditou, E., *et al.* 2002c. Exploitation patterns of the cuttlefish, *Sepia officinalis* (Sepioidea: Sepiidae), in the Mediterranean Sea. Bulletin of Marine Science, 71: 187–196.

Belcari, P., De Ranieri, S., Ligas, A., Reale, B., Sartor, P., and Viva, C. 2007. Selectivity of two diamond mesh size cod-ends in the trawl fishery of the northern Tyrrhenian Sea (western Mediterranean). Rapports de la Commission Internationale de la Mer Méditerranée, 38: 428.

Bellido, J. M., Pierce, G. J., and Wang, J. 2001. Modelling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalized additive models. Fisheries Research, 52: 23–39.

Bello, G. 1985. Preliminary note on cephalopods in the stomach content of swordfish, *Xiphias gladius* L., from the Ionian and Adriatic seas. Rapports de la Commission Internationale de la Mer Méditerranée, 29: 231–232.

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

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

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

Bello, G. 2001. Dimorphic growth in male and female cuttlefish *Sepia orbignyana* (Cephalopoda: Sepiidae) from the Adriatic Sea. Helgoland Marine Research, 55: 124–127.

Bello, G., and Borri, M. 1990. Nomi italiani dei cefalopodi delle Schede FAO d'identificazione delle specie di interesse alieutico. Notiziario SIM, 9(1–2): 9–20.

Besteiro, C. 1985. Fishery prospect expedition on the fishery of squid (*Todarodes sagittatus* (Lamarck, 1880)) and red-fish (*Sebastes marinus* (Linneo, 1758)) in the waters of the economic exclusive zone of Norway (August–November of 1981). Trabajos Compostelanos de Biologia, 11: 61–102.

Bettencourt, V., and Guerra, A. 2001. Age studies based on daily increments in statoliths and growth lamellae in cuttlebone of cultured *Sepia officinalis*. Marine Biology, 139: 327–334.

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

Beuerlein, K., Ruth, P., Westermann, B., Lohr, S., and Schipp, R. 2002. Hemocyanin and the branchial heart complex of *Sepia officinalis*: are the hemocytes involved in hemocyanin metabolism of coleoid cephalopods? Cell and Tissue Research, 310: 373–381.

Biagi, V. 1997. Polpi, Seppie e Totani nel mare di Piombino e dell'isola d'Elba. Baldecchi e Vivaldi, Pontedera, Italy. 131 pp.

Bjørke, H., and Gjøsæter, H. 2004. Cephalopods in the Norwegian Sea. *In* The Norwegian Sea Ecosystem, pp. 371–394. Ed. by H. R. Skjoldal, O. A. Misund, R. Sætre, A. Færnö, and I. Røttingen. Tapir Academic Press, Trondheim, Norway. 559 pp.

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

Boletzky, S. v. 1975. Le développement d´*Eledone moschata* (Mollusca, Cephalopoda) élevée au laboratoire. Bulletin de la Société Zoologique de France, 100: 361–367.

Boletzky, S. v. 1979a. Observations on early post-embryonic development of *Loligo vulgaris* (Mollusca, Cephalopoda). Rapports de la Commission Internationale de la Mer Méditerranée, 25/26: 1–10.

Boletzky, S. v. 1979b. Growth and life span of *Sepia officinalis* under artificial conditions. Rapports de la Commission Internationale de la Mer Méditerranée, 25/26: 159–168.

Boletzky, S. v. 1983. *Sepia officinalis*. *In* Cephalopod Life Cycles. Vol. I: Species Accounts, pp. 31–52. Ed. by P. R. Boyle. Academic Press, London. 516 pp.

Boletzky, S. v. 1988. Preliminary observations on laboratory-reared *Sepia orbignyana* (Mollusca cephalopoda). Rapports de la Commission Internationale de la Mer Méditerranée, 31: 256.

Boletzky, S. v. 2004. A brief survey of cephalopod culture techniques. Turkish Journal of Aquatic Life, 2: 229–240.

Boletzky, S. v., and Hanlon, R. T. 1983. A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. Memoirs of the National Museum of Victoria, 44: 147–187.

Borges, T. C. 2001. Cephalopod resources dynamics and fisheries trends in the Algarve and the Gulf of Cadiz (ALCACEPH). Final Report to the Commission of the European Communities Directorate General of Fisheries. University of the Algarve, Faro, Portugal. 432 pp.

Börjesson, P., Berggren, P., and Ganning, B. 2003. Diet of harbour porpoises in the Kattegat and Skagerrak Sea: accounting for individual variation and sample size. Marine Mammal Science, 19: 38–58.

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

Boucaud-Camou, E., and Boismery, J. 1991. The migration of the cuttlefish (*Sepia officinalis* L.) in the English Channel. *In* La Seiche: the Cuttlefish, 1st International Symposium on the Cuttlefish *Sepia*, 1–3 June 1989, Caën, pp. 179–189. Ed. by E. Boucaud-Camou. Centre de Publications de l'Université de Caën, Caën, France. 358 pp.

Boucaud-Camou, E., Koueta, N., Boismery, J., and Medhioub, A. 1991. The sexual cycle of *Sepia officinalis* L. from the Bay of Seine. *In* La Seiche: the Cuttlefish, 1st International Symposium on the Cuttlefish *Sepia*, 1–3 June 1989, Caën, pp. 141–151. Ed. by E. Boucaud-Camou. Centre de Publications de l'Université de Caën, Caën, France. 358 pp.

Boyle, P. R. 1983. *Eledone cirrhosa*. *In* Cephalopod Life Cycles. Vol. I: Species Accounts, pp. 365–386. Ed. by P. R. Boyle. Academic Press, London. 475 pp.

Boyle, P. R. 1991. The UFAW handbook on the care and management of cephalopods in the laboratory. Universities Federation for Animal Welfare, Potters Bar, UK. 63 pp.

Boyle, P. R. (Ed.). 2000. Cephalopod Resource Dynamics: Patterns in Environmental and Genetic Variation, 1997–2000. Final Report for EU Integrated Project FAIR-CT96-1520. University of Aberdeen, UK.

Boyle, P. R., and Knobloch, D. 1981. Hole boring of crustacean prey by the octopus *Eledone cirrhosa* (Mollusca: Cephalopoda). Journal of Zoology, 193: 1–10.

Boyle, P. R., and Knobloch, D. 1982. On growth of the octopus *E. cirrhosa*. Journal of the Marine Biological Association of the UK, 62: 277–296.

Boyle, P. R., and Knobloch, D. 1983. The female reproductive cycle of the octopus, *E. cirrhosa*. Journal of the Marine Biological Association of the UK, 63: 71–83.

Boyle, P. R., and Pierce, G. J. (Eds). 1994. Fishery biology of the Northeast Atlantic squid. Fisheries Research, 21: 1–314.

Boyle, P. R., and Rodhouse, P. G. 2005. Cephalopods. Ecology and Fisheries. Blackwell Science, Oxford. 452 pp.

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

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

Boyle, P. R., Collins, M. A., and Pierce, G. J. (Eds). 2002. Cephalopod biomass and production. Bulletin of Marine Science, 71: 1–1146.

Brackoniecki, T. F. 1986. A generic revision of the family Loliginidae (Cephalopoda: Myopsida) based primarily on the comparative morphology of the hectocotylus. PhD thesis, University of Miami, FL.

Bravo de Laguna, J. 1989. Managing an international multispecies fishery: the Saharan trawl fishery for cephalopods. *In* Marine Invertebrate Fisheries: Their Assessment and Management, pp. 591–612. Ed. by J. F. Caddy. John Wiley and Sons, New York. 752 pp.

Brierley, A. S., Thorpe, J., Pierce, G. J., Clarke, M. R., and Boyle, P. R. 1995. Genetic variation in the neritic squid *Loligo forbesi* (Myopsida: Loliginidae) in the Northeast Atlantic Ocean. Marine Biology, 122: 79–86.

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

Browning, J. 1979. Octopus microvasculature: permeability to ferritin and carbon. Tissue and Cell, 11: 371–383.

Bruno, I. 2008. Short-finned squid fishery landings of the Spanish fishing fleet operating in the northern Atlantic of the Iberian Peninsula. *In* Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH), pp. 37–49. ICES Document CM 2008/LRC:14. 49 pp.

Bustamante, P., Caurant, F., Fowler, S. W., and Miramand, P. 1998a. Cephalopods as a vector for the transfer of cadmium to top marine predators in the North East Atlantic Ocean. Science of the Total Environment, 220: 71–80.

Bustamante, P., Cherel, Y., Caurant, F., and Miramand, P. 1998b. Cadmium, copper and zinc in octopuses from Kerguelen Islands, Southern Indian Ocean. Polar Biology, 19: 264–271.

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

Bustamante, P., Teyssié, J-L., Fowler, S. W., Cotret, O., Danis, B., Miramand, P., and Warnau, M. 2002a. Biokinetics of zinc and cadmium accumulation and depuration at different stages of the life cycle of the cuttlefish *Sepia officinalis*. Marine Ecology Progress Series, 231: 167–177.

Bustamante, P., Cosson, R. P., Gallien, I., Caurant, F., and Miramand, P. 2002b. Cadmium detoxification processes in the digestive gland of cephalopods in relation to accumulated cadmium concentrations. Marine Environmental Research, 53: 227–241.

Bustamante, P., Teyssié, J-L., Danis, B., Fowler, S. W., Miramand, P., Cotret, O., Miramand, P., *et al.* 2004. Uptake, transfer and distribution of silver and cobalt in tissues of the common cuttlefish *Sepia officinalis* at different stages of its life cycle. Marine Ecology Progress Series, 269: 185–195.

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

Bustamante, P., González, A. F., Rocha, F., Miramand, P., and Guerra, A. 2008. Metal and metalloid concentrations in the giant squid *Architeuthis dux* from Iberian waters. Marine Environmental Research, 66: 278–287.

Butty, J. S., and Holdway, D. A. 1997. Assessment of the octopus *Octopus pallidus*, as a potential bioindicator of xenobiotic challenge: baseline studies. Marine Pollution Bulletin, 34: 564–570.

Caballero-Alfonso, A. M., Ganzedo-López, U., Díez-Díez, G., and Castro, J. J. 2008. New record of *Ocythoe tuberculata* (Cephalopoda: Ocythoidae) in the North-east Atlantic related to sea warming. JMBA2–Biodiversity Records. 3 pp.

Cabranes, C., Fernández-Rueda, P., and Martinez, J. L. 2008. Genetic structure of *Octopus vulgaris* around the Iberian Peninsula and Canary Islands as indicated by microsatellite DNA variation. ICES Journal of Marine Science, 65: 12–16.

Caddy, J. F. 1991. Daily rings on squid statoliths: an opportunity to test standard population models? *In* Squid Age Determination Using Statoliths, pp. 53–66. Ed. by P. Jereb, S. Ragonese, and S. v. Boletzky. Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy, 9–14 October 1989. NTR-ITTP Special Publication No. 1. 124 pp.

Calabrese, A., MacInnes, J. R., and Nelson, D. A. 1984. Effects of long-term exposure to silver or copper on growth, bioaccumulation and histopathology in the blue mussel *Mytilus edulis*. Marine Environmental Research, 11: 253–274.

Carlini, D. B., Kunkle, L. K., and Vecchione, M. 2006. A molecular systematic evaluation of the squid genus *Illex* (Cephalopoda: Ommastrephidae) in the North Atlantic ocean and Mediterranean Sea. Molecular Phylogenetics and Evolution, 41: 496–502.

Carneiro, M. C., Martins, R., and Rebordão, F. R. 2006. Contribuição para o conhecimento das artes de pesca utilizadas no Algarve. Publicações Avulsas do IPIMAR, 13. 60 pp.

Carrasco, J. F., Arronte, J. C., and Rodríguez, C. 2006. Paralarval rearing of the common octopus, *Octopus vulgaris* (Cuvier). Aquaculture Research, 37: 1601–1605.

Carvalho, G. R., and Pitcher, T. J. (Eds). 1995. Molecular genetics in fisheries. Chapman and Hall, New York. 141 pp.

Casali, P., Manfrin-Piccinetti, G., and Soro, S. 1998. Distribuzione di cefalopodi in alto e medio Adriatico. Biologia Marina Mediterranea, 5: 307–317.

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

Castro, B. G. 1991. Can *Sepia officinalis* L be reared on artificial food? Marine Behaviour and Physiology, 19: 35–38.

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

Castro, B. G., and Lee, P. G. 1994. The effects of semi-purified diets on growth and condition for *Sepia officinalis* L. (Mollusca: Cephalopoda). Comparative Biochemistry and Physiology A, Physiology, 109: 1007–1016.

Castro, B. G., Di Marco, F. P., DeRusha, R. H., and Lee, P. G. 1993. The effects of surimi and pelleted diets on the laboratory survival, growth, and feeding rate of the cuttlefish *Sepia officinalis* L. Journal of Experimental Marine Biology and Ecology, 170: 241–252.

Casu, M., Maltagliati, F., Meloni, M., Casu, D., Cossu, P., Binelli, G., Curini-Galetti, M., *et al.* 2002. Genetic structure of *Octopus vulgaris* (Mollusca, Cephalopoda) from the Mediterranean Sea as revealed by a microsatellite locus. Italian Journal of Zoology, 68: 295–300.

Caverivière, A., Domain, F., and Diallo, A. 1999. Observations on the influence of temperature on the length of embryonic development in *Octopus vulgaris* (Senegal). Aquatic Living Resources, 12: 151–154.

Cerezo Valverde, J., Hernández, M. D., Aguado-Giménez, F., and Garcia Garcia, B. 2008. Growth, feed efficiency and condition of common octopus (*Octopus vulgaris*) fed on two formulated moist diets. Aquaculture, 275: 266–273.

Ceriola, L., Ungaro, N., and Toteda, F. 2006. Some information on the biology of *Illex coindetii* Verany, 1839 (Cephalopoda, Ommastrephidae) in the south-western Adriatic Sea (Central Mediterranean). Fisheries Research, 82: 41–49.

Ceriola, L., Ungaro, N., and Toteda, F. 2007. A "Traffic Light" approach for the assessment of the Broadtail shortfin squid *Illex coindetii* Verany, 1839 in the Southern Adriatic Sea (Central Mediterranean). Reviews in Fish Biology and Fisheries, 17: 145–157.

Challier, L., Dunn, M. R., and Robin, J-P. 2005a. Trends in age-at-recruitment and juvenile growth of cuttlefish, *Sepia officinalis*, from the English Channel. ICES Journal of Marine Science, 62: 1671–1682.

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

Chapela, A. G., González, A. F., Dawe, E. G., Rocha, F. J., and Guerra, A. 2006. Growth of common octopus (*Octopus vulgaris*) in cages suspended from rafts. Scientia Marina, 70: 121–129.

Chavez, F. P., Ryan, J. P., Lluch-Cota, S. E., and Ñiquen, C. M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science, 299: 217–221.

Chen, C. S., Pierce, G. J., Wang, J., Robin, J-P., Poulard, J. C., Pereira, J., Zuur, A. F., *et al.* 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: trends in *Loligo* spp. abundance in the northeast Atlantic and possible environmental influences. Fisheries Research, 78: 44–54.

Chen, X. J., Zhao, X. H., and Chen, Y. 2007. Influence of *El Niño/La Niña* on the western winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) in the northwestern Pacific Ocean. ICES Journal of Marine Science, 64: 1152–1160.

Chen, X. K., and Long, L. J. 1991. Research and production of live feeds in China. *In* Rotifer and Microalgae Culture Systems. Proceedings of a US–Asia Workshop, 28–31 January 1991, Honolulu, Hawaii, pp. 187–202. Ed. by W. Fulks and K. L. Main. The Oceanic Institute, Hawaii, USA. 364 pp.

Chen, Y., Cheung, S. G., and Shin, P. K. S. 2008. The diet of amphioxus in subtropical Hong Kong as indicated by fatty acid and stable isotopic analyses. Journal of the Marine Biological Association of the UK, 88: 1487–1491.

Cheng, T. C. 1988a. *In vivo* effects of heavy metals on cellular defence mechanisms of *Crassostrea virginica*: total and differential cell counts. Journal of Invertebrate Pathology, 51: 207–214.

Cheng, T. C. 1988b. *In vivo* effects of heavy metals on cellular defence mechanisms of *Crassostrea virginica*: phagocytic and endocytotic indexes. Journal of Invertebrate Pathology, 51: 215–220.

Cherel, Y., and Hobson, K. A. 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. Proceedings of the Royal Society of London B: Biological Sciences, 272: 1601–1607.

Cherel, Y., Ridoux, V., Spitz, J., and Richard, P. 2009a. Stable isotopes document the trophic structure of a deep-sea cephalopod assemblage including giant octopod and giant squid. Biological Letters, 5: 364–367.

Cherel, Y., Fontaine, C., Jackson, J. D., Jackson, C. H., and Richard, P. 2009b. Tissue, ontogenic and sex-related differences in δ13C and δ15N values of the oceanic squid *Todarodes filippovae* (Cephalopoda: Ommastrephidae). Marine Biology, 156: 699–708.

Children, J. G. 1823. Lamarck's genera of shells, translated from the French, with plates from original drawings by Miss Anna Children. Quarterly Journal of Science, 14: 64–86, 298–322; 15: 23–52, 216–258; 16: 49–79, 241–264. (See Kennard, A. S., Salisbury, A. E., and Woodward, B. B. 1931. The Types of Lamarck's Genera of Shells as Selected by J. G. Children in 1823. Smithsonian Miscellaneous Collections, 82(17). 40 pp.)

Christensen, V., and Walters, C. 2000. Ecopath with Ecosim: methods, capabilities and limitations. *In* Methods for Assessing the Impact of Fisheries on Marine Ecosystems of the North Atlantic, pp. 79–105. Ed. by D. Pauly and T. Pitcher. Fisheries Centre Research Reports, 8(2). University of British Columbia, Vancouver. 195 pp.

Clarke, M. R. 1966. A review of the systematic and ecology of oceanic squids. Advances in Marine Biology, 4: 91–300.

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

Clarke, M. R., and Lu, C. C. 1995. Cephalopoda of Madeiran Waters. Boletim do Museu Municipal do Funchal, 4: 181–200.

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

Clarke, M. R., and Pascoe, P. L. 1997. Cephalopod species in the diet of a sperm whale (*Physeter catodon*) stranded at Penzance, Cornwall. Journal of the Marine Biological Association of the UK, 7: 1255–1258.

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

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

Coelho, M. L., Domingues, P., Balguerías, E., Fernández, M., and Andrade, J. P. 1997. A comparative study of the diet of *Loligo vulgaris* (Lamarck, 1799; Mollusca: Cephalopoda) from the south coast of Portugal and the Saharan Bank (Central-East Atlantic). Fisheries Research, 29: 245–255.

Collie, J. S., Wood, A. D., and Jeffries, H. P. 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1352–1365.

Collins, M. A., Burnell, G. M., and Rodhouse, P. G. 1995. Reproductive strategies of male and female *Loligo forbesi* (Cephalopoda: Loliginidae). Journal of the Marine Biological Association of the UK, 75: 621–634.

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

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

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

Cooper, E. L. 2002. Comparative immunology. Current Pharmaceutical Design, 8: 99–110.

Costa, P. R., Rosa, R., Duarte-Silva, A., Brotas, V., and Sampayo, M. A. M. 2005a. Accumulation, transformation and tissue distribution of domoic acid, the amnesic shellfish poisoning toxin, in the common cuttlefish, *Sepia officinalis*. Aquatic Toxicology, 74: 82–91.

Costa, P. R., Rosa, R., Pereira, J., and Sampayo, M. A. M. 2005b. Detection of domoic acid, the amnesic shellfish toxin, in the digestive gland of *Eledone cirrhosa* and *E. moschata* (Cephalopoda, Octopoda) from the Portuguese coast. Aquatic Living Resources, 18: 395–400.

Cuccu, D., Damele, F., Follesa, M. C., Murenu, M., and Cau, A. 2003. Aspetti biologici di *E. cirrhosa* (Cephalopoda Octopoda) nei mari circostanti la Sardegna. Biologia Marina Mediterranea, 10(2): 119–126.

Cuccu, D., Jereb, P., Addis, P., Pendugiu, A. A., Sabatini, A., and Cau, A. 2005. Eccezionali catture di *Todarodes saggitatus* (Cephalopoda: Ommastrophidae) nei mari sardi. Biologia Marina Mediterranea, 12(1): 500–503.

Cunha, M. M., and Moreno, A. 1994. Recent trends in the Portuguese squid fishery. Fisheries Research, 21: 231–242.

Daly, H. I., Pierce, G. J., Santos, M. B., Royer, J., Cho, S. K., Stowasser, G., and Robin, J-P. 2001. Cephalopod consumption by fish in UK waters. Fisheries Research, 52: 51–64.

Danis, B., Bustamante, P., Cotret, O., Teyssié, J-L., Fowler, S. W., and Warnau, M. 2005. Bioaccumulation of PCBs in the cuttlefish *Sepia officinalis* from seawater, sediment and food pathways. Environmental Pollution, 134: 113–122.

Daszak, P., Cunningham, A. A., and Hyatt, A. D. 2001. Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta Tropica, 78: 103–116.

Dawe, E. G., Colbourne, E. B., and Drinkwater, K. F. 2000. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). ICES Journal of Marine Science, 57: 1002–1013.

Dawe, E. G., Hendrickson, L. C., Colbourne, E. B., Drinkwater, K. F., and Showell, M. A. 2007. Ocean climate effects on the relative abundance of short-finned (*Illex illecebrosus*) and long-finned (*Loligo pealeii*) squid in the northwest Atlantic Ocean. Fisheries Oceanography, 16: 303–316.

De Guardo, G., Marruchella, G., Agrimi, U., and Kennedy, S. 2005. Morbillivirus infections in aquatic mammals: a brief overview. Journal of Veterinary Medicine Series A. Physiology Pathology and Clinical Medicine, 52: 88–93.

De Heij, A., and Baayen, R. P. 2005. Seasonal distribution of cephalopod species living in the central and southern North Sea. Basteria, 69: 91–120.

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

De Rusha, R. H., Forsythe, J. W, DiMarco, F. P., and Hanlon, R. T. 1989. Alternative diets for maintaining and rearing cephalopods in captivity. Laboratory Animal Science, 39: 306–312.

Delgado de Molina, *et al*. 1993. Parametros biologico-pesqueros de algunas especies de la familia Sepiidae Keferstein, 1866 obtenidos en las campanas IBNSINA (1980–1982). Boletin del Instuto Español de Oceanografía, 9(1): 41–56.

Denis, V., and Robin, J-P. 2002. Present status of the French Atlantic fishery for cuttlefish (*Sepia officinalis*). Fisheries Research, 52: 11–22.

Denis, V., Lejeune, J., and Robin, J-P., 2002. Spatio-temporal analysis of commercial trawler data using General Additive models: patterns of Loliginid squid abundance in the northeast Atlantic. ICES Journal of Marine Science, 59: 633–648.

Diffenbaugh, N. S., Snyder, M. A., and Sloan, L. C. 2004. Could CO_2-induced land-cover feedbacks alter nearshore upwelling regimes? Proceedings of the National Academy of Sciences of the USA, 101: 27–32.

Dillane, E., Galvin, P., Coughlan, J., Lipinski, M., and Cross, T. F. 2005. Genetic variation in the lesser flying squid *Todaropsis eblanae* (Cephalopod: Ommastrephidae) in east Atlantic and Mediterranean waters. Marine Ecology Progress Series, 292: 225–232.

Di Marco, F. P., Turk, P. E., Scimeca, J. R., Browning, W. J., and Lee, P. G. 1993. Laboratory survival, growth, and digestive gland histology of squids reared on living and non-living fish diets. Laboratory Animal Science, 43: 1–6.

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

Domain, F., Caverivière, A., Fall, M., and Jouffre, D. 2002. Expériences de marquages du poulpe *Octopus vulgaris* au Sénégal. *In* Le poulpe *Octopus vulgaris*: Sénégal et côtes nord–ouest africaines, pp. 41–57. Ed. by A. Caverivière, M. Thiam, and D. Jouffre. IRD Éditions, Paris. 385 pp.

Domingues, P., Sykes, A., and Andrade, J. P. 2002. The effects of temperature in the life cycle of two consecutive generations of the cuttlefish *Sepia officinalis* (Linnaeus, 1758), cultured in the Algarve (South Portugal). Aquaculture International, 10: 207–220.

Domingues, P., Poirier, R., Dickel, L., Almansa, E., Sykes, A., and Andrade, J. P. 2003a. Effects of culture density and live prey on growth and survival of juvenile cuttlefish, *Sepia officinalis*. Aquaculture International, 11: 225–242.

Domingues, P., Sykes, A., Sommerfield, A., and Andrade, J. P. 2003b. Effects of feeding live or frozen prey on growth, survival and the life cycle of the cuttlefish, *Sepia officinalis* (Linnaeus, 1758). Aquaculture International, 11: 397–410.

Domingues, P., Sykes, A., Sommerfield, A., Almansa, E., Lorenzo, A., and Andrade, J. P. 2004. Growth and survival of cuttlefish (*Sepia officinalis*) of different ages fed crustaceans and fish. Effects of frozen and live prey. Aquaculture, 229: 239–254.

Domingues, P., Bettencourt, V., and Guerra, A. 2006. Growth of *Sepia officinalis* in captivity and in nature. Vie et Milieu, 56: 109–120.

Domingues, P., Ferreira, A., Marquez, L., Andrade, J. P., Lopez, N., and Rosas, C. 2008. Growth, absorption and assimilation efficiency by mature cuttlefish (*Sepia officinalis*) fed with alternative and artificial diets. Aquaculture International, 16: 215–229.

Domingues, P. M. 1999. Development of alternative diets for the mass culture of the European cuttlefish *Sepia officinalis*. PhD thesis, University of Algarve, Faro, Portugal. 95 pp.

Domingues, P. M., Kingston, T., Sykes, A., and Andrade, J. P. 2001a. Growth of young cuttlefish, *Sepia officinalis* (Linnaeus 1758) at the upper end of the biological distribution temperature range. Aquaculture Research, 32: 923–930.

Domingues, P. M., Sykes, A., and Andrade, J. P. 2001b. The use of *Artemia* sp. or mysids as food source for hatchlings of the cuttlefish (*Sepia officinalis* L.), effects on growth and survival throughout the life cycle. Aquaculture International, 9: 319–331.

Domingues, P. M., Di Marco, F. P., Andrade, J. P., and Lee, P. G. 2005. The effects of diets with amino acid supplementation on the survival, growth and body composition of the cuttlefish *Sepia officinalis*. Aquaculture International, 13: 423–440.

D'Onghia, G., Tursi, A., Papaconstantinou, C., and Matarrese, A. 1992. Teuthofauna of the North Aegean Sea: preliminary results on catch composition and distribution. FAO Fisheries Report No. 477: 69–84.

Dorval, E., McDaniel, J., and Crone, P. 2009. Fecundity, egg-escapement, and F-based biological reference points in the market squid fishery off California. *In* Cephalopod International Advisory Council (CIAC) Symposium, 3–11 September 2009, Vigo, Spain, Abstracts, pp. 45–46. CIAC. 98 pp. Available online at http://www.abdn.ac.uk/ciac.

Dos Santos, A., Santos, A. M., and Conway, D. V. P. 2007. Horizontal and vertical distribution of cirripede cyprid larvae in an upwelling system off the Portuguese coast. Marine Ecology Progress Series, 329: 145–155.

Doubleday, Z. A. 2009. An integrative approach to understanding the population structure and dispersal patterns of two commercial octopus species (*Octopus maorum* and *Octopus pallidus*). PhD thesis, University of Tasmania, Australia.

Doubleday, Z. A., Semmens, J. M., Pecl, G. T., and Jackson, G. D. 2006. Assessing the validity of stylets as ageing tools in *Octopus pallidus*. Journal of Experimental Marine Biology and Ecology, 338: 35–42.

Ducrotoy, J. P. 1999. Indications of change in the marine flora of the North Sea in the 1990s. Marine Pollution Bulletin, 38: 646–654.

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

Eastwood, P. D., Meaden, G. J., and Grioche, A. 2001. Modelling spatial variations in spawning habitat suitability for the sole *Solea solea* using regression quantiles and GIS procedures. Marine Ecology Progress Series, 224: 251–266.

EC. 1987. Glossarium on Fishing Gear. Office of Official Publications of European Communities, Luxembourg. 381 pp.

Edwards, M., and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430: 881–884.

Edwards, M., Reid, P., and Planque, B. 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). ICES Journal of Marine Science, 58: 39–49.

Edwards, M., Beaugrand, G., Reid, P. C., Rowden, A. A., and Jones, M. B. 2002. Ocean climate anomalies and the ecology of the North Sea. Marine Ecology Progress Series, 239: 1–10.

Eltink, A. T. G., Newton, A. W., Morgado, C., Santamaria, M. T. G., and Modin, J. 2000. Guidelines and tools for age reading comparisons. Available online at http://www.efan.no.

Esch, G. W., and Fernández, J. C. 1993. A Functional Biology of Parasitism: Ecological and Evolutionary Implications. Chapman and Hall, London. 337 pp.

Ezzeddine-Najai, S. 1997. Maturation sexuelle d'*Eledone moschata* (Cephalopoda, Octopoda) du Golfe de Gabès. Vie et Milieu, 47: 69–76.

Fabry, V. J., Seibel, B. A., Feely, R. A., and Orr, J. C. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science, 65: 414–432.

FAO. 1995. Code of Conduct for Responsible Fisheries. FAO, Rome. 41 pp.

FAO. 2004. Fishstat Plus (v. 2.30). Commodities trade and production (1976–2002). Available online at http://www.fao.org/fi/statist/fisoft/fishplus.asp.

FAO. 2007. Aquaculture Production 2005. FAO Yearbook of Fishery Statistics, 100/2. FAO, Rome. 202 pp.

Faraj, A., and Bez, N. 2007. Spatial considerations for the Dakhla stock of *Octopus vulgaris*: indicators, patterns, and fisheries interactions. ICES Journal of Marine Science, 64: 1820–1828.

Farto, R., Armada, S. P., Montes, M., Guisande, J. A., Pérez, M. J., and Nieto, T. P. 2003. *Vibrio lentus* associated with diseased wild octopus (*Octopus vulgaris*). Journal of Invertebrate Pathology, 83: 149–156.

Faure, V. 2002. Environnement et variabilité des populations de poulpes *Octopus vulgaris* en Afrique de l'Ouest. *In* Le poulpe *Octopus vulgaris*: Sénégal et côtes nord-ouest africaines, pp. 129–142. Ed. by A. Caverivière, M. Thiam, and D. Jouffre. IRD Éditions, Paris. 385 pp.

Faure, V., Inejih, C. A., Demarq, H., and Cury, P. 2000. The importance of retention processes in upwelling areas for recruitment of *Octopus vulgaris*: the example of the Arguin Bank (Mauritania). Fisheries Oceanography, 9: 343–355.

Fernández-Rueda, P., and García-Flórez, L. 2007. *Octopus vulgaris* (Mollusca: Cephalopoda) fishery management assessment in Asturias (North-West Spain). Fisheries Research, 83: 351–354.

Ferretti, M., Tarulli, E., and Palladino, S. 2002. Classificazione e descrizione degli attrezzi da pesca in uso nelle marinerie italiane con particolare riferimento al loro impatto ambientale. Quaderni ICRAM No. 3. 126 pp.

Fiedler, P. C. 2002. Ocean Environment. *In* Encyclopedia of Marine Mammals, pp. 824–830. Ed. by W. F. Perrin, B. Wursig, and J. G. M. Thewissen. Academic Press, San Diego. 1414 pp.

Fisheries Research Services. 2004. Scottish Ocean Climate Status Report 2002 and 2003. Ed. by S. L. Hughes. Fisheries Research Services, Aberdeen. 50 pp.

Fluckiger, M., Jackson, G. D., Nichols, P., Virtue, P., Daw, A., and Wotherspoon, S. 2008. An experimental study of the effect of diet on the fatty acid profiles of the European cuttlefish (*Sepia officinalis*). Marine Biology, 154: 363–372.

Fonseca, P., Campos, A., and Garcia, A. 2002. Bottom trawl codend selectivity for cephalopods in Portuguese continental waters. Fisheries Research, 59: 263–271.

Fonseca, T., Campos, A., Afonso-Dias, M., Fonseca, P., and Pereira, J. 2008. Trawling for cephalopods off the Portuguese coast – fleet dynamics and landings composition. Fisheries Research, 92: 180–188.

Foote, K. G., Hanlon, R. T., Iampietro, P. J., and Kvitek, R. G. 2006. Acoustic detection and quantification of benthic egg beds of the squid *Loligo opalescens* in Monterey Bay, California. Journal of the Acoustical Society of America, 119: 844–856.

Ford, L. A. 1992. Host defense mechanisms of cephalopods. Annual Review of Fish Diseases, 2: 25–41.

Form, A., and Oelschlägel, A. 2004. Untersuchungen zur Nahrungsökologie zweier Kalmar-Arten (*Loligo forbesi* + *Todaropsis eblanae*) in der Nordsee. Student Thesis, University of Kiel, Kiel, Germany. 42 pp.

Forsythe, J. W. 2004. Accounting for the effect of temperature on squid growth in nature: from hypothesis to practice. Marine and Freshwater Research, 55: 331–339.

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

Forsythe, J. W., and van Heukelem, W. F. 1987. Growth. *In* Cephalopod Life Cycles. Vol. II: Comparative Reviews, pp. 135–156. Ed. by P. R. Boyle. Academic Press, London. 441 pp.

Forsythe, J. W., Hanlon, R. T., and Lee, P. G. 1987. A synopsis of cephalopod pathology in captivity. *In* Proceedings of the 18th Annual IAAAM Conference, May 1987, Monterey, CA, Vol. 1, pp. 130–135. Ed. by T. D. Williams. International Association for Aquatic Animal Medicine.

Forsythe, J. W., Hanlon, R. T., and Lee, P. G. 1990. A formulary for treating cephalopod mollusc diseases. *In* Pathology in Marine Science. Proceedings of the 3rd International Colloquium on Pathology in Marine Aquaculture, 2–6 October 1988, in Gloucester Point, VA, pp. 51–63. Ed. by F. O. Perkins and T. C. Cheng. Academic Press, San Diego. 538 pp.

Forsythe, J. W., Hanlon, R. T., Bullis, R. A., and Noga, E. J. 1991. *Octopus bimaculoides* (Pickford and McConnaughey, 1949): a marine invertebrate host for ectoparasitic protozoans. Journal of Fish Diseases, 14: 431–442.

Forsythe, J. W., De Rusha, R. H., and R. T. Hanlon. 1994. Growth, reproduction and life span of *Sepia officinalis* (Cephalopoda: Mollusca) cultured through seven consecutive generations. Journal of Zoology, 233: 175–192.

Forsythe, J. W., Walsh, L. S., Turk, P. E., and Lee, P. G. 2001. Impact of temperature on juvenile growth and age at first egg-laying of the Pacific reef squid *Sepioteuthis lessoniana* reared in captivity. Marine Biology, 138: 103–112.

Fry, D. M. 1995. Reproductive effects in birds exposed to pesticides and industrial chemicals. Environmental Health Perspectives, 103(Suppl. 7): 165–171.

Fuhrman, J. A. 1999. Marine viruses and their biogeochemical and ecological effects. Nature, 399: 541–548.

Furuya, H., Hochberg, F. G., and Tsuneki, K. 2003. Reproductive traits in dicyemids. Marine Biology, 142: 693–706.

Furuya, H., Ota, M., Kimura, R., and Tsuneki, K. 2004. Renal organs of cephalopods: A habitat for dicyemids and chromidinids. Journal of Morphology, 262: 629–643.

Galloway, T. S., and Depledge, M. H. 2001. Immunotoxicity in invertebrates: measurement and ecotoxicological relevance. Ecotoxicology, 10: 5–23.

García, B., and Aguado, F. 2002. Influence of the diet on ongrowing and nutrient utilization in the common octopus (*Octopus vulgaris*). Aquaculture, 211: 497–182.

García García, J., Rodríguez, L. M., and García García, B. 2004. Cost analysis of octopus ongrowing installation in Galicia. Spanish Journal of Agricultural Research, 2: 531–537.

Garoia, F., Guarniero, I., Ramsak, A., Ungaro, N., Landi, M., Piccinetti, C., Mannini, P., *et al.* 2004. Microsatellite DNA variation reveals high gene flow and panmictic populations in the Adriatic shared stocks of the European squid and cuttlefish (Cephalopoda). Heredity, 93: 166–174.

Garstang, W. 1900. The plague of octopus on the south coast, and its effect on the crab and lobster fisheries. Journal of the Marine Biological Association of the UK, 6: 260–273.

Gauvrit, E., Le Goff, R., and Daguzan, J. 1997. Reproductive cycle of the cuttlefish, *Sepia officinalis* (L.), in the northern part of the Bay of Biscay. Journal of Molluscan Studies, 63: 19–28.

Georgakarakos, S., Koutsoubas, D., and Valavanis, V. 2006. Time series analysis and forecasting techniques applied on loliginid and ommastrephid landings in Greek waters. Fisheries Research, 78: 55–71.

Gestal, C., Belcari, P., Abollo, E., and Pascual, S. 1999. Parasites of cephalopods in the northern Tyrrhenian Sea (western Mediterranean): new host record and host specificity. Scientia Marina, 63: 39–43.

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

Glass, C. W., Sarno, B., Milliken, H. O., Morris, G. D., and Carr, H. A. 1999. Bycatch reduction in Massachusetts inshore squid (*Loligo pealeii*) trawl fisheries. Marine Technology Society Journal, 33: 35–42.

Godinho, V. M. 1985. Os Descobrimentos e a Economia Mundial, Vol. II. Editorial Presença, Lisbon. 228 pp.

Goerke, H., Weber, K., Bornemann, H., Ramdohr, S., and Plötz, J. 2004. Increasing levels and biomagnification of persistent organic pollutants (POPs) in Antarctic biota. Marine Pollution Bulletin, 48: 295–302.

Gómez-Muñoz, V. M. 1990. A model to estimate catches from a short fishery statistics survey. Bulletin of Marine Science, 46: 719–722.

González, A. F., and Guerra, A. 1996. Reproductive biology of the short-finned squid *Illex coindetii* (Cephalopoda: Ommastrephilae) of the Northeastern Atlantic. Sarsia, 81: 107–118.

González, A. F., López, A., Guerra, A., and Barreiro, A. 1994a. Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. Fisheries Research, 21: 179–191.

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

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

González, A. F., Trathan, P., Yau, C., and Rodhouse, P. G. 1997. Interactions between oceanography, ecology and fisheries of ommastrephid squid in the South Atlantic. Marine Ecology Progress Series, 152: 205–215.

González, A. F., Dawe, E. G., Beck, P. C., and Perez, J. A. A. 2000. Bias associated with statolith-based methodologies for ageing squid; a comparative study on *Illex illecebrosus* (Cephalopoda: Ommastrephidae). Journal of Experimental Marine Biology and Ecology, 244: 161–180.

Gonźalez, A. F., Pascual, S., Gestal, C., Abollo, E., and Guerra, A. 2003. What makes a cephalopod a suitable host for a parasite? The case of Galician waters. Fisheries Research, 60: 177–183.

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

González, A. F., Otero, J., Pierce, G. J., and Guerra, A. 2010. Age, growth and mortality of *Loligo vulgaris* wild paralarvae: implications for understanding of the life cycle and longevity. ICES Journal of Marine Science, doi:10.1093/icesjms/fsq014.

González, M., and Sánchez, P. 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. Scientia Marina, 66(Suppl. 2): 199–208.

Gowland, F. C. 2002. Developmental variability in loliginid squid (*Loligo forbesi* and *Sepioteuthis australis*). PhD thesis, University of Aberdeen, UK.

Grisley, M. S., and Boyle, P. R. 1988. Recognition of food in octopus digestive tract. Journal of Experimental Marine Biology and Ecology, 118: 7–32.

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

Guerra, A. 1984. Cephalopods of the Ria de Vigo (NW of Spain): preliminary results. Cuadernos da Area de Ciencias Marinas. Seminario de Estudos Galegos, 1: 333–348.

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

Guerra, A. 1992. Mollusca, Cephalopoda. Fauna Ibérica, Vol. 1, Museo Nacional de Ciencias Naturales, Madrid. 327 pp.

Guerra, A., and Castro, B. G. 1988. On the life cycle of *Sepia officinalis* (Cephalopoda, Sepioidea) in the Ria Vigo (NW Spain). Cahiers de Biologie Marine, 29: 395–405.

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

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

Guerra, A., Simon, F., and González, A. F. 1993. Cephalopods in the diet of the swordfish, *Xiphias gladius*, from the northeastern Atlantic Ocean. *In* Recent Advances in Cephalopod Fisheries Biology, pp. 159–164. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokyo University Press, Tokyo. 752 pp.

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

Guerra, A., Gracia, J., González, A., and Rocha, F. (Eds). 2000. Development of software to estimate unreported and misreported catch and effort data and to apply fishery management models. Final Report to the Commission of the European Communities Directorate General for Fisheries on Study No. 97/0107. Instituto de Investigaciones Marinas, CSIC, Vigo, Spain.

Guerra, A., Perez-Losada, M., Rocha, F., and Sanjuan, A. 2001. Species differentiation of *Sepia officinalis* and *Sepia hierredda* (Cephalopoda: Sepiidae) based on morphological and allozyme analyses. Journal of the Marine Biological Association of the UK, 81: 271–281.

Gutowska, M. A., and Melzner, F. 2009. Abiotic conditions in cephalopod (*Sepia officinalis*) eggs: embryonic development at low pH and high pCO_2. Marine Biology, 156: 515–519.

Gutowska, M. A., Pörtner, H. O., and Melzner, F. 2008. Growth and calcification in the cephalopod *Sepia officinalis* under elevated seawater pCO_2. Marine Ecology Progress Series, 373: 303–309.

Hamabe, M., Hamuro, M., and Ogura, M. 1982. Squid Jigging from Small Boats. FAO Fishing Manuals, Fishing News Books, Farnham, Surrey, UK. 84 pp.

Hanlon, R. T., and Forsythe, J. W. 1990a. Diseases caused by microorganisms. *In* Diseases of Marine Animals. Vol. III: Cephalopoda to Urochordata: Diseases of Mollusca: Cephalopoda, pp. 23–46. Ed. by O. Kinne. Biologische Anstalt Helgoland, Hamburg. 696 pp.

Hanlon, R. T., and Forsythe, J. W. 1990b. Structural abnormalities and neoplasia. *In* Diseases of Marine Animals. Vol. III: Cephalopoda to Urochordata: Diseases of Mollusca: Cephalopoda, pp. 203–204. Ed. by O. Kinne. Biologische Anstalt Helgoland, Hamburg. 696 pp.

Hanlon, R. T., and Messenger, J. 1998. Cephalopod Behaviour. Cambridge University Press, Cambridge, UK. 248 pp.

Hanlon, R. T., Turk, P. E., and Lee, P. G. 1991. Squid and cuttlefish mariculture: an updated perspective. Journal of Cephalopod Biology, 2: 31–40.

Hansen, B., Turrell, W. R., and Østerhus, S. 2001. Decreasing overflow from the Nordic seas into the Atlantic Ocean through the Faroe Bank channel since 1950. Nature, 411: 927–930.

Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofmann, E. E., *et al.* 1999. Emerging marine diseases–climate links and anthropogenic factors. Science, 285: 1505–1510.

Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S., and Samuel, M. D. 2002. Ecology–climate warming and disease risks for terrestrial and marine biota. Science, 296: 2158–2162.

Harwood, J. 2001. Marine mammals and their environment in the twenty-first century. Journal of Mammalogy, 82: 630–640.

Hastie, L. C. 1996. Estimation of trawl codend selectivity for squid (*Loligo forbesi*), based on Scottish research vessel survey data. ICES Journal of Marine Science, 53: 741–744.

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

Hastie, L. C., Pierce, G. J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U., and Robin, J-P. 2009a. Cephalopods in the north-east Atlantic: species, biogeography, ecology, exploitation and conservation. Oceanography and Marine Biology: An Annual Review, 47: 111–190.

Hastie, L. C., Nyegaard, M., Collins, M. A., Moreno, A., Pereira, J. M. F., Piatkowski, U., and Pierce, G. J. 2009b. Reproductive biology of the loliginid squid, *Alloteuthis subulata*, in the north-east Atlantic and adjacent waters. Aquatic Living Resources, 22: 35–44.

Heath, M. R., Adams, R. D., Brown, F., Dunn, J., Fraser, S., Hay, S. J., Kelly, M. C., *et al.* 1999a. Plankton Monitoring Off the East Coast of Scotland in 1997 and 1998. Fisheries Research Services, Aberdeen, UK, Report No. 13/99. 32 pp.

Heath, M. R., Beare, D. J., Dunn, J., Fraser, J. G., Hay, S. J., and Turrell, W. R. 1999b. Monitoring the Effects of Climate Change – Overwintering Abundance of *Calanus finmarchicus* in the Faroe-Shetland Channel. Fisheries Research Services, Aberdeen, UK, Report No. 14/99. 24 pp.

Henderson, A. C., and Williams, R. S. 2001. A new record of the sharpnose seven-gill shark *Heptranchias perlo*, from the north-east Atlantic. Journal of the Marine Biological Association of the UK, 81: 707–708.

Hendrickson, L. C., and Hart, D. R. 2006. An age-based cohort model for estimating the spawning mortality of semelparous cephalopods with an application to per-recruit calculations for the northern shortfin squid, *Illex illecebrosus*. Fisheries Research, 78: 4–13.

Hermosilla, C. A., Rocha, F., Gonzalez, A. F., Guerra, A., and Fiorito, G. 2009. Age validation in common octopus, *Octopus vulgaris* using stylet increment analysis. *In* Cephalopod International Advisory Council (CIAC) Symposium, 3–11 September 2009, Vigo, Spain, Abstracts, p. 73. CIAC. 98 pp. Available online at http://www.abdn.ac.uk/ciac.

Hernández-García, V. 1992. Preliminary notes about feeding of three species of flying squids (Cephalopoda, Ommastrephidae) in the Northwest Africa CECAF area. ICES Document CM 1992/K:24. 13 pp.

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

Hernández-García, V., Piatkowski, U., and Clarke, M. R. 1998a. Development of the darkening of *Todarodes sagittatus* beaks and its relation to growth and reproduction. South African Journal of Marine Science, 20: 363–373.

Hernández-García, V., Hernández-López, J. L., and Castro, J. J. 1998b. The octopus (*Octopus vulgaris*) in the small-scale trap fishery off the Canary Islands (Central-East Atlantic). Fisheries Research, 35: 183–189.

Hernández-García, V., Hernández-López, J. L., and Castro-Hernández, J. J. 2002. On the reproduction of *Octopus vulgaris* off the coast of the Canary Islands. Fisheries Research, 57: 197–203.

Hernández-López, J. L., Castro-Hernández, J. J., and Hernández-Garcia, V. 2001. Age determined from the daily deposition of concentric rings on common octopus (*Octopus vulgaris*) beaks. Fisheries Bulletin, 99: 679–684.

Hoberg, E. P., and Klassen, G. J. 2002. Revealing the faunal tapestries, co-evolution and historical biogeography of hosts and parasites in marine systems. Parasitology, 124: S3–S22.

Hobson, K. A., and Cherel, Y. 2006. Isotopic reconstruction of marine food webs using cephalopod beaks: new insight from captively raised Sepia *officinalis*. Canadian Journal of Zoology, 84: 766–770.

Hobson, K. A., Piatt, J. F., and Pitocchelli, J. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology, 63: 786–798.

Hochberg, F. G. 1983. The parasites of cephalopods, a review. Memoirs of the National Museum of Victoria, 44: 109–145.

Hochberg, F. G. 1990. Diseases caused by protistans and mesozoans. *In* Diseases of Marine Animals. Vol. III: Cephalopoda to Urochordata: Diseases of Mollusca: Cephalopoda, pp. 47–202. Ed. by O. Kinne. Biologische Anstalt Helgoland, Hamburg. 696 pp.

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

Hornborg, S. 2005. The Swedish Cephalopod Fauna. Species composition and patterns of abundance. MSc thesis, University of Göteborg, Sweden. 39 pp.

Howard, F. G. 1979. Recent trends in the Scottish fishery for *Loligo forbesi* together with some notes on the biology of the species. ICES Document CM 1979/K:36. 4 pp., 17 figures.

Howard, F. G., Ngoile, M. A., and Mason, J. 1987. *Loligo forbesi*: its present status in Scottish fisheries. ICES Document CM 1987/K:5. 4 pp., 17 figures.

Hubert, W. A. 1996. Passive capture techniques. *In* Fisheries Techniques, pp. 157–192. Ed. by B. R. Murphy and D. W. Willis. American Fisheries Society, Bethesda, MD. 732 pp.

Hughes, S. E. 1998. Growth history patterns in squid as assessed by gladius structure. PhD thesis, University of Aberdeen, UK.

Hulme, M., Jenkins, G. J., Lu, X., Turnpenny, J. R., Mitchell, T. D., Jones, R. G., Lowe, J., *et al.* 2002. Climate Change Scenarios for the UK: The UKCIP02 Scientific Report. Tyndall Centre for Climate Change Research, Norwich. 120 pp.

ICES. 2000. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH). ICES Document CM 2000/G:04. 61 pp.

ICES. 2004a. Report of the Working Group on Cephalopod Fisheries and Life History. ICES Document CM 2004/G:02. 37 pp.

ICES. 2004b. The Annual ICES Ocean Climate Status Summary 2003/2004. ICES Cooperative Research Report No. 269. 32 pp.

ICES. 2008. Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH). ICES Document CM 2008/LRC:14. 49 pp.

ICES. 2009. Report of the Working Group on Cephalopod Life History and Fisheries (WGCEPH). ICES Document CM 2009/LRC:06. 72 pp.

Ichii, T., Mahapatra, K., Okamura, H., and Okada, Y. 2006. Stock assessment of the autumn cohort of neon flying squid (*Ommastrephes bartramii*) in the North Pacific based on past large-scale high seas driftnet fishery data. Fisheries Research, 78: 286–297.

Iglesias, J., Sánchez, F. J., and Otero, J. J. 1996. The octopus (*Octopus vulgaris* Cuvier): a candidate for aquaculture? ICES Document CM 1996/F:10. 5 pp.

Iglesias, J., Sánchez, F. J., and Otero, J. J. 1997. Primerias experiencias sobre el cultivo integral del pulpo (*Octopus vulgaris* Cuvier) en el Instituto Español de Oceanografía. *In* Actas del VI Congreso Nacional de Acuicultura, 9–11 July 1997, Cartegena, Spain, pp. 221–226. Ed. by J. Costa, E. Abellan, A. Garcia, B. Ortega, and S. Zamora. Ministerio de Agricultura, Pesca y Alimentación, Madrid.

Iglesias, J., Sánchez, F. J., Otero, J. J., and Moxica, C. 2000. Culture of octopus: present, knowledge, problems and perspectives. Cahiers Options Méditerranéennes, 47*:* 313–321.

Iglesias, J., Otero, J. J., Moxica, C., Fuentes, L., and Sánchez, F. J. 2004. The completed life cycle of the octopus (*Octopus vulgaris*, Cuvier) under culture conditions: paralarval rearing using *Artemia* and zoeae, and first data on juvenile growth up to 8 months of age. Aquaculture International, 12: 481–487.

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

Iglesias, J., Sánchez, F. J., Bersano, J. G. F., Carrasco, J. F., Dhont, J., Fuentes, L., Linares, L., *et al.* 2007. Rearing of *Octopus vulgaris* paralarvae: present status, bottlenecks and trends. Aquaculture, 266: 1–15.

Ikeda, Y., Onaka, S., Takai, N., Kidokoro, H., Arai, N., and Sakamoto, W. 1998. Migratory routes of the Japanese common squid (*Todarodes pacificus*) inferred from analyses of statolith trace elements, and nitrogen and carbon stable isotopes. ICES Document CM 1998/M:11. 4 pp.

Ikeda, Y., Arai, N., Kidokoro, H., and Sakamoto, W. 2003. Strontium: calcium ratios in statoliths of Japanese common squid *Todarodes pacificus* (Cephalopoda: Ommastrephidae) as indicators of migratory behaviour. Marine Ecology Progress Series, 251: 169–179.

ICZN (International Commission on Zoological Nomenclature). 1954. Opinion 233: Suppression under the plenary powers, of the name "Octopodia", Schneider, 1784 (Class Cephalopoda), and certain reputed names published by the same author in 1784. Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature, 4: 275–296.

ICZN (International Commission on Zoological Nomenclature). 1997. Opinion 1861: *Octopus vulgaris* Cuvier, 1797 and *Loligo vulgaris* Lamarck, 1798 (Mollusca, Cephalopoda): Specific Names Conserved. Bulletin of Zoological Nomenclature, 54: 59–61.

IPCC. 2001. Climate Change 2001: The Scientific Basis. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK. 881 pp.

Ishimatsu, A., Hayashi, M., and Kikkawa, T. 2008. Fishes in high-CO_2, acidified oceans. Marine Ecology Progress Series, 373: 295–302.

IUCN, UNEP, and WWF. 1980. World Conservation Strategy: Living Resource Conservation for Sustainable Development. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Iverson, S. J., Field, C., Bowen, W. D., and Blanchard, W. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs, 74: 211–235.

IWC. 1997. Report of the IWC workshop on climate change and cetaceans. Report of the International Whaling Commission, 47: 293–313.

Jackson, G. D. 1994. Application and future potential of statolith increment analysis in squids and sepioids. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2612–2625.

Jackson, G. D., and Moltschaniwskyj, N. A. 2002. Spatial and temporal variation in growth rates and maturity in the Indo-Pacific squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae). Marine Biology, 140: 747–754.

Jackson, G. D., and O'Dor, R. K. 2001. Time, space and the ecophysiology of squid growth, life in the fast lane. Vie et Milieu, 51: 205–215.

Jackson, G. D., Forsythe, J. W., Hixon, R. F., and Hanlon, R. T. 1997. Age, growth, and maturation of *Lolliguncula brevis* (Cephalopoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length–frequency vs. statolith age analysis. Canadian Journal of Fisheries and Aquatic Sciences, 54: 2907–2919.

Jackson, G. D., Alford, R. A., and Choat, J. H. 2000. Can length frequency analysis be used to determine squid growth? – An assessment of ELEFAN. ICES Journal of Marine Science, 57: 948–954.

Jackson, G. D., Bustamante, P., Cherel, Y., Fulton, E. A., Grist, E. P. M., Jackson, C. H., Nichols, P. D., *et al.* 2007. Applying new tools to cephalopod trophic dynamics and ecology: perspectives from the Southern Ocean Cephalopod Workshop, 2–3 February 2006. Reviews in Fish Biology and Fisheries, 17: 79–99.

Jackson, L. E., Kurtz, J. C., and Fisher, W. S. (Eds). 2000. Evaluation Guidelines for Ecological Indicators. EPA/620/R-99/005. US Environmental Protection Agency, Office of Research and Development, Research Triangle Park, NC. 107 pp.

Jaeckel, S. 1937. Tintenfische in der westlichen Ostsee. Archiv für Molluskenkunde, 69: 129–136.

Jangaard, P. M., and Ackman, R. G. 1965. Lipids and component fatty acids of the Newfoundland squid *Illex illecebrosus* (LeSueur). Journal of the Fisheries Research Board of Canada, 22: 131–137

Jereb, P., and Ragonese, S. 1986. Un esemplare di *Loligo forbesi* di notevoli dimensioni proveniente dalla pesca locale di Mazara del Vallo (Canale di Sicilia). Nova Thalassia, 8(Suppl. 3): 675–676).

Jereb, P., and Ragonese, S. 1990. Sui Cefalopodi di scarso o nullo interesse commerciale nel Canale di Sicilia. Oebalia, 16: 689–692.

Jereb, P., and Ragonese, S. 1991. *Sepia elegans* and *Sepia orbignyana*: first studies on the presence of the elegant and pink cuttlefish in the Sicilian Channel. *In* La Seiche: the Cuttlefish, 1st International Symposium on the Cuttlefish *Sepia*, 1–3 June 1989, Caën, pp. 17–29. Ed. by E. Boucaud-Camou. Centre de Publications de l'Université de Caën, Caën, France. 358 pp.

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

Jereb, P., and Roper, C. F. E. (Eds). 2005. Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Volume 1. Chambered Nautiluses and Sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO Species Catalogue for Fisheries Purposes No. 4(1). 294 pp.

Jereb, P., Ragonese, S., and Boletzky, S. v. 1991. Squid Age Determination Using Statoliths. Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy, 9–14 October 1989. NTR-ITTP Special Publication No. 1. 124 pp.

Jónsson, E. 1998. Study of biology of European flying squid, *Todarodes sagittatus* (Lamarck), occurring in deep waters south off Iceland. ICES Document CM 1998/M:48. 14 pp.

Joubin, L. 1895. Contribution à l'étude des Céphalopodes de l'Atlantique Nord. Resultats des Campagnes Scientifiques Accomplies par le Prince Albert I, Monaco, 9: 1–63.

Joy, J. B. 1990. The fishery biology of *Todarodes sagittatus* in Shetland waters. Journal of Cephalopod Biology, 1: 1–20.

Kaiser, S., and Barnes, D. K. A. 2008. Southern Ocean deep-sea biodiversity: sampling strategies and predicting responses to climate change. Climate Research, 37: 165–179.

Kang, D. Y., Mukai, T., Iida, K., Hwang, D. J., and Myoung, J. G. 2005. The influence of tilt angle on the acoustic target strength of the Japanese common squid (*Todarodes pacificus*). ICES Journal of Marine Science, 62: 779–789.

Kang, Y. S., Kim, J. Y., Kim, H. G., and Park, J. H. 2002. Long-term changes in zooplankton and its relationship with squid, *Todarodes pacificus*, catch in Japan/East Sea. Fisheries Oceanography, 11: 337–346.

Katsanevakis, S., and Verriopoulos, G. 2004. Abundance of *Octopus vulgaris* on soft sediment. Scientia Marina, 68: 553–560.

Katsanevakis, S., and Verriopoulos, G. 2006. Modelling the effect of temperature on hatching and settlement patterns of meroplanktonic organisms: the case of the octopus. Scientia Marina, 70: 699–708.

Kawabata, A. 1999. Measurement of the target strength of Japanese flying squid, *Todarodes pacificus* Steenstrup. Bulletin of Tohoku National Fisheries Research Institute, 61: 29–40.

Kawabata, A. 2005. Target strength measurements of suspended live ommastrephid squid, *Todarodes pacificus*, and its application in density estimations. Fisheries Science, 71: 63–72.

Kear, A. J. 1992. The diet of Antarctic squid – comparison of conventional and serological gut contents analyses. Journal of Experimental Marine Biology and Ecology, 156: 161–178.

Keyl, F., Argüelles, J., Mariátegui, L., Tafur, R., Wolff, M., and Yamashiro, C. 2008. A hypothesis on range expansion and spatio-temporal shifts in size-at-maturity of jumbo squid (*Dosidicus gigas*) in the eastern Pacific Ocean. CalCOFI Report, 49: 119–128.

Khromov, D. N., Lu, C. C., Guerra, A., Dong, Zh., and Boletzky, S. v. 1998. A synopsis of Sepiidae outside Australian waters (Cephalopoda: Sepioidea). *In* Systematics and Biogeography of Cephalopods, pp. 77–157. Ed. by N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney. Smithsonian Contributions to Zoology No. 586(I). Smithsonian Institution Scholarly Press, Washington, DC. 276 pp.

Kikkawa, T., Watanabe, Y., Katayama, Y., Kita, J., and Ishimatsu, A. 2008. Acute CO_2 tolerance limits of juveniles of three marine invertebrates, *Sepia lycidas*, *Sepioteuthis lessoniana*, and *Marsupenaeus japonicus*. Plankton and Benthos Research, 3: 184–187.

Kishi, M. J., Nakajima, K., Fujii, M., and Hashioka, T. 2009. Environmental factors which affect growth of Japanese common squid, *Todarodes pacificus*, analyzed by a bioenergetics model coupled with a lower trophic ecosystem model. Journal of Marine Systems, 78: 278–287.

Korzun, Y., Nesis, K. N., Nigmatullin, C., Ostapenko, A. A., and Pinchukov, M. A. 1979. New data on the distribution of squids, family Ommastrephidae, in the world ocean. Oceanologia, 19: 472–475.

Koueta, N., and Boucaud-Camou, E. 1999. Food intake and growth in reared early juvenile cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda). Journal of Experimental Marine Biology and Ecology, 240: 93–109.

Koueta, N., and Boucaud-Camou, E. 2001. Basic growth relations in experimental rearing of early juvenile cuttlefish *Sepia officinalis* L. (Mollusca, Cephalopoda). Journal of Experimental Marine Biology and Ecology, 265: 75–87.

Koueta, N., and Boucaud-Camou, E. 2003. Combined effects of photoperiod and feeding frequency on survival and growth of juvenile cuttlefish *Sepia officinalis* L. in experimental rearing. Journal of Experimental Marine Biology and Ecology, 296: 215–226.

Koueta, N., Boucaud-Camou, E., and Noel, B. 2002. Effects of enriched natural diet on survival and growth of juvenile cuttlefish *Sepia officinalis* L. Aquaculture, 203: 293–310.

Koueta, N., Andrade, J. P., and Boletzky, S. v. (Eds). 2006. The cuttle *Sepia officinalis*. Vie et Milieu, 56.

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

Lacoue-Labarthe, T., Warnau, M., Oberhänsli, F., Teyssié, J-L., Koueta, N., and Bustamante, P. 2008a. Differential bioaccumulation behaviour of Ag and Cd during the early development of the cuttlefish *Sepia officinalis*. Aquatic Toxicology, 86: 437–446.

Lacoue-Labarthe, T., Warnau, M., Oberhänsli, F., Teyssié, J-L., Jeffree, R., and Bustamante, P. 2008b. First experiments on the maternal transfer of heavy metals in the cuttlefish, *Sepia officinalis*. Marine Pollution Bulletin, 57: 826–831.

Lacoue-Labarthe, T., Bustamante, P., Hörlin, E., Luna-Acosta, A., Bado-Nilles, A., and Thomas-Guyon, H. 2009a. Phenoloxidase activation in the embryo of the common cuttlefish *Sepia officinalis* and responses to the Ag and Cu exposure. Fish and Shellfish Immunology, 27: 516–521.

Lacoue-Labarthe, T., Martin, S., Oberhänsli, F., Teyssié, J-L., Markich, S., Jeffree, R., and Bustamante, P. 2009b. Effects of increased pCO_2 and temperature on trace element (Ag, Cd and Zn) bioaccumulation in the eggs of the common cuttlefish, *Sepia officinalis*. Biogeosciences Discussions, 6: 4865–4894.

Lafferty, K. D. 1997. Environmental parasitology: what can parasite tell us about human impacts on the environment? Parasitology Today, 13: 251–255.

Lafferty, K. D., and Holt, R. D. 2003. How should environmental stress affect the population dynamics of disease? Ecology Letters, 6: 654–664.

Lahaye, V., Bustamante, P., Spitz, J., Dabin, W., Das, K., Pierce, G. J., and Caurant, F. 2005. Long-term dietary segregation of common dolphins (*Delphinus delphis*) in the Bay of Biscay, determined using cadmium as an ecological tracer. Marine Ecology Progress Series, 305: 275–285.

Landman, N. H., Cochran, J. K., Cerrato, R., Mak, J., Roper, C. F. E., and Lu, C. C. 2004. Habitat and age of the giant squid (*Architeuthis sanctipauli*) inferred from isotopic analysis. Marine Biology, 144: 685–691.

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

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

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

Le Bihan, E. 2006. Valorisation de co-produits issus de la pêche des céphalopodes: applications á la seiche *Sepia officinalis.* PhD thesis, University of Caën, France. 316 pp.

Lee, P. G. 1994. Nutrition of cephalopods: fuelling the system. Marine and Freshwater Behaviour and Physiology, 25: 35–51.

Lee, P. G., Forsythe, J. W., DiMarco, F. P., DeRusha, R. H., and Hanlon, R. T. 1991. Initial palatability and growth trials on pelleted diets for cephalopods. Bulletin of Marine Science, 49: 362–372.

Lefkaditou, E. 2006. Taxonomy and biology of cephalopods in the North Aegean Sea. PhD thesis, University of Patras, Greece. 298 pp.

Lefkaditou, E., and Adamidou, A. 1997. Beach-seine fisheries in the Thracian Sea. Preliminary results. *In* Proceedings of the 5th Pan-Hellenic Symposium of Oceanography and Fisheries, Kavala, Greece, 15–18 April 1997, Vol. II, pp. 21–24 (in Greek, abstract in English).

Lefkaditou, E., and Papaconstantinou, C. 1995. Distribution, growth and maturity of *Eledone cirrhosa* (Cephalopoda: Octopoda) in the Thracian Sea (Eastern Mediterranean). Rapports de la Commission Internationale de la Mer Méditerranée, 34: 247.

Lefkaditou, E., Siapatis, A., and Papaconstantinou, C. 1998a. Seasonal and spatial changes in the abundance and distribution of *Eledone moschata* (Cephalopoda: Octopoda), in the South Aegean Sea (Eastern Mediterranean). ICES Document CM 1998/M:44. 8 pp.

Lefkaditou, E., Sánchez, P., Tsangridis, A., and Adamidou, A. 1998b. A preliminary investigation on how meteorological changes may affect beach-seine catches of *Loligo vulgaris* in the Thracian Sea (Eastern Mediterranean). South African Journal of Marine Science, 20: 453–461.

Lefkaditou, E., Souplet, A., Peristeraki, N., González, M., Kavadas, S., Vidoris, P., Cuccu, D., *et al.* 2000. Preliminary investigation of factors affecting the spatial distribution and abundance of *Eledone cirrhosa* (Cephalopoda: Octopoda) in the Mediterranean Sea. *In* Demersal Resources in the Mediterranean, pp. 53–63. Ed. by J. A. Bertrand and G. Relini. Actes de Colloques 26, Ifremer, Plouzané, France. 240 pp.

Lefkaditou, E., Papaconstantinou, C., Tsangridis, A., and Leondarakis, P. 2001. Contribution of cephalopods to the artisanal and trawl fisheries in the Thracian Sea. *In* 10th Panhellenic Ichthyological Congress on Management and Sustainable Development of Water Resources and Nearby Regions, Chania, Greece, 18–20 October, pp. 45–48 (in Greek, abstract in English).

Lefkaditou, E., Kavadas, S., and Papaconstantinou, C. 2002. Cephalopod fisheries statistics in Greek waters (NE Mediterranean). ICES Document CM 1999/G:4. 6 pp.

Lefkaditou, E., Mytilineou, C., Maiorano, P., and D'Onghia, G. 2003a. Cephalopod species captured by deep-water exploratory trawling in the northeastern Ionian Sea. Journal of Northwest Atlantic Fishery Science, 31: 431–440.

Lefkaditou, E., Adamidou, A., Leondarakis, P., Tsangridis A., and Papaconstantinou, C. 2003b. Fyke net fishery of the common octopus, *Octopus vulgaris,* in the Thracian Sea. *In* Proceedings of the 11th Panhellenic Ichthyological Congress on Advances and Development of Science and Technology in Fisheries-Aquaculture and Management of Water Resources, Preveza, Greece, 10–13 April 2003, pp. 295–298 (in Greek, abstract in English).

Lefkaditou, E., Haralabous, J., Sarikas, D., Karamelidou, S., and Kavadas, S. 2004. The cephalopods in the small-scale fishery in the eastern Thracian Sea (NE Mediterranean). ICES Document CM 2004/CC:19. 12 pp.

Lefkaditou, E., Verriopoulos, G., and Valavanis, V. 2007. The research on cephalopod resources in Greece. *In* State of Hellenic Fisheries, pp. 440–451. Ed. by C. Papaconstantinou, A. Zenetos, C. Vassilopoulou, and G. Tserpes. Hellenic Centre for Marine Research, Institute of Marine Biological Resources, Athens, Greece. 466 pp.

Lefkaditou, E., Politou, C. Y., Palialexis, A., Dokos, J., Cosmopoulos, P., and Valavanis, V. D. 2008. Influences of environmental variability on the population structure and distribution patterns of the short-fin squid *Illex coindetii* (Cephalopoda: Ommastrephidae) in eastern Ionian Sea. Hydrobiologia, 612: 71–90.

Lenzi, F., Cittolin, G., Ingle, E., and Tibaldi, E. 2002. Allevamento del polpo *(Octopus vulgaris)*: riproduzione e allevamento larvale in avannotteria industriale. *In* Ricerca per lo sviluppo dell'Acquacoltura Toscana, pp. 73–83. Ed. by D. Lanari and E. Ribaldi. Associazione Piscicoltori Italiani, Verona. 209 pp.

Leporati, S. C., Semmens, J. M., and Pecl, G. T. 2008. Determining the age and growth of wild octopus using stylet increment analysis. Marine Ecology Progress Series, 367: 213–222.

Lipinski, M., and Soule, M. 2007. A new direct method of stock assessment of the loliginid squid. Reviews in Fish Biology and Fisheries, 17: 437–453.

Lipinski, M., Payne, A., and Rose, B. 1992. The importance of cephalopods as prey for hake and other groundfish in South African waters. South African Journal of Marine Science, 12: 651–662.

Lipinski, M. R., and Durholtz, M. D. 1994. Problems associated with ageing squid from their statoliths: towards a more structured approach. Antarctic Science, 6: 215–222.

Lo Bianco, S. 1909. Notizie biologiche reguardanti specialmente il periodo di maturàsessuale degli animali del Golfo di Napoli. Mitteilungen aus der Zoologischen Station zu Neapel, 19: 51–761.

López, A. 2002. Estatus dos pequenos cetáceos da plataforma de Galicia. PhD thesis, University of Santiago de Compostela, Spain. 337 pp.

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

Lordan, C., Burnell, G. M., and Cross, T. F. 1998. The diet and ecological importance of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Irish waters. South African Journal of Marine Science, 20: 153–163.

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

Lordan, C., Warnes, S., Cross, T. F., and Burnell, G. M. 2001b. The distribution and abundance of cephalopod species caught during demersal trawl surveys west of Ireland and in the Celtic Sea. Irish Fisheries Investigations (New Series), 8: 1–26.

Lorrain, A., Graham, B., Ménard, F., Popp, B., Bouillon, S., van Breugel, P., and Cherel, Y. 2009. Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. Marine Ecology Progress Series, 391: 293–306.

Lourenço, S., and Pereira, J. 2006. Estimating standardised landings per unit effort for an octopus mixed components fishery. Fisheries Research, 78: 89–95.

Lozier, J. D., Aniello, P., and Hickerson, M. J. 2009. Predicting the distribution of Sasquatch in western North America: anything goes with ecological niche modelling. Journal of Biogeography, 36: 1623–1627.

Luaces, C. M., and Rey-Mendez, M. 2001. El engorde industrial del pulpo (*Octopus vulgaris*) en jaulas: análisis de dos años de cultivo en la Ría de Camariñas (Galicia). *In* Convergencia entre investigación y empresa: un reto para el siglo XXI. Selección de comunicaciones presentada en el 7º Congreso Nacional de Acuicultura, celebrado en Las Palmas de Gran Canaria 19, 20 y 21 de mayo de 1999, pp. 184–189. Ed. by H. Fernández-Palacios Barber and M. Izquierdo. Monografías del Instituto Canario de Ciencias Marinas 4. 586 pp.

Lukeneder, A., Harzhauser, M., Mullegger, S., and Piller, W. E. 2008. Stable isotopes ($\delta^{18}O$ and $\delta^{13}C$) in *Spirula spirula* shells from three major oceans indicate developmental changes paralleling depth distributions. Marine Biology, 154: 175–182.

Lum-Kong, A. 1989. The reproductive biology of female *Loligo forbesi* Steenstrup (Cephalopoda: Myopsia). PhD thesis, University of Aberdeen, UK.

Lum-Kong, A., and Hastings, T. S. 1992. The accessory nidamental glands of *Loligo forbesi* (Cephalopoda: Loliginidae): characterization of symbiotic bacteria and preliminary experiments to investigate factors controlling sexual maturation. Journal of Zoology, London, 228: 395–403.

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

Luque, J. L., and Oliva, M. E. 1999. Metazoan parasite infracommunities of *Menticirrhus ophicephalus* (Teleostei: Sciaenidae): an amphi-oceanic approximation. Journal of Parasitology, 85: 379–381.

Machias, A., Vassilopoulou, V., Vatsos, D., Bekas, P., Kallianiotis, A., Papaconstantinou, C., and Tsimenides, N. 2001. Bottom trawl discards in the northeastern Mediterranean Sea. Fisheries Research, 53: 181–195.

Madelaine, B., and Aquab, T. 1991. Cuttlefish trapping fishery on Calvados coasts. *In* La Seiche: the Cuttlefish, 1st International Symposium on the Cuttlefish *Sepia*, 1–3 June 1989, Caën, p. 350. Ed. by E. Boucaud-Camou. Centre de Publications de l'Université de Caën, Caën, France. 358 pp.

Madureira, L., Habiaga, R., Soares, C., Weigert, S., Ferreira, C., Eliseire, D., and Duvoisin, A. C. 2005. Identification of acoustic records of the Argentinean Calamar *Illex argentinus* (Castellanos, 1960) along the outer shelf and shelf break of the south and southeast coast of Brazil. Fisheries Research, 73: 251–257.

Malham, S. K., and Runham, N. W. 1998. A brief review of the immunobiology of *Eledone cirrhosa*. South African Journal of Marine Science, 20: 385–391.

Malham, S. K., Lacoste, A., Cueff, A., Jalabert, F., Gélébart, F., and Poulet, S. A. 2002. A first insight into stress-induced neuroendocrine and immune changes in the octopus *Eledone cirrhosa*. Aquatic Living Resources, 15: 187–192.

Maltagliati, F., Belcari, P., Casu, D., Casu, M., Sartor, P., Vargiu, G., and Castelli, A. 2002. Allozyme genetic variability and gene flow in *Octopus vulgaris* (Cephalopoda, Octopodidae) from the Mediterranean Sea. Bulletin of Marine Science, 71: 473–486.

Mangold, K. 1983. *Eledone moschata*. *In* Cephalopod Life Cycles. Vol. I: Species Accounts, pp. 381–400. Ed. by P. R. Boyle. Academic Press, London. 475 pp.

Mangold, K. 1987. Reproduction. *In* Cephalopod Life Cycles. Vol. II: Comparative Reviews, pp. 157–200. Ed. by P. R. Boyle. Academic Press, London. 441 pp.

Mangold, K. 1997. *Octopus vulgaris*: review of the biology. *In* Proceedings of the Workshop on the Fishery and Market Potential of Octopus in California, pp. 85–90. Ed. by M. A. Lang and F. G. Hochberg. Smithsonian Institution, Washington, DC. 190 pp.

Mangold, K., and Boletzky, S. v. 1973. New data on reproductive biology and growth of *Octopus vulgaris.* Marine Biology, 19: 7–12.

Mangold, K., and Boletzky, S. v. 1987. Cephalopodes. *In* Fiches FAO d'identification des espèces pour les besoins de la pêche. Méditeranée et Mer Noire – Zone de Pêche, 37(1): Végétaux et Invertébrés, pp. 633–714. FAO, Rome. 760 pp.

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

Marcogliese, D. J. 2001. Implications of climate change for parasitism of animals in the aquatic environment. Canadian Journal of Zoology, 79: 1331–1352.

Marshall, C. T., O'Brien, L., Tomkiewicz, J., Marteinsdóttir, G., Morgan, M. J., Saborido-Rey, F., Köster, F., *et al.* 2003. Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. Journal of Northwest Atlantic Fishery Science, 33: 161–190.

Marshall, C. T., Needle, C. L., Thorsen, A., Kjesbu, O. S., and Yaragina, N. A. 2006. Systematic bias in estimates of reproductive potential of a cod (*Gadus morhua*) stock: implications for stock/recruit theory and management. Canadian Journal of Fisheries and Aquatic Sciences, 63: 980–994.

Martinez, P., Belcari, P., Sanjuan, A., and Guerra, A. 2005. Allozyme analysis of geographical and seasonal variation of *Illex coindetii* (Cephalopoda: Ommastrephidae) from central Mediterranean and Iberian Atlantic. Journal of the Marine Biological Association of the UK, 85: 177–184.

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

Martins, M. C. 2003. Outros moluscos: o polvo *Octopus vulgaris*. Portugala: noticiário malacológico, 2: 5–6.

Massuti, E., Deudero, S., Sánchez, P., and Morales-Nin, B. 1998. Diet and feeding of dolphin (*Coryphaena hippurus*) in western Mediterranean waters. Bulletin of Marine Science, 63: 329–341.

Massy, M. 1928. The Cephalopoda of the Irish Coast. Proceedings of the Royal Irish Academy, 33: 25–37.

Mattei, N., Cesarini, A., and Tibaldi, E. 2002. Allevamento del polpo (*Octopus vulgaris*): esperienze di allevamento e condizionamento alla riproduzione di adulti selvatici. *In* Ricerca per lo sviluppo dell'Acquacoltura Toscana, pp. 85–92. Ed. by D. Lanari and E. Ribaldi. Associazione Piscicoltori Italiani, Verona. 209 pp.

Mazon, M. J., Piedecausa, M. A., Hernández, M. D., and Garcia Garcia, B. 2007. Evaluation of environmental nitrogen and phosphorus contributions as a result of intensive ongrowing of common octopus (*Octopus vulgaris*). Aquaculture, 266: 226–235.

McAllister, M. K., Hill, S. L., Agnew, D. J., Kirkwood, G. P., and Beddington, J. R. 2004. A Bayesian hierarchical formulation of the DeLury stock assessment model for abundance estimation of Falkland Islands' squid. Canadian Journal of Fisheries and Aquatic Sciences, 61: 1048–1059.

Meyer, M., and Smale, M. J. 1991. Predation patterns of demersal teleosts from the Cape South and West coasts of South Africa. 1. Pelagic predators. South African Journal of Marine Science, 10: 173–191.

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

Mikalsen, K. H., and Jentoft, S. 2008. Participatory practices in fisheries across Europe: Making stakeholders more responsible. Marine Policy, 32: 169–177.

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

Miramand, P., Bustamante, P., Bentley, D., and Kouéta, N. 2006. Variation of heavy metal concentrations (Ag, Cd, Co, Cu, Fe, Pb, V, and Zn) during the life cycle of the common cuttlefish *Sepia officinalis*. Science of the Total Environment, 361: 132–143.

Miyahara, K., Ota, T., Kohno, N., Ueta, Y., and Bower, J. R. 2005. Catch fluctuations of the diamond squid *Thysanoteuthis rhombus* in the Sea of Japan and models to forecast cpue based on analysis of environmental factors. Fisheries Research, 72: 71–79.

Moline, M. A., Claustre, H., Frazer, T. K., Schofields, O., and Vernet, M. 2004. Alterations of the food web along the Antarctic Peninsula in response to a regional warming trend. Global Change Biology, 10: 1973–1980.

Moltschaniwskyj, N. A., Staudinger, M., van Gelderen, R., Villanueva, R., Warnke, K., Hall, K., Lipinski, M. R., *et al.* 2007. Ethical and welfare considerations when using cephalopods as experimental animals. Reviews in Fish Biology and Fisheries, 17: 455–476.

Montevecchi, W. A., and Myers, R. A. 1997. Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the northwest Atlantic: implications for climate change. ICES Journal of Marine Science, 54: 608–614.

Moreno, A. 2001. Idade e crescimento da lula vulgar (*Loligo vulgaris* Lamarck, 1798) da costa portuguesa através da análise da micro-estrutura dos estatólitos. Provas de Acesso à Categoria de Assistente de Investigação, IPIMAR, Lisbon. 169 pp.

Moreno, A. 2008. Geographic variation in cephalopod life history traits. Provas de Acesso à Categoria de Investigador Auxiliar, IPIMAR, Lisbon. 181 pp.

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

Moreno, A., Pereira, J. M. F., and Cunha, M. M. 1996. Age and growth of the squid *Loligo vulgaris* from Portuguese waters. ICES Document CM 1996/K:14. 17 pp.

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

Moreno, A., Pereira, J., and Cunha, M. M. 2005. Environmental influences on age and size-at-maturity of *Loligo vulgaris*. Aquatic Living Resources, 18: 377–384.

Moreno, A., Azevedo, M., Pereira, J., and Pierce, G. J. 2007. Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. Marine Biology Research, 3: 49–59.

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

Moriyasu, M. 1981. Biologie des peches de céphalopodes benthiques application aux *E. cirrhosa* (Lam. 1798) du Golfe du Lion. PhD thesis, Université des Sciences et Techniques du Languedoc, Montpellier, France.

Moriyasu, M. 1983. Etude biometrique de la croissance d'*E. cirrhosa* (Lam. 1798 (Cephalopoda, Octopoda)) du Golfe du Lion. Oceanologica Acta, 6: 35–41.

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

Morte, M. S., Redon, M. J., and Sanz-Brau, A. 2002. Diet of *Phycis blennoides* (Gadidae) in relation to fish size and season in the western Mediterranean (Spain). Marine Ecology, 23: 141–155.

Moxica, C., Linares, F., Otero, J. J., Iglesias, J., and Sánchez, F. J. 2002. Cultivo intensivo de paralarvas de pulpo, *Octopus vulgaris* Cuvier, 1797, en tanques de 9 m^3. Boletín del Instituto Español de Oceanografía, 18: 31–36.

Muirhead, S. J., and Furness, R. W. 1988. Heavy metal concentrations in the tissues of seabirds from Gough Island, South Atlantic Ocean. Marine Pollution Bulletin, 19: 278–283.

Murphy, J. M., Balguerías, E., Key, L. N., and Boyle, P. R. 2002. Microsatellite DNA markers discriminate between two *Octopus vulgaris* (Cephalopoda: Octopoda) fisheries along the northwest African coast. Bulletin of Marine Science, 7: 545–553.

Muus, B. J. 1959. Skallus, Søtænder, Blæksprutter. Danmarks Fauna, 65: 1–239.

Muus, B. J. 2002. The *Bathypolypus–Benthoctopus* problem of the North Atlantic (Octopodidae, Cephalopoda). Malacologia, 44: 175–222.

Naef, A. 1921. Das System der dibranchiaten Cephalopoden und die mediterranean Arten derselben. Mitteilungen aus der Zoologischen Station zu Neapel, 22: 527–542.

Naef, A. 1923. Die Cephalopoden (Systematik). *In* Fauna e Flora de Golfo di Napoli, Monograph 35(I-1), Pubblicazioni della Stazione Zoologica di Napoli. R. Friedländer and Sohn, Berlin. 863 pp.

Nakazoe, J. 2000. Chapter 2: General properties of squid and cuttlefish. *In* Nutritional and Functional Properties of Squid and Cuttlefish, pp. 9–21. Ed. by M. Okozumi and T. Fujii. National Cooperative Association of Squid Processors, Tokyo. 223 pp.

Natsukari, Y. 1984. Morphological and taxonomical studies on the family Loliginidae Steenstrup, 1861 (Cephalopoda: Mollusca). PhD thesis, University of Kyushu, Japan.

Navarro, J. C., and Villanueva, R. 2000. Lipid and fatty acid composition of early stages of cephalopods: an approach to their lipid requirements. Aquaculture, 183: 161–177.

Navarro, J. C., and Villanueva, R. 2003. The fatty acid composition of *Octopus vulgaris* paralarvae reared with live and inert food: deviation from their natural fatty acid profile. Aquaculture, 219: 613–631.

Nesis, K. N. 1987. Cephalopods of the World. TNP Publications, New York, NY. 351 pp.

Ngoile, M. A. K. 1987. Fishery biology of the squid *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Scottish waters. PhD thesis, University of Aberdeen, UK.

Nigmatullin, Ch. M. 1975. The food of commercial cephalopods from the shelf waters off Spanish Sahara and Mauritania. Oceanological Studies, Fishery Biology and Fisheries in the Atlantic Ocean and the Baltic Sea, 58 (in Russian, with English abstract).

Norman, J., Murphy, J. M., Pierce, G. P., and Boyle, P. R. 1994. Preliminary molecular genetic analysis of stock structure in the squid *Loligo forbesi* (Steenstrup). ICES Document CM 1994/K:23. 8 pp.

Nürnberger, T., and Brunner, F. 2002. Innate immunity in plants and animals: emerging parallels between the recognition of general elicitors and pathogen-associated molecular patterns. Current Opinion in Plant Biology, 5: 1–7.

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

O'Dor, R. K., and Wells, M. J. 1987. Energy and nutrient flow. *In* Cephalopod Life Cycles. Vol. II: Comparative reviews, pp. 109–134. Ed. by P. R. Boyle. Academic Press, London. 441 pp.

Oehlmann, J., and Schulte-Oehlmann, U. 2003. Endocrine disruption in invertebrates. Pure and Applied Chemistry, 75: 2207–2218.

Okumura, S., Kurihara, A., Iwamoto, A., and Takeuchi, T. 2005. Improved survival and growth in *Octopus vulgaris* paralarvae by feeding large type *Artemia* and Pacific sandeel, *Ammodytes personatus*. Aquaculture, 244: 147–157.

Oliver, L. M., and Fisher, W. S. 1999. Appraisal of prospective bivalve immunomarkers. Biomarkers, 4: 510–530.

Oosthuizen, A., Roberts, M. J., and Sauer, W. H. H. 2002. Temperature effects on the embryonic development and hatching success of the squid *Loligo vulgaris reynaudii.* Bulletin of Marine Science, 71: 619–632.

Orsi-Relini, L. 1994. The stomach content of some bottlenose dolphins (*Tursiops truncatus*) from the Ligurian Sea. European Research on Cetaceans, 8: 192–195.

Orsi-Relini, L., Mannini, A., Fiorentino, F., Palandri, G., and Relini, G. 2006. Biology and fishery of *Eledone cirrhosa* in the Ligurian Sea. Fisheries Research, 78: 72–88.

Otero, J. 2006. Ecología del pulpo común (*Octopus vulgaris* Cuvier, 1797) en un área de afloramiento costero (Galicia, NE Atlántico). PhD thesis, University of Vigo, Spain.

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

Otero, J., González, A. F., Pilar-Sieiro, M., and Guerra, A. 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. Fisheries Research, 85: 122–129.

Otero, J., Álvarez–Salgado, X. A., González, A. F., Miranda, A., Groom, S. B., Cabanas, J. M., Smyth, T., *et al.* 2008. Bottom–up control of *Octopus vulgaris* abundance in a wind-driven upwelling ecosystem (NE Atlantic). Marine Ecology Progress Series, 362: 181–192.

Otero, J., Álvarez-Salgado, X. A., González, A. F., Gilcoto, M., and Guerra, A. 2009. High-frequency coastal upwelling events influence *Octopus vulgaris* larval dynamics on the NW Iberian shelf. Marine Ecology Progress Series, 386: 123–132.

Otero, J. J., Moxica, C., Sánchez, F. J., and Iglesias, J. 2001. Engorde de pulpo *Octopus vulgaris* Cuvier, 1797 a diferentes densidades de estabulación. *In* Convergencia entre investigación y empresa: un reto para el siglo XXI. Selección de comunicaciones presentada en el 7º Congreso Nacional de Acuicultura, celebrado en Las Palmas de Gran Canaria 19, 20 y 21 de mayo de 1999, pp. 180–184. Ed. by H. Fernández-Palacios Barber and M. Izquierdo. Monografías del Instituto Canario de Ciencias Marinas, 4. 586 pp.

Ozogul, Y., Duysak, O., Ozogul, F., Ozkutuk, A. S., and Tuereli, C. 2008. Seasonal effects in the nutritional quality of the body structural tissue of cephalopods. Food Chemistry, 108: 847–852.

Öztürk, B., Salman, A., Öztürk, A. A., and Tonay, A. 2007. Cephalopod remains in the diet of striped dolphins (*Stenella coeruleoalba*) and Risso's dolphins (*Grampus griseus*) in the eastern Mediterranean Sea. Vie et Milieu, 57: 57–63.

Pan, M., McBeath, A. J. A., Hay, S. J., Pierce, G. J., and Cunningham, C. O. 2008. Real-time PCR assay for detection and relative quantification of *Liocarcinus depurator* larvae from plankton samples. Marine Biology, 153: 859–870.

Papaconstantinou, C., Politou, C-Y., Caragitsou, E., Stergiou, K., Mytilineou, Ch., Vassilopoulou, V., Fourtouni, A., *et al.* 1994. Assessment of demersal fish stocks with commercial importance in the Thermaikos Gulf and the Thracian Sea. General Secretariat for Research and Technology of Greece, Project code 14. NCMR Final Report, National Centre for Marine Research, Athens. 356 pp. (in Greek).

Parry, M. 2008. Trophic variation with length in two ommastrephid squids, *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis*. Marine Biology, 153: 249–256.

Pascoe, P. L. 1986. Size data and stomach contents of common dolphins, *Delphinus delphis*, near Plymouth. Journal of the Marine Biological Association of the UK, 66: 319–322.

Pascual, E. 1978. Crecimiento y alimentacion de tres generaciones de *Sepia officinalis* en cultivo. Investigacion Pesquera, 42: 421–442.

Pascual, S., Gestal, C., Estévez, J., Rodríguez, H., Soto, M., Abollo, E., and Árias, C. 1996. Parasites in commercially exploited cephalopods (Mollusca, Cephalopoda) in Spain: an updated perspective. Aquaculture, 142: 1–10.

Pascual, S., González, A., and Guerra, A. 2007a. Parasites and cephalopod fisheries uncertainty: towards a waterfall understanding. Reviews in Fish Biology and Fisheries, 17: 635–635.

Pascual, S., González, A. F., and Guerra, A. 2007b. Parasite recruitment and oceanographic regime: a working hypothesis on a global scale. Biological Reviews, 82, 257–263.

Pauly, D. 1998. Why squid, though not fish, may be better understood by pretending they are. South African Journal of Marine Science, 20: 47–58.

Pauly, D., Christensen, V., Guenette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R., *et al.* 2002. Towards sustainability in world fisheries. Nature, 418: 689–695.

Payne, A. G., Agnew, D. J., and Pierce, G. J. (Eds). 2006. Trends and Assessment of Cephalopod Fisheries – Proceedings of the CEPHSTOCK Cephalopod Assessment Workshop. Fisheries Research, 78: 1–106.

Payne, A. I. L., Lipinski, M. R., Clarke, M. R., and Roeleveld, M. A. C. (Eds). 1998. Cephalopod Biodiversity, Ecology and Evolution. South African Journal of Marine Science, 20. 469 pp.

Pecl, G., and Jackson, G. D. 2008. The potential impacts of climate change on inshore squid: biology, ecology and fisheries. Reviews in Fish Biology and Fisheries, 18: 373–385.

Perales-Raya, C., Garcia-Santamaria, M. T., Bartolome, A., Pascual, P., and Almansa, E. 2009. Age reading comparison between sagittal sections and lateral walls of the octopus beaks

(*Octopus vulgaris* Cuvier, 1797). *In* Cephalopod International Advisory Council. (CIAC) Symposium, 3–11 September 2009, Vigo, Spain, Abstracts, p. 55. CIAC. 98 pp. Available online at http://www.abdn.ac.uk/ciac.

Pereira, J. M. F. (Ed). 2001. Data collection for assessment of cephalopod fisheries. Final Report to the Commission of the European Communities Directorate General for Fisheries on Study No. 99/063. Instituto de Investigação das Pescas e do Mar, Lisbon.

Pereira, J. M. F., Morais da Cunha, M., and Moreno, A. 1997. Portuguese cephalopod fisheries from ICES Division IXa. ICES Document CM 1997/K:2. 11 pp.

Pereira, J. M. F., Moreno, A., and Morais da Cunha, M. 1998. Western European squid distribution: a review. ICES Document CM 1998/M:29. 20 pp.

Pérez-Losada, M., Guerra, A., and Sanjuan, A. 1999. Allozyme differentiation in the cuttlefish S*epia officinalis* (Mollusca: Cephalopoda) from the NE Atlantic and Mediterranean. Heredity, 83: 280–289.

Pérez-Losada, M., Guerra, A., Carvalho, G. R., Sanjuan, A., and Shaw, P. W. 2002. Fine population structuring of the cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda) around the Iberian peninsula revealed by microsatellite DNA markers. Heredity, 89: 417–424.

Pérez-Losada, M., Nolte, M., Crandall, K. A., and Shaw, P. W. 2007. Testing population structuring hypotheses in the NE Atlantic Ocean and Mediterranean Sea using the common cuttlefish *Sepia officinalis*. Molecular Ecology, 16: 2667–2679.

Peristeraki, P., Tserpes, G., and Lefkaditou, E. 2005. What cephalopod remains from *Xiphias gladius* stomachs can imply about predator prey interactions in the Mediterranean Sea? Journal of Fish Biology, 67: 549–554.

Perrin, A. 2004. Etude expérimentale des capacités digestives chez la seiche *Sepia officinalis* (Mollusque Céphalopode): Impact de l'alimentation, indice de condition nutritionnelle et formulation d'un aliment artificiel. PhD thesis, University of Caën, France. 153 pp.

Perrin, A., Le Bihan, E., and Koueta, N. 2004. Experimental study of enriched frozen diet on digestive enzymes and growth of juvenile cuttlefish *Sepia officinalis* L. (Mollusca Cephalopoda). Journal of Experimental Marine Biology and Ecology, 311: 267–285.

Perugini, M., Cavaliere, M., Giammarino, A., Mazzone, P., Olivieri, V., and Amorena, M. 2004. Levels of polychlorinated biphenyls and organochlorine pesticides in some edible marine organisms from the Central Adriatic Sea. Chemosphere, 57: 391–400.

Peterman, R. M., and Bradford, M. J. 1987. Wind-speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science, 235: 354–356.

Phillips, K. L., Jackson, G. D., and Nichols, P. D. 2001. Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analysis. Marine Ecology Progress Series, 215: 179–189.

Phillips, K. L., Nichols, P. D., and Jackson, G. D. 2003a. Dietary variation of the squid *Moroteuthis ingens* at four sites in the Southern Ocean: stomach contents, lipids and fatty acid profiles. Journal of the Marine Biological Association of the UK, 83: 523–534.

Phillips, K. L., Jackson, G. D., and Nichols, P. D. 2003b. Temporal variations in the diet of the squid *Moroteuthis ingens* at Macquarie Island: stomach contents and fatty acid analyses. Marine Ecology Progress Series, 256: 135–149.

Phillips, K. L., Nichols, P. D., Jackson, G. D. 2003c. Size-related dietary changes observed in the squid *Moroteuthis ingens* at the Falkland Islands: stomach contents and fatty acid analyses. Polar Biology, 26: 474–485.

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

Piatkowski, U., and Hagen, W. 1994. Distribution and lipid composition of early life stages of the cranchiid squid *Galiteuthis glacialis* (Chun) in the Weddell Sea, Antarctica. Antarctic Science, 6: 235–239.

Piatkowski, U., Hernández-Garcia, V., and Clarke, M. R. 1998. On the biology of the European flying squid *Todarodes sagittatus* (Lamarck, 1798; Cephalopoda, Ommastrephidae) in the central eastern Atlantic. South African Journal of Marine Science, 20: 375–383.

Piatkowski, U., Pierce, G. J., and Morais da Cunha, M. (Eds). 2001. Impact of cephalopods in the food chain and their interaction with the environment. Fisheries Research, 52: 1–142.

Pierce, G. J. (Ed). 1999. Data collection for assessment of cephalopod fished stocks. Final Report to the Commission of the European Communities Directorate General for Fisheries on Study No. 96/081. University of Aberdeen, UK.

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

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

Pierce, G. J., and Santos, M. B. 1996. Trophic interactions of squid *Loligo forbesi* in Scottish waters. *In* Aquatic Predators and Their Prey, pp. 58–64. Ed. by S. P. R. Greenstreet and M. L. Tasker. Fishing News Books, Oxford. 191 pp.

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

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

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

Pierce, G. J., Hastie, L. C., Guerra, A., Thorpe, R. S., Howard, F. G., and Boyle, P. R. 1994c. Morphometric variation in *Loligo forbesi* and *Loligo vulgaris*: regional, seasonal, maturity and worker differences. Fisheries Research, 21: 127–148.

Pierce, G. J., Boyle, P. R., Hastie, L. C., and Santos, M. B. 1994d. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. Fisheries Research, 21: 149–164.

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

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

Pierce, G. J., Wang, J., and Valavanis, V. 2002. Application of GIS to cephalopod fisheries: workshop report. Bulletin of Marine Science, 71: 35–46.

Pierce, G. J., Santos, M. B., Learmonth, J. A., Mente, E., and Stowasser, G. 2004. Methods for dietary studies on marine mammals. *In* Investigating the Role of Cetaceans in Marine Ecosystems, pp. 29–36. CIESM Workshop Monograph 25, Commission Internationale pour l'exploration Scientifique de la mer Méditerranée, Monaco. 144 pp.

Pierce, G. J., Portela, J. M., and Robin, J-P. (Eds). 2005a. Environmental effects on cephalopod life history and fisheries. Aquatic Living Resources, 18: 325–400.

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

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

Pierce, G. J., Valavanis, V. D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J. M., Katara, I., *et al*. 2008b. A review of cephalopod-environment interactions in European Seas and other world areas. Hydrobiologia, 612: 49–70.

Pipe, R. K., Coles, J. A., Carissan, F. M. M., and Ramanathan, K. 1999. Copper induced immunomodulation in the marine mussel, *Mytilus edulis*. Aquatic Toxicology, 46: 43–54.

Planque, B., and Taylor, A. H. 1998. Long-term changes in plankton and the climate of the North Atlantic. ICES Journal of Marine Science, 78: 1015–1018.

Porteiro, F. M., and Martins, H. 1994. Biology of *Loligo forbesi* Steenstrup, 1856 (Mollusca: Cephalopoda) in the Azores: sample composition and maturation of squid caught by jigging. Fisheries Research, 21: 103–114.

Pörtner, H. O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. Marine Ecology Progress Series, 373: 203–217.

Pörtner, H. O., and Reipschläger, A. 1996. Ocean disposal of anthropogenic CO_2: physiological effects on tolerant and intolerant animals. *In* Ocean Storage of Carbon Dioxide. Workshop 2 – Environmental Impact, pp. 57–81. Ed. by B. Ormerod and M. V. Angel. International Energy Agency, Greenhouse Gas R&D Programme, Cheltenham, UK. 131 pp.

Pörtner, H. O., and Reipschläger, A. 1996. Ocean disposal of anthropogenic CO_2: physiological effects on tolerant and intolerant animals. *In* Ocean Storage of Carbon Dioxide. Workshop 2 – Environmental Impact, pp. 57–81. Ed. by B. Ormerod and M. V. Angel. International Energy Agency, Greenhouse Gas R&D Programme, Cheltenham, UK. 131 pp.

Pörtner, H. O., Langebuch, M., and Reipschläger, A. 2004. Biological impact of elevated ocean CO_2 concentration: lessons from animal physiology and Earth history. Journal of Oceanography, 60: 705–718.

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

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

Quetglas, A., Alemany, F., Carbonell, A., Merella, P., and Sánchez, P. 1999. Diet of the European flying squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) in the Balearic Sea (western Mediterranean). Journal of the Marine Biological Association of the UK, 79: 479–486.

Quintana, D., Domingues, P., and García, S. 2008. Effect of two artificial wet diets agglutinated with gelatin on feed and growth performance of common octopus (*Octopus vulgaris*) sub-adults. Aquaculture, 280: 161–164.

Ragonese, S., and Bianchini, M. L. 1990. Oceanic squid jigging in the Sicilian channel: Potential and drawbacks. Quaderni dell' Istituto di Idriobiologia e Acquacoltura 'G. Brunelli', 10: 65–79.

Ragonese, S., and Jereb, P. 1991. Length-width relationship and growth of the pink and elegant cuttlefish *Sepia orbignyana* and *Sepia elegans* in the Sicilian Channel. *In* La Seiche: the Cuttlefish, 1st International Symposium on the Cuttlefish *Sepia*, 1–3 June 1989, Caën, pp. 31–47. Ed. by E. Boucaud-Camou. Centre de Publications de l'Université de Caën, Caën, France. 358 pp.

Rama-Villar, A. C., and Rey-Mendez, M. 1997. Engorde del pulpo (*Octopus vulgaris*) en batea. *In* Actas del VI Congresso Nacional de Acuicultura, 9–11 July 1997, Cartegena, Spain, pp.

245–250. Ed. By J. Costa, E. Abellan, B. Garcia, A. Ortega, and S. Zamora. Ministerio de Agricultura, Pesca y Alimentación, Madrid.

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

Raya, C. P. 2001. Determinación de la edad y estudio del crecimiento del choco (*Sepia hierredda* Rang, 1837), el calamar (*Loligo vulgaris* Lamarck, 1798) y el pulpo (*Octopus vulgaris* Cuvier, 1797) de la costa Noroccidental Africana. PhD thesis, Universidad de La Laguna, Spain. 192 pp.

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

Redfern, J. V., Ferguson, M. C., Becker, E. A., Hyrenbach, K. D., Good, C., Barlow, J., Kaschner, K., *et al.* 2006. Techniques for cetacean-habitat modelling. Marine Ecology Progress Series, 310: 271–295.

Rees, W. J. 1950. The distribution of *Octopus vulgaris* in British waters. Journal of the Marine Biological Association of the UK, 29: 361–378.

Rees, W. J., and Lumby, J. R. 1954. The abundance of *Octopus vulgaris* in the English Channel. Journal of the Marine Biological Association of the UK, 33: 515–536.

Reichow, D., and Smith, M. J. 2001. Microsatellites reveal high levels of gene flow among populations of the California squid *Loligo opalescens*. Molecular Ecology, 10: 1101–1109.

Reid, A., Jereb, P., and Roper, C. F. E. 2005. Family Sepiidae. *In* Cephalopods of the World. An Annotated and Illustrated Catalogue of Species Known to Date. Vol. 1. Chambered Nautiluses and Sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae), pp. 57–152. Ed. by P. Jereb and C. F. E. Roper. FAO Species Catalogue for Fisheries Purposes No. 4(1). FAO, Rome. 294 pp.

Reid, D. G., Edwards, M., Beaugrand, G., Skogen, M., and Stevens, D. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fisheries Oceanography, 12: 260–269.

Reis, C. A., Cabido, M. T. J., and Leal, F. M. G. P. 1984. Distribuição na costa portuguesa de 4 especies da familia Octopodidae (Mollusca: Cephalopoda). Actas do IV Simpósio Ibérico de Estudos do Bentos Marinho, 21–25 May 1984, Lisboa, 1: 203–217.

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

Relini, G., Zamboni, A., Massi, D., and Fiorentino, F. 1998. Behaviour of the exploited demersal resources of the Ligurian Sea through twelve year series of biomass indices. Rapports de la Commission Internationale de la Mer Méditerranée, 35: 89–98.

Richard, A. 1971. Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle de *Sepia officinalis* L. (Moll., Céphalopode). PhD thesis, University of Lille, France, 264 pp.

Richard, A. 1976. L'élevage de la seiche (*Sepia officinalis* L., Mollusque). *In* Proceedings of the 10th European Symposium on Marine Biology, Ostend, Belgium, 17–23 September 1975, Vol. 1: Research in Mariculture at Laboratory and Pilot Scale, pp. 359–380. Ed. by G. Persoone and E. Jaspers. Universa Press, Wetteren, Belgium. 620 pp.

Roa-Ureta, R., and Arkhipkin, A. I. 2007. Short-term stock assessment of *Loligo gahi* at the Falkland Islands: sequential use of stochastic biomass projection and stock depletion models. ICES Journal of Marine Science, 64: 3–17.

Roberts, M. J., Barange, M., Lipinski, M. R., and Prowse, M. R. 2002. Direct hydroacoustic observations of chokka squid *Loligo vulgaris reynaudii* spawning activity in deep water. South African Journal of Marine Science, 24: 387–393.

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

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

Rocha, F. 1994. Aspectos biológicos y ecológicos de *Loligo vulgaris* y *Loligo forbesi* (Cephalopoda: Loliginidae) en las costas de Galicia. PhD thesis. Universidad de Oviedo, Spain. 240 pp.

Rocha, F., and Guerra, A. 1996. Signs of an extended and intermittent terminal spawning in the squids *Loligo vulgaris* Lamarck and *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae). Journal of Experimental Marine Biology and Ecology, 207: 177–189.

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

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

Rocha, F., Guerra, A., Prego, R., and Piatkowski, U. 1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). Journal of Plankton Research, 21: 21–33.

Rocha, F., Guerra, A., and González, A. F. 2001. A review of reproductive strategies in cephalopods. Biological Reviews, 76: 291–304.

Rocha, F., Otero, J., Outeiral, R., González, A. F., Gracia, J., and Guerra, A. 2006. Modelling small-scale coastal fisheries of Galicia (NW Spain) based on data obtained from fisheries: the case of *Sepia officinalis.* Scientia Marina, 70: 593–601.

Rodhouse, P. G. 2001. Managing and forecasting squid fisheries in variable environments. Fisheries Research, 54: 3–8.

Rodhouse, P. G., and Nigmatullin, C. 1996. Role as consumers. Philosophical Transactions of the Royal Society of London B, 351: 1003–1022.

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

Rodhouse, P. G., Symon, C., and Hatfield, E. M. G. 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the Southwest Atlantic Ocean. Marine Ecology Progress Series, 89: 183–195.

Rodríguez, C., Carrasco, J. F., Arronte, J. C., and Rodríguez, M. 2006. Common octopus (*Octopus vulgaris* Cuvier, 1797) juvenile ongrowing in floating cages. Aquaculture, 254: 293–300.

Rodríguez-Rúa, A., Pozuelo, I., Prado, M. A., Gómez, M. J., and Bruzon, M. A. 2005. The gametogenic cycle of *Octopus vulgaris* (Mollusca: Cephalopoda) as observed on the Atlantic coast of Andalusia (south of Spain). Marine Biology, 147: 927–933.

Roel, B. A., and Butterworth, D. S. 2000. Assessment of the South African chokka squid *Loligo vulgaris reynaudii* – is disturbance of aggregations by the recent jig fishery having a negative impact on recruitment? Fisheries Research, 48: 213–228.

Rohde, K. 2002. Ecology and biogeography of marine parasites. Advances in Marine Biology, 43: 1–7.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and Pounds, A. 2003. Fingerprints of global warming on wild plants and animals. Nature, 421: 57–60.

Roper, C. F. E., and Mangold, K. M. 1998. Systematic and distributional relationships of *Illex coindetii* to the genus *Illex* (Cephalopoda, Ommastrephidae). *In* Squid Recruitment Dynamics. The Genus *Illex* as a Model. The Commercial *Illex* Species. Influences on Variability, pp. 13–26. Ed. by P. G. Rodhouse, E. G. Dawe, and R. K. O′Dor. FAO Fisheries Technical Paper No. 376. FAO, Rome. 273 pp.

Roper, G. F. E., Sweeney, M. J., and Nauen, E. 1984. FAO Species Catalogue. Vol. 3: Cephalopods of the World. An Annotated and Illustrated Catalogue of Species of Interest to Fisheries. FAO Fisheries Synopsis, 125(3). 277 pp.

Roper, C. F. E., Lu, C. C., and Vecchione, M. 1998. A revision of the systematics and distribution of *Illex* species (Cephalopoda: Ommastrephidae). *In* Systematics and Biogeography of Cephalopods, pp. 405–423. Ed. by N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney. Smithsonian Contributions to Zoology No. 586(II). Smithsonian Institution Scholarly Press, Washington, DC. 323 pp.

Rosa, R., and Seibel, B. A. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. Proceedings of the National Academy of Sciences of the USA, 105: 20776–20780.

Rosa, R., Marques, A. M., Nunes, M. L., Bandarra, N., and Sousa-Reis, C. 2004. Spatial-temporal changes in dimethyl acetal (octadecanal) levels of *Octopus vulgaris* (Mollusca, Cephalopoda): relation to feeding ecology. Scientia Marina, 68: 227–236.

Rosa, R., Pereira, J., and Nunes, M. L. 2005. Biochemical composition of cephalopods with different life strategies, with special reference to a giant squid, *Architeuthis* sp. Marine Biology, 146: 739–751.

Rosas, C., Tut, J., Baeza, J., Sanchez, A., Sosa, V., Pascual, C., Arena, L., *et al.* 2008. Effect of type of binder on growth, digestibility, and energetic balance of *Octopus maya*. Aquaculture, 275: 291–297.

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

Rossetti, I. 1998. Biologia e pesca di *Eledone cirrhosa* (Cephalopoda: Octopoda) nel mar Tirreno settentrionale. Diploma thesis (Tesi di laurea), Pisa University, Italy.

Rossi, A., Pellegrini, D., Belcari, P., and Barghigiani, C. 1993. Mercury in *Eledone cirrhosa* from the northern Tyrrhenian Sea: contents and relations with life cycle. Marine Pollution Bulletin, 26: 683–686.

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

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

Ruiz-Cooley, R. I., Gendron, D., Aguiniga, S., Mesnick, S., and Carriquiry, J. D. 2004. Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. Marine Ecology Progress Series, 277: 275–283.

Ruiz-Cooley, R. I., Markaida, U., Gendron, D., and Aguinaga, S. 2006. Stable isotopes in jumbo squid (*Dosidicus gigas*) beaks to estimate its trophic position: comparison between stomach contents and stable isotopes. Journal of the Marine Biological Association of the UK, 86: 437–445.

Rungger, D., Rastelli, M., Braendle, E., and Malsberg, R. G. 1971. A virus-like particle associated with lesions in muscles of *Octopus vulgaris*. Journal of Invertebrate Pathology, 17: 72–80.

Sakaguchi, H., Hamano, T., and Nakazono, A. 1999. Occurrence of planktonic juveniles of *Octopus vulgaris* in eastern Iyo-Nada of the Seto Inland Sea, Japan. Bulletin of the Japanese Society of Fisheries Oceanography, 63: 181–187.

Salas, F., Patrício, J., and Marques, J. C. 2006. Ecological Indicators in Coastal and Estuarine Environmental Quality Assessment. A User-friendly Guide for Practitioners. Coimbra University Press, Coimbra. 165 pp.

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

Salman, A., Bilecenoglu, M., and Güçlüsoy, H. 2001. Stomach contents of two Mediterranean monk seals (*Monachus monachus*) from the Aegean Sea, Turkey. Journal of the Marine Biological Association of the UK, 81: 719–720.

Sánchez, F. J., Iglesias, J., Moxica, C., and Otero, J. J. 1998. Growth of octopus (*Octopus vulgaris*) males and females under culture conditions. ICES Document CM 1998/M:47. 3 pp.

Sánchez, P. 1981. Regime alimentaire d'*E. cirrhosa* (Lamarck, 1798; Mollusca, Cephalopoda) dans la Mer Catalane. Rapports de la Commission Internationale de la Mer Méditerranée, 27: 209–212.

Sánchez, P. 1984. Determinación de la edad y de los parámetros del crecimiento de *Illex coindetii* (Verany, 1837) en el mar Catalán (Mediterráneo Occidental). Investigacion Pesquera, 48: 59–70.

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

Sánchez, P., and Obarti, R. 1993. The biology and fishery of *Octopus vulgaris* caught with clay pots on the Spanish Mediterranean coast. *In* Recent Advances in Fisheries Biology, pp. 477–487. Ed. by T. Okutani, R. K. O' Dor, and T. Kubodera. Tokai University Press, Tokyo. 752 pp.

Sánchez, P., Lefkaditou, E., and Tsangridis, A. 1995. Experimental squid jigging with light attraction. Final Report to the Commission of the European Communities Directorate General of Fisheries on Study EU-MED/93/19. Barcelona. 116 pp.

Sánchez, P., González, F., Jereb, P., Laptikhovski, V., Mangold, K., Nigmatullin, Ch., and Ragonese, S. 1998. *Illex coindetii. In* Squid Recruitment Dynamics. The Genus *Illex* as a Model. The Commercial *Illex* Species. Influences on Variability, pp. 59–76. Ed. by P. G. Rodhouse, E. G. Dawe, and R. K. O´Dor. FAO Fisheries Technical Paper No. 376. FAO, Rome. 273 pp.

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

Sánchez, P., Demestre, M., Recasens, L., Maynou, F., and Martin, P. 2008. Combining GIS and GAMs to identify potential habitats of squid *Loligo vulgaris* in the Northwestern Mediterranean. Hydrobiologia, 612: 91–98.

Sanjuan, A., Perez-Losada, M., and Guerra, A. 1996. Genetic differentiation in three *Sepia* species (Mollusca: Cephalopoda) from Galician waters (northwest Iberian Peninsula). Marine Biology, 126: 253–259.

Santos, A. M. P., Chicharo, A., Dos Santos, A., Moita, T., Oliveira, P., Peliz, A., and Ré, P. 2007. Physical–biological interactions in the life history of small pelagic fish in the Western Iberia Upwelling Ecosystem. Progress in Oceanography, 74: 192–209.

Santos, M. B., Pierce, G. J., González, A. F., and López, A. 1997. Dieta do Arroás, *Tursiops truncatus* en Galicia (NW Spain). Eubalaena, 10: 30–39.

Santos, M. B., Pierce, G. J., Boyle, P. R., Reid, R. J., Ross, H. M., Patterson, I. A. P., Kinze, C. C., *et al.* 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. Marine Ecology Progress Series, 183: 281–294.

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

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

Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Ross, H. M., Patterson, I. A. P., Reid D. G., *et al.* 2004a. Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. Marine Mammal Science, 20: 1–27.

Santos, M. B., Pierce, G. J., López, A., Martínez, J. A., Fernández, R., Ieno, E., Porteiro, F., *et al.* 2004b. Variability in the diet of common dolphins (*Delphinus delphis*) in Galician waters 1991–2003 and relationship with prey abundance. ICES Document CM 2004/Q:09. 40 pp.

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

Santos, M. B., Pierce, G. J., Ieno, E. N., Addink, M., Smeenk, C., and Kinze, C. C. 2005b. Harbour porpoise (*Phocoena phocoena*) feeding ecology in the eastern North Sea. ICES Document CM 2005/R:15. 25 pp.

Santos, M. B., Fernández, R., López, A., Martínez, J. A., and Pierce, G. J. 2007. Variability in the diet of bottlenose dolphin, *Tursiops truncatus* (Montagu), in Galician waters, NW Spain, 1990–2005. Journal of the Marine Biological Association of the UK, 87: 231–242.

Santulli, A., and Bertolino, F. (Eds). 1997. La pesca artigianale nella Provincia di Trapani. Consorzio Universitario di Trapani. 204 pp.

Santurtun, M., Lucio, P., Quincoces, I., Díez, G., and Iriondo, A. 2004. Brief note on cephalopod discards at the Spain national sampling programme (ICES Subareas VI and VII, and Divisions VIIIa, b, d, and c). ICES Document CM 2004/G:02. 37 pp.

Sartor, P., Belcari, P., Carbonell, A., González, M., Quetglas, A., and Sánchez, P. 1998. The importance of cephalopods to trawl fisheries in the western Mediterranean. South African Journal of Marine Science, 20: 67–72.

Sato, K., Kajiwara, N., Hashimoto, S., Kidokoro, H., Shibata, Y., and Ohtsuki, A. 2000. Accumulative characteristics of organochlorine compounds (OCs) in squid. Nippon Suisan Gakkaishi, 66: 658–665.

Sauer, W. H. H., Lipinski, M. R., and Augustyn, C. J. 2000. Tag recapture studies of the chokka squid *Loligo vulgaris* reynaudii d'Orbigny, 1845 on inshore spawning grounds on the south-east coast of South Africa. Fisheries Research, 45: 283–289.

Scimeca, J. M. 2006. Cephalopods. *In* Invertebrate Medicine, pp. 79–90. Ed. by G. A. Lewbart. Blackwell Publishing Ltd, Oxford, UK. 327 pp.

Sear, C., Hulme, M., Adger, N., and Brown, K. 2001a. The Impacts of Global Climate Change on the UK Overseas Territories: Issues and Recommendations – A Summary Report. Natural Resources Institute, Chatham, and Tyndall Centre for Climate Change Research, Norwich. 10 pp.

Sear, C., Hulme, M., Adger, N., and Brown, K. 2001b. The Impacts of Global Climate Change on the UK Overseas Territories: Technical Report and Stakeholder Survey. Natural Resources Institute, Chatham, and Tyndall Centre for Climate Change Research, Norwich. 50 pp.

Seibel, B. A. 2007. On the depth and scale of metabolic rate variation: scaling of oxygen consumption and enzymatic activity in the Class Cephalopoda (Mollusca). Journal of Experimental Biology, 210: 1–11.

Seibel, B. A., and Drazen, J. C. 2007. The rates of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. Philosophical Transactions of the Royal Society B, 362: 2061–2071.

Seibel, B. A., Hochberg, F. G., and Calini, D. B. 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): deep-sea spawning and post-spawning egg care. Marine Biology, 137: 519–526.

Seibel, B. A., Robison, B. H., and Haddock, S. H. D. 2005. Post-spawning egg care by a squid. Nature, 438: 929.

Seixas, P., Rey-Méndez, M., Valente, L. M. P., and Otero, A. 2008. Producing juvenile Artemia as prey for *Octopus vulgaris* paralarvae with different microalgal species of controlled biochemical composition. Aquaculture, 283: 83–91.

Seixas, S. 2004. Trace elements and pollutants in *Octopus vulgaris* in Portuguese Waters. PhD thesis, University of Lisbon, Portugal. 424 pp.

Seixas, S., and Pierce, G. J. 2005a. Bioaccumulation of lead, calcium and strontium and their relationships in the octopus *Octopus vulgaris*. Water, Air and Soil Pollution, 163: 137–152.

Seixas, S., and Pierce, G. J. 2005b. Vanadium, rubidium and potassium in *Octopus vulgaris* (Mollusca: Cephalopoda). Scientia Marina, 69: 215–222.

Seixas, S., Bustamante, P., and Pierce, G. J. 2005a. Interannual patterns of variation in concentrations of trace elements in arms of *Octopus vulgaris*. Chemosphere, 59: 1113–1124.

Seixas, S., Bustamente, P., and Pierce, G. J. 2005b. Accumulation of mercury in the tissues of the common octopus *Octopus vulgaris* (L.) in two localities on the Portuguese coast. Science of the Total Environment, 340: 113–122.

Şen, H. 2007. Food preference of *Eledone moschata* Lamarck, 1799 (Cephalopoda: Octopodidae) in captive conditions. International Journal of Natural and Engineering Sciences, 1: 29–31.

Şen, H., and Sunlu, U. 2007. Effects of cadmium ($CdCl_2$) on development and hatching of eggs in European squid (*Loligo vulgaris* Lamarck, 1798; Cephalopoda: Loliginidae). Environmental Monitoring and Assessment, 133: 371–378.

Sendao, S. J., Goncalves, I., and Borges, T. C. 2002. By-catch and discards of cephalopods in the fisheries of the South Portuguese coast. Bulletin of Marine Science, 71: 1139.

Shadwick, R. E., and Nilsson, E. K. 1990. The Importance of vascular elasticity in the circulatory system of the cephalopod *Octopus vulgaris*. Journal of Experimental Biology, 152: 471–484.

Shaw, P. W., and Boyle, P. R. 1997. Multiple paternity within the brood of single females of *Loligo forbesi* (Cephalopoda: Loliginidae), demonstrated with microsatellite DNA markers. Marine Ecology Progress Series, 160: 279–282.

Shaw, P. W., and Sauer, W. H. H. 2004. Multiple paternity and complex fertilisation dynamics in the squid *Loligo vulgaris reynaudii*. Marine Ecology Progress Series, 270: 173–179.

Shaw, P. W., Pierce, G. J., and Boyle, P. R. 1999. Subtle population structuring within a highly vagile marine invertebrate, the veneid squid *Loligo forbesi*, demonstrated with microsatellite DNA markers. Molecular Ecology, 8: 407–417.

Shaw, P. W., Adcock, G. J., Burnett, W. J., Carvalho, G. R., and Arkhipkin, A. I. 2004. Temporally distinct spawning cohorts and geographically distinct spawning aggregations within the Patagonian squid *Loligo gahi* do not represent genetically differentiated sub-populations. Marine Biology, 144: 961–970.

Shaw, R. 1994. An economic description and assessment of the squid catching industry in the UK, Portugal and Spain. Fisheries Research, 21: 287–303.

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

Silva, L., Ramos, R., and Sobrino, I. 2004. Reproductive biology of *Eledone moschata* (Cephalopoda, Octopodidae) in the Spanish waters of the Gulf of Cadiz (SW Spain, ICES Division IXa). Journal of the Marine Biological Association of the UK, 84: 1221–1226.

Silva, M. 1999. Diet of common dolphins, *Delphinus delphis*, off the Portuguese continental coast. Journal of the Marine Biological Association of the UK, 79: 531–540.

Simón, F., Rocha, F., and Guerra, A. 1995. The small-scale squid hand-jig fishery off the northwestern Iberian Peninsula: application of a model based on a short survey of fishery statistics. Fisheries Research, 25: 253–263.

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

Smith, C. D. 2003. Diet of *Octopus vulgaris* in False Bay, South Africa. Marine Biology, 143: 1127–1133.

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

Smith, V. H. 2002. Effects of resource supplies on the structure and function of microbial communities. Antonie van Leeuwenhoek, 81: 99–106.

Sobrino, I., Silva, L., Bellido, J. M., and Ramos, F. 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cádiz (SW Spain). Bulletin of Marine Science, 71: 851–865.

Söller, R., Warnke, K., Saint-Paul, U., and Blohm, D. 2000. Sequence divergence of mitochondrial DNA indicates cryptic biodiversity in *Octopus vulgaris* and supports the taxonomic distinctiveness of *Octopus mimus* (Cephalopoda: Octopodidae). Marine Biology, 136: 29–35.

Solow, A. R. 2002. Fisheries recruitment and the North Atlantic Oscillation. Fisheries Research, 54: 295–297.

Souissi, N., Ellouz-Triki, Y., Bougatef, A., Blibech, M., and Nasri, M. 2008. Preparation and use of media for protease-producing bacterial strains based on by-products from cuttlefish (*Sepia officinalis*) and wastewaters from marine-products processing factories. Microbiological Research, 163: 473–480.

Southward, A. J., Hawkins, S. J., and Burrows, M. T. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology, 20: 127–155.

Spooner, J. T., Maggiore, M., Ordóñez, R., and Passino, K. M. 2002. Stable Adaptive Control and Estimation for Nonlinear Systems: Neural and Fuzzy Approximator Techniques. John Wiley and Sons, New York. 568 pp.

Starr, R. M., and Thorne, R. E. 1998. Acoustic assessment of squid stocks. *In* Squid Recruitment Dynamics. The Genus *Illex* as a Model. The Commercial *Illex* Species. Influences on Variability, pp. 181–198. Ed. by P. G. Rodhouse, E. G. Dawe, and R. K. O′Dor. FAO Fisheries Technical Paper No. 376. FAO, Rome. 273 pp.

Stebbing, A. R. D., Turk, S. M. T., Wheeler, A., and Clark, K. R. 2002. Immigration of southern fish species to south-west England linked to warming of the North Atlantic 1960–2001. Journal of the Marine Biological Association of the UK, 82: 177–180.

Steenstrup, J. 1856. Hectocotyldannelsen hos Octopodslægterne Argonatua og Tremoctopus oplyst ved Iagttagelse af lignende Dannelser hos Blæksprutterne. I Almindelighed. Kongelige Danske Videnskabernes Selskabs Skrifter, 5: 185–216.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K. S., and Lima, M. 2002. Ecological effects of climate fluctuations. Science, 297: 1292–1296.

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

Storelli, M. M., Barone, G., D'Addabbo, R., and Marcotrigiano, G. O. 2006. Concentrations and composition of organochlorine contaminants in different species of cephalopod molluscs from the Italian waters (Adriatic Sea). Chemosphere, 64: 129–134.

Stowasser, G., Pierce, G. J., Moffat, C. F., Collins, M. A., and Forsythe, J. W. 2006. Experimental study on the effect of diet on fatty acid and stable isotope profiles of the squid *Lolliguncula brevis*. Journal of Experimental Marine Biology and Ecology, 333: 97–114.

Strugnell, J., Norman, M., Jackson, J., Drummond, A. J., and Cooper, A. 2005. Molecular phylogeny of coleoid cephalopods (Mollusca: Cephalopoda) using a multigene approach; the effect of data partitioning on resolving phylogenies in a Bayesian framework. Molecular Phylogenetics and Evolution, 37: 426–441.

Strugnell, J. M., and Lindgren, A. R. 2007. A barcode of life database for the Cephalopoda? Considerations and concerns. Reviews in Fish Biology and Fisheries, 17: 337–344.

Sundet, J. H. 1985. A short review on the biology and fishery of the squid *Todarodes sagittatus*. ICES Document CM 1985/K:44. 10 pp., 4 figures.

Suzuki, T. 1990. Japanese common squid-*Todarodes pacificus* Steenstrup. Marine Behaviour and Physiology, 18: 73–109.

Sweeney, M. J., and Roper, C. F. E. 1998. Classification, type localities, and type repositories of recent Cephalopoda. *In* Systematics and Biogeography of Cephalopods, pp. 561–599. Ed. by N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney. Smithsonian Contributions to Zoology No. 586(II). Smithsonian Institution Scholarly Press, Washington, DC. 323 pp.

Sweeney, M. J., and Vecchione, M. 1998. Generic and specific names introduced in the squid family Loliginidae (Cephalopoda: Myopsida). *In* Systematics and Biogeography of Cephalopods, pp. 223–237. Ed. by N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney. Smithsonian Contributions to Zoology No. 586(I). Smithsonian Institution Scholarly Press, Washington, DC. 276 pp.

Sykes, A. V., Domingues, P. M., Correia, M., and Andrade, J. P. 2006. Cuttlefish culture – state of the art and future trends. Vie et Milieu, 56: 129–137.

Symondson, W. O. C. 2002. Molecular identification of prey in predator diets. Molecular Ecology, 11: 627–641.

Takai, N., Onaka, S., Ikeda, Y., Yatsu, A., Kidokorom, H., and Sakamoto, W. 2000. Geographical variations in carbon and nitrogen stable isotope ratios in squid. Journal of the Marine Biological Association of the UK, 80: 675–684.

Takeda, R. 1990. The distribution of planktonic juveniles of *Octopus vulgaris* Cuvier in Harima Nada. Suisanzoshoku, 38: 183–190 (in Japanese).

Tasende, M., Quintero, F., Arnáiz, Bañón, R., Campelos, J. M., Lamas, F., Gancedo, A., *et al.*, 2005. La pesquería de calamar (*Loligo vulgaris*) y puntilla (*Alloteuthis* spp) con boliche en las Rías Baixas gallegas (1999–2003). *In* Los Recursos Marinos de Galicia. Serie Técnica No. 3, Consellería de Pesca e Asuntos Marítimos, Xunta de Galicia. 108 pp.

Tavakoli, O., and Yoshida, H. 2006. Squid oil and fat production from squid wastes using subcritical water hydrolysis: Free fatty acids and transesterification. Industrial and Engineering Chemistry Research, 45: 5675–5680.

Thomas, H. J. 1973. Squid. Scottish Fishery Bulletin, 39: 35–39.

Toll, R. B., and Strain, C. H. 1988. Freshwater and terrestrial food organisms as an alternative diet for laboratory culture of cephalopods. Malacologia, 29: 195–200.

Tollit, D. J., and Thompson, P. M. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. Canadian Journal of Zoology, 74: 1110–1121.

Tollit, D. J., Schulze, A. D., Trites, A. W., Olesiuk, P. F., Crockford, S. J., Gelatt, T. S., Ream, R. R., *et al.* 2009. Development and application of DNA techniques for validating and improving pinniped diet estimates. Ecological Applications, 19: 889–905.

Tsangridis, A., Lefkaditou, E., and Adamidou, A. 1998. Analysis of catch and effort data of *Loligo vulgaris* in the W. Thracian Sea (NE Mediterranean, Greece) using a depletion model. Rapports de la Commission Internationale de la Mer Méditerranée, 35: 494–495.

Tsangridis, A., Sánchez, P., and Ioannidou, D. 2002. Exploitation patterns of *Octopus vulgaris* in two Mediterranean areas. Scientia Marina, 66: 59–68.

Tsutsumi, T., Amakura, Y., Sasaki, K., and Maitani, T. 2007. Dioxin concentrations in the edible parts of Japanese common squid and saury. Journal of the Food Hygienic Society of Japan, 48: 8–12.

Turk, P. E., Hanlon, R. T., Bradford, L. A., and Yang, W. T. 1986. Aspects of feeding, growth and survival of the European squid, *Loligo vulgaris* Lamarck, 1799, reared through the early growth stages. Vie et Milieu, 36: 9–13.

Turrell, W. R. 1999. Scottish Ocean Climate Status Report 1998. Fisheries Research Services, Aberdeen, UK, Report No. 9/99. 12 pp.

Tursi, A., and D'Onghia, G. 1992. Cephalopods of the Ionian Sea (Mediterranean Sea). Oebalia, 18(N. S.): 25–43.

Tynan, C. T., and DeMaster, D. P. 1997. Observations and predictions of Arctic climate change: potential effects on marine mammals. Arctic, 50: 308–322.

Ueda, T., Nakahara, M., and Ishii, T. 1979. Amount of trace elements in marine cephalopods. Journal of Radiation Research, 20: 338–342.

Ueno, D., Inoue, S., Ikeda, K., Tanaka, H., Yamada, H., and Tanabe, S. 2003. Specific accumulation of polychlorinated biphenyls and organochlorine pesticides in Japanese common squid as a bioindicator. Environmental Pollution, 125: 227–235.

Unger, M. A., Harvey, E., Vadas, G. G., and Vecchione, M. 2008. Persistent pollutants in nine species of deep-sea cephalopods. Marine Pollution Bulletin, 56: 1486–1512.

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

Valavanis, V. D. (Ed). 2008. Essential Fish Habitat Mapping in the Mediterranean. Developments in Hydrobiology. Springer, Dordrecht. 300 pp.

Valavanis, V. D., Pierce, G. J., Zuur, A. F., Palialexis, A., Saveliev, A., Katara, I., and Wang, J. 2008. Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. Hydrobiologia, 612: 5–20.

Vaz-Pires, P., Seixas, P., and Barbosa, A. 2004. Aquaculture potential of the common octopus (*Octopus vulgaris* Cuvier, 1797): a review. Aquaculture, 238: 221–238.

Vecchione, M., Brakoniecki, T. F., Natsukari, Y., and Hanlon, R. T. 1998. A provisional generic classification of the Loliginidae. *In* Systematics and Biogeography of Cephalopods, pp. 215–222. Ed. by N. A. Voss, M. Vecchione, R. B. Toll, and M. J. Sweeney. Smithsonian Contributions to Zoology No. 586 (I). Smithsonian Institution Scholarly Press, Washington, DC. 276 pp.

Vecchione, M., Shea, E., Bussarawit, S., Anderson, F., Alexyev, D., Lu, C. C., Okutani, T., *et al.* 2005. Systematics of Indo-west Pacific loliginids. Phuket Marine Biological Centre Research Bulletin, 66: 23–26.

Vecchione, M., Allcock, L., Piatkowski, U., Jorgensen, E., and Barratt, I. 2009. Persistent elevated abundance of octopods in an overfished Antarctic area. *In* Smithsonian at the

Poles: Contributions to International Polar Year Science, pp. 197–204. Ed. by I. Krupnik, M. A. Lang, and S. E. Miller. Smithsonian Institution Scholarly Press, Washington, DC. 405 pp.

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

Viana, M., Pierce, G. J., Illian, J., MacLeod, C. D., Bailey, N., Wang, J., and Hastie, L. C. 2009. Seasonal movements of veined squid *Loligo forbesi* in Scottish (UK) waters. Aquatic Living Resources, 22: 291–305.

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

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

Villanueva, R., and Bustamante, P. 2006. Composition in essential and non-essential elements of early stages of cephalopods and dietary effects on the elemental profiles of *Octopus vulgaris* paralarvae. Aquaculture, 261: 225–240.

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

Villanueva, R., Koueta, N., Riba, J., and Boucaud-Camou, E. 2002a. Growth and proteolytic activity of *Octopus vulgaris* paralarvae with different food rations during first-feeding, using *Artemia* nauplii and compound diets. Aquaculture, 205: 269–286.

Villanueva, R., Collins, M. A., Sánchez, P., and Voss, N. A. 2002b. Systematics, distribution and biology of the cirrate octopods of the genus *Opisthoteuthis* (Mollusca, Cephalopoda) in the Atlantic Ocean, with description of two new species. Bulletin of Marine Science, 71: 933–985.

Villanueva, R., Riba, J., Ruiz-Capillas, C., González, A. V., and Baeta, M. 2004. Amino acid composition of early stages of cephalopods and effect of amino acid dietary treatments on *Octopus vulgaris* paralarvae. Aquaculture, 242: 455–478.

Villanueva, R., Escudero, J. M., Deulofeu, R., Bozzano, A., and Casoliva, C. 2009. Vitamin A and E content in early stages of cephalopods and their dietary effects in *Octopus vulgaris* paralarvae. Aquaculture, 286: 277–282.

Volpi, C., Auteri, R., Borri, M., and Mannini, P. 1990. Distribution and reproduction of *Sepia elegans* in the North Tyrrhenian Sea. Rapports de la Commission Internationale de la Mer Méditerranée, 32: 244.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., *et al.* 2002. Ecological responses to recent climate change. Nature, 416: 389–395.

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

Waluda, C. M., Trathan, P. N., and Rodhouse, P. G. 1999. Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the South Atlantic. Marine Ecology Progress Series, 183: 159–167.

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

Waluda, C. M., Rodhouse, P. G., Trathan, P. N., and Pierce, G. J. 2001b. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. Fisheries Oceanography, 10: 207–216.

Wang, J., Pierce, G. J., Boyle, P. R., Denis, V., Robin, J-P., and Bellido, J. M. 2003. Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences –

a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters. ICES Journal of Marine Science, 60: 1149–1158.

Ware, D. M., and Thomson, R. E. 2005. Bottom–up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science, 308: 1280–1284.

Warnke, K., Söller, R., Blohm, D., and Saint-Paul, U. 2004. A new look at geographic and phylogenetic relationships within the species group surrounding *Octopus vulgaris* (Mollusca, Cephalopoda): indications of very wide distribution from mitochondrial DNA sequences. Journal of Zoological Systematics and Evolutionary Research, 42: 306–312.

Wasserman, P. D. 1989. Neural Computing Theory and Practice. Van Nostrand Reinhold, New York. 230 pp.

Weaver, A. J., and Zwiers, F. W. 2000. Uncertainty in climate change. Nature, 407: 571–572.

Wells, M. J. 1978. Octopus: Physiology and Behaviour of an Advanced Invertebrate. Chapman and Hall, London. 417 pp.

Wells, M. J. 1983. Circulation in cephalopods. *In* The Mollusca. Vol. 5: Physiology, Part 2, pp. 239–290. Ed. by A. S. M. Saleuddin and K. M. Wilbur. Academic Press, London. 500 pp.

Wells, M. J., and Smith, P. J. S. 1987. The performance of the octopus circulatory system. A triumph of engineering over design. Experientia, 43: 487–499.

Wiborg, K. F. 1972. *Todarodes sagittatus* (Lamarck). Investigation in Norwegian and North Atlantic waters in 1970–1972. Fisken og Havet, 1972(3): 5–14.

Wiborg, K. F. 1978. *Todarodes sagittatus* (Lamarck) occurrence in Norwegian coastal waters during autumn 1977–spring 1978. Fisken og Havet, 1978(2): 43–59.

Wiborg, K. F. 1979a. *Gonatus fabricii* (Lichenstein), a possible fishery resource in the Norwegian Sea. Fisken og Havet, 1979(1): 33–46.

Wiborg, K. F. 1979b. *Todarodes sagittatus* (Lamarck). Investigation in Norwegian coastal waters, in the northern North Sea and south of the Faroes during October 1978–1979. Fisken og Havet, 1979(3): 9–19.

Wiborg, K. F. 1987. Investigation on the squid, *Todarodes sagittatus* (Lamarck), in Norwegian coastal and bank waters in September–December 1984, April and August–September 1985, at Shetland in July 1984, and at the Faroes in August 1985. Fisken og Havet, 1987(2): 1–8.

Wise, L., Murta, A. G., Carvalho, J. P., Abreu, P., Fernandes, A. C., Ferreira, A. L., Henriques, E., *et al.* 2009. Cognitive maps from onboard observers as a tool for fishery management. ICES Document CM 2009/L:07. 14 pp.

Wommack, K. E., and Colwell, R. R. 2000. Virioplankton: Viruses in aquatic ecosystems. Microbiology and Molecular Biology Reviews, 64: 69–114.

Worms, J. 1983. *Loligo vulgaris*. *In* Cephalopod Life Cycles. Vol. I: Species Accounts, pp. 143–157. Ed. by P. R. Boyle. Academic Press, London. 475 pp.

Wülker, G. 1920. Über Cephalopoden des Roten Meeres. Senckenbergiana, 2: 48–58.

Würsig, B., Reeves, R. R., and Ortega-Ortiz, J. G. 2002. Global climate change and marine mammals. *In* Marine Mammals: Biology and Conservation, pp. 589–608. Ed. by P. G. H. Evans and J. A. Raga. Kluwer Academic/Plenum Publishers, New York. 626 pp.

Wurtz, M., Matricardi, G., and Rebora, F. 1991. Abundance estimates and distribution of *Sepia orbignyana* and *Sepia elegans* in two fishing areas of central Mediterranean. Trawl-survey 1985–87. *In* La Seiche: the Cuttlefish, 1st International Symposium on the Cuttlefish *Sepia*, 1–3 June 1989, Caën, pp. 301–311. Ed. by E. Boucaud-Camou. Centre de Publications de l'Université de Caën, Caën, France. 358 pp.

Wurtz, M., Matricardi, G., and Belcari, P. 1992. Distribution and abundance of the octopus *Eledone cirrhosa* in the Tyrrhenian Sea, Central Mediterranean. Fisheries Research, 13: 53–66.

Yamada, H., Takayanagi, K., Tateishi, M., Tagata, H., and Ikeda, K. 1997. Organotin compounds and polychlorinated biphenyls of livers in squid collected from coastal waters and open oceans. Environmental Pollution, 96: 217–226.

Yatsu, A., Mochioka, N., Morishita, K., and Toh, H. 1998. Strontium/Calcium ratios in statoliths of the neon flying squid *Ommastrephes bartrami* (Cephalopoda) in the North Pacific Ocean. Marine Biology, 131: 275–282.

Yatsu, A., Watanabe, T., Mori, J., Nagasawa, K., Ishida, Y., Meguro, T., Kamei, Y., *et al.* 2000. Interannual variability in stock abundance of the neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean during 1979–1998: impact of driftnet fishing and oceanographic conditions. Fisheries Oceanography, 9: 163–170.

Yau, C. 1994. The ecology and ontogeny of cephalopod juveniles in Scottish waters. PhD thesis, University of Aberdeen, UK.

Yeatman, J., and Benzie, J. A. H. 1994. Genetic structure and distribution of *Photololigo* spp. in Australia. Marine Biology, 118: 79–87.

Young, I. A. G., Pierce, G. J., Daly, H. I., Santos, M. B., Key, L. N., Bailey, N., Robin, J-P., *et al.* 2004. Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). Fisheries Research, 69: 211–227.

Young, I. A. G., Pierce, G. J., Stowasser, G., Santos, M. B., Wang, J., Boyle, P. R., Shaw, P. W., *et al.* 2006a. The Moray Firth directed squid fishery. Fisheries Research, 78: 39–43.

Young, I. A. G., Pierce, G. J., Murphy, J., Daly, H. I., and Bailey, N. 2006b. Application of the Gómez-Muñoz model to estimate catch and effort in squid fisheries in Scotland. Fisheries Research, 78: 26–38.

Zeidberg, L. D., and Robison, B. H. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. Proceedings of the National Academy of Sciences of the USA, 104: 12946–12948.

Zeidberg, L. D., Hamner, W. M., Nezlin, N. P., and Henry, A. 2006. The fishery for California market squid (*Loligo opalescens*; Cephalopoda: Myopsida), from 1981 through 2003. Fishery Bulletin US, 104: 46–59.

Zimmer, I., Piatkowski, U., and Brey, T. 2007. The trophic link between squid and the emperor penguin *Aptenodytes forsteri* at Pointe Géologie, Antarctica. Marine Biology, 152: 1187–1195.

Zuev, G. V., and Nesis, K. N. 1971. Squid (Biology and Fishing). *In* Selected English Translations of Published Works on Cephalopods by Kir N. Nesis, Vol. II. Compiled by M. J. Sweeney. Smithsonian Institution Libraries 2003, Washington, DC. 291 pp.

Zuev, G. V., Nesis, K. N., and Nigmatullin, Ch. M. 1976. Distribution of the genera *Ommastrephes* D'Orbigny, 1835, *Sthenoteuthis* Verrill, 1880 and *Todarodes S*teenstrup, 1880 (Cephalopoda, Oegopsida) in the Atlantic Ocean. Bulletin of the Moscow Society of Naturalists (Biological Section), 81: 53–63 (in Russian).

Zumholz, K. 2000. Fischereibiologische Untersuchungen zür Cephalopoden-Fauna der Nordsee. Diploma thesis, University of Kiel, Germany.

Zumholz, K. 2005. The influence of environmental factors on the micro-chemical composition of cephalopod statoliths. PhD thesis, University of Kiel, Germany.

Zumholz, K., and Piatkowski, U. 2005. Research cruise data on the biology of the lesser flying squid, *Todaropsis eblanae*, in the North Sea. Aquatic Living Resources, 18: 373–376.

Zumholz, K., Hansteen, T. H., Klügel, A., and Piatkowski, U. 2006. Food effects on statolith composition of the common cuttlefish (*Sepia officinalis*). Marine Biology, 150: 237–244.

Zumholz, K., Klügel, A., Hansteen, T. H., and Piatkowski, U. 2007a. Statolith microchemistry traces environmental history of the boreoatlantic armhook squid *Gonatus fabricii*. Marine Ecology Progress Series, 333: 195–204.

Zumholz, K., Hansteen, T. H., Piatkowski, U., and Croot, P. 2007b. Influence of temperature and salinity on the trace element incorporation into statoliths of the common cuttlefish (*Sepia officinalis*). Marine Biology, 151: 1321–1330.

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

Annex 1 CEPHSTOCK project deliverables

The project deliverables (prefixed D) are listed by workpackage, and most are unpublished reports. Almost all are multi-authored, and author names are indicated below if given in the report. Copies of reports may be requested from the authors and/or workpackage leaders.

WP1 Coordination

Workpackage leader: Graham Pierce (University of Aberdeen, UK)

Deliverable No	Deliverable title	Delivery date
D1.1	Annual Progress Report, Year 1	12 months
D1.2	Annual Progress Report, Year 2	24 months
D1.3	Annual Progress Report, Year 3	36 months
D1.4	Final Report	36 months
D1.5	Dissemination Report	36 months

WP2 Fishery databases and GIS for cephalopod stocks

Workpackage leader: Jianjun Wang (University of Aberdeen, UK)

The final GIS and databases (D2.5, D2.6, D2.7) were delivered as CD-ROMs. D2.8 was a website (unfortunately no longer active).

Deliverable No	Deliverable title	Delivery date
D2.1	CD-ROM FOR COMMON DATABASES (DRAFT)	24 MONTHS
D2.2	CD-ROM for common GIS outputs (draft)	24 months
D2.3	CD-ROM for GIS routines (draft)	24 months
D2.4	Evaluation version of web interface	24 months
D2.5	CD-ROM for common databases (final)	36 months
D2.6	CD-ROM for common GIS outputs (final)	36 months
D2.7	CD-ROM for GIS routines (final)	36 months
D2.8	Final version of web interface	36 months
D2.9	Report on commercial development of GIS	36 months

WP3 Review and analysis of fishery–environment interactions

Workpackage leader: Vasilis Valavanis (HCMR, Greece)

D3.3 subsumed the content of D3.1 and D3.2, as well as adding new material.

Deliverable No	Deliverable title	Delivery date
D3.1	Review of modelling studies of cephalopod stock dynamics and relationships with environmental factors	12 months
D3.2	Summary report on new modelling results	24 months
D3.3	Report on stock trends and fishery forecasting	36 months

WP4 Review of cephalopod stock genetics

Workpackage leader: Paul Shaw (Royal Holloway, University of London, UK)

The content of D4.1, D4.3, and D4.4 was subsumed entirely within D4.2 and D4.5.

Deliverable No	Deliverable title	Delivery date
D4.1	Draft report on molecular genetics applications in cephalopod fisheries	18 months
D4.2	Final report on molecular genetics applications in cephalopod fisheries	36 months
D4.3	Annual summary recommendations for genetic data collection	12 months
D4.4	Annual summary recommendations for genetic data collection	24 months
D4.5	Annual summary recommendations for genetic data collection	36 months

WP5 Review of life cycle, ecology, and movements

Workpackage leader: Uwe Piatkowski (IFM-GEOMAR, Germany)

D5.2 was extended to include reviews of additional, less commercially important species. D5.3 was merged with D5.2 (the common database) and was provided on a CD-ROM. D5.4, a compilation of beak size–body size relationships, is currently available online at http://researchservices1.qub.ac.uk/BiolBio/.

Deliverable No	Deliverable title	Delivery date
D5.1a–f	Life-history review papers for main species (draft)	18 months
D5.2a–f	Life-history review papers for main species (final)	36 months
D5.3	Life-history data CD-ROM	36 months
D5.4	Beak size–body size CD-ROM	36 months

WP6 Review of cephalopod immunology and physiology

Workpackage leader: Shelagh Malham (Bangor University, UK)

Deliverable No	Deliverable title	Delivery date
D6.1	Report and map of nutrient and pollutant distribution in cephalopod fishery areas – S. Malham, D. Norris, M. L. M. Jones, J. Latchford, J. King, S. Seixas, P. Bustamante, J. Wang, and G. J. Pierce	12 months
D6.2	Report on diseases in cephalopods – S. Malham, J. Latchford, S. Seixas, P. Bustamante, and S.Pascual	24 months
D6.3	Report on methodology for testing immuno-competence – S. Malham, M. L. M. Jones, J. Latchford, S. Seixas, P. Bustamante, and G. J. Pierce	36 months

WP7 Review of cephalopod culture and capture fisheries

Workpackage leader: Noussithé Koueta (University of Caën, France)

The two final deliverables (D7.3, D7.4) were combined in a single report. D7.3 also included a series of annexes.

Deliverable No	Deliverable title	Delivery date
D7.1	Status report on European cephalopod fisheries (draft)	18 months
D7.2	Prospects for cephalopod culture (technical aspects; draft)	18 months
D7.3	Status report on European cephalopod fisheries (final)	36 months
Annex 1	The Moray Firth Directed Squid Fishery – G. J. Pierce, I. A. G. Young, G. Stowasser, M. B. Santos, J. Wang, P. R. Boyle, P. W. Shaw, N. Bailey, I. Tuck, and M. A. Collins	
Annex 2	Cuttlefish Fisheries in the Coastal Zone of Normandy – V. Legrand, P. Freitas, L. Challier, J. Royer, and J. P. Robin	
Annex 3	The Galician Gillnet Fishery in San Simon – F. Rocha, A. Guerra, , A. F. González, and S. Cerviño	

Annex 4	Artisanal Fisheries Off South Coast of Portugal, Algarve – T. C Borges and J. Sendão	
Annex 5	Characterization of the Artisanal Cephalopods Fisheries off Spanish South Atlantic Region (Gulf Of Cádiz): Fishing Gear and Methods - I. Sobrino and L. Silva	
Annex 6	Review of Cephalopod Culture and Capture Fisheries: The Italian Situation – Patrizia Jereb and Sabrina Agnesi	
Annex 7	Review of cephalopod fisheries in the Greek Seas – E. Lefkaditou, S. Kavadas, G. Petrakis, D. Koutsoubas, A. Chilari, and J. Nikolaou	
Annex 8	Falklands Fishery – A. G. Payne and D. J. Agnew	
Annex 9	Spanish Cephalopod Fisheries in West Africa (Eastern Central Atlantic) – Eduardo Balguerías Guerra	
D7.4	Prospects for cephalopod culture (technical aspects; final)	36 months

WP8 Socio-economic review of cephalopod fisheries

Workpackage leader: João Pereira (IPIMAR, Portugal)

Deliverable No	Deliverable title	Delivery date
D8.1	Socio-economic report on European cephalopod fisheries (draft)	18 months
D8.2	Prospects for cephalopod culture (socio-economic aspects; draft)	18 months
D8.3	Socio-economic report on European cephalopod fisheries (final)	36 months
D8.4	Prospects for cephalopod culture (socio-economic aspects; final)	36 months

WP9 Data collection requirements for stock assessment

Workpackage leader: Marina Santurtun (AZTI, Spain)

Deliverable No	Deliverable title	Delivery date
D9.1	First report on data collection protocols	12 months
D9.2	Second report on data collection protocols	24 months
D9.3	Third report on data collection protocols	36 months

WP10 Stock status reviews

Workpackage leader: Jean-Paul Robin (University of Caën, France)

Deliverable No	Deliverable title	Delivery date
D10.1	Outline stock status reports	12 months
D10.2	Draft stock status reports	24 months
D10.3	Final stock status reports	36 months

WP11 Stock assessment workshops

Workpackage leader: Adam Payne (Renewable Resources Assessment Group, Imperial College, London, UK)

D11.3 comprised the special issue of *Fisheries Research* edited by David Agnew, Adam Payne, and Graham Pierce, arising from the 2004 stock assessment workshop.

Deliverable No	Deliverable title	Delivery date
D11.1	First assessment workshop report	24 months
D11.2	Second assessment workshop report	36 months
D11.3	Review and results of stock assessments	36 months

WP12 Fishery management recommendations

Workpackage leader: João Pereira (IPIMAR, Portugal)

Deliverable No	Deliverable title	Delivery date
D12.1	Summary report on management regimes	24 months
D12.2	Report on management recommendations	36 months

WP13 New research priorities

Workpackage leader: Graham Pierce (University of Aberdeen, UK)

Deliverable No	Deliverable title	Delivery date
D13.1	Research priorities	36 months
D13.2	Framework 6 RTD proposal(s)	36 months

Annex 2 CEPHSTOCK project publications

A2.1 Journal special issues

Koueta, N., Andrade, J. P., and Boletzky, S. v. (Eds). 2006. The cuttle *Sepia officinalis*. Vie et Milieu, 56(2): 69–201.

Pierce, G. J., Portela, J. M., and Robin, J-P. (Eds). 2005. Environmental effects on cephalopod life history and fisheries. Aquatic Living Resources 18: 325–400.

Payne, A. G., Agnew, D. J., and Pierce, G. J. (Eds). 2006. Trends and Assessment of Cephalopod Fisheries – Proceedings of the CEPHSTOCK Cephalopod Assessment Workshop. Fisheries Research, 78: 1–106.

A2.2 Journal papers

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

Chen, C. S., Pierce, G. J., Wang, J., Robin, J-P., Poulard, J. C., Pereira, J., Zuur, A. F., *et al.* 2006. The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: trends in *Loligo* spp. abundance in the northeast Atlantic and possible environmental influences. Fisheries Research, 78: 44–54.

Georgakarakos, S., Koutsoubas, D., and Valavanis, V. D. 2006. Time series analysis and forecasting techniques applied on loliginid and ommastrephid landings in Greek waters. Fisheries Research, 78: 55–71.

Payne, A. G., Agnew, D. J., and Pierce, G. J. 2006. Foreword: Trends and assessment of cephalopod fisheries. Fisheries Research, 78: 1–3.

Pierce, G. J., Portela, J., and Robin, J-P. 2005. Foreword: Environmental effects on cephalopod life history and fisheries. Aquatic Living Resources, 18: 325–326.

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

Pierce, G. J., Valavanis, V. D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J. M., Katara, I., *et al.* 2008. A review of cephalopod–-environment interactions in European Seas and other world areas. Hydrobiologia, 612: 49–70.

Rosa, R., Pereira, J., Costa, P. R., and Nunes, M. L. 2006. Distribution, abundance, biology, and biochemistry of the stout bobtail squid *Rossia macrosoma* from the Portuguese coast. Marine Biology Research, 2: 14–23.

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

Seixas, S., Bustamante, P., and Pierce, G. J. 2005. Interannual patterns of variation in concentrations of trace elements in arms of *Octopus vulgaris*. Chemosphere, 59: 1113–1124.

Semmens, J. M., Pecl, G. T., Villanueva, R., Jouffre, D., Sobrino, I., Wood, J. B., and Rigby, P. R. 2004. Understanding octopus growth: patterns, variability and physiology. Marine and Freshwater Research, 55: 367–377.

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

Valavanis, V. D., Kapantagakis, A., Katara, I., and Palialexis, A. 2004. Critical regions: A GIS-based model of marine productivity hotspots. Aquatic Sciences, 66: 139–148.

Valavanis, V. D., Georgakarakos, S., Kapantagakis, A., Palialexis, A., and Katara, I. 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling, 178: 417–427.

Valavanis, V. D., Katara, I., and Palialexis, A. 2005. Marine GIS: Identification of mesoscale oceanic thermal fronts. International Journal of Geographical Information Science, 19: 1131–1147.

Villanueva, R., and Bustamante, P. 2006. Composition in essential and non-essential elements of early stages of cephalopods and dietary effects on the elemental profiles of *Octopus vulgaris* paralarvae. Aquaculture, 261: 225–240.

Villanueva, R., Arkhipkin, A., Jereb, P., Lefkaditou, E., Lipinski, M. R., Perales-Raya, C., Riba, J., *et al.* 2003. Embryonic life of the loliginid squid *Loligo vulgaris*: comparison between statoliths of Atlantic and Mediterranean populations. Marine Ecology Progress Series, 253: 197–208.

Villanueva, R., Riba, J., Ruiz-Capillas, C., Gonzalez, A. V., and Baeta, M. 2004. Amino acid composition of early stages of cephalopods and effect of amino acid dietary treatments on *Octopus vulgaris* paralarvae. Aquaculture, 242: 455–478.

Villanueva, R., Moltschaniwskyj, N. A., and Bozzano, A. 2007. Abiotic influences on embryo growth: statoliths as experimental tools in the squid early life history. Reviews in Fish Biology and Fisheries, 17: 101–110.

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

Young, I. A. G., Pierce, G. J., Murphy, J., Daly, H. I., and Bailey, N. 2006. Application of the Gómez-Muñoz model to estimate catch and effort in squid fisheries in Scotland. Fisheries Research, 78: 26–38.

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

Author and Editor Contact Information

Editors

Graham J. Pierce
Author: Sections 1, 3.1, 3.3, 4, 5, 6
University of Aberdeen, Oceanlab
Main Street, Newburgh
Aberdeenshire
AB41 6AA
UK
g.j.pierce@abdn.ac.uk
and
Instituto Español de Oceanografía, Centro Oceanográfico de Vigo
Apdo. 1552
36200 Vigo
Spain

Louise Allcock
Author: Sections 2, 3.1
Martin Ryan Marine Science Institute
National University of Ireland, Galway
University Road
Galway, Ireland
louise.allcock@gmail.com

Isabel Bruno
Author: Section 4
Instituto Español de Oceanografía
Centro Oceanográfico de Vigo
Apdo. 1552
36200 Vigo
Spain
isabel.bruno@vi.ieo.es

Paco Bustamante
Author: Sections 3.4, 6
Littoral, Environnement et Sociétés (LIENSs)
UMR 6250
CNRS-Université de La Rochelle
2 rue Olympe de Gouges
17042 La Rochelle Cedex 01
France
paco.bustamante@univ-lr.fr

Angel González
Author: Sections 3.1, 3.3, 6
Instituto de Investigaciones Marinas (CSIC)
Eduardo Cabello 6
36208 Vigo
Spain
afg@iim.csic.es

Ángel Guerra
Author: Sections 3.1, 4, 6
Instituto de Investigaciones Marinas (CSIC)
Eduardo Cabello 6
36208 Vigo
Spain
angelguerra@iim.csic.es

Patrizia Jereb
Author: Sections 3.1, 4, 6
ISPRA
Via di Casalotti 300
00166 Roma
Italy
p.jereb@icram.org
patrizia.jereb@isprambiente.it

Eugenia Lefkaditou
Author: Sections 3.1, 4, 5, 6
Institute of Marine Biological Resources
Hellenic Centre for Marine Research
Ag. Kosmas
16777 Helliniko
Athens
Greece
teuthis@ath.hcmr.gr

Shelagh Malham
Author: Section 3.4
Bangor University, School of Ocean Sciences, Centre for Applied Marine Sciences
Menai Bridge
Anglesey
LL59 5AB
UK
s.malham@bangor.ac.uk

Ana Moreno
Author: Section 3.1, 3.3, 6
INRB/L-IPIMAR, Instituto Nacional de Recursos Biológicos
Av. Brasilia, s/n
1400-038 Lisboa
Portugal
amoreno@ipimar.pt

João Pereira
Author: Sections 3.1, 4, 5, 6
INRB/L-IPIMAR, Instituto Nacional de Recursos Biológicos
Av. Brasilia, s/n
1400-038 Lisboa
Portugal
pereira@notes.horta.uac.pt

Uwe Piatkowski
Author: Sections 3.1, 6
IFM-GEOMAR
Leibniz-Institut für Meereswissenschaften an der Universität Kiel
Forschungsbereich Marine Ökologie
Düsternbrooker Weg 20
24105 Kiel
Germany
upiatkowski@ifm-geomar.de

Mario Rasero
University of Aberdeen, Oceanlab
Main Street, Newburgh
Aberdeenshire
AB41 6AA
UK
mariorasero@yahoo.es

Pilar Sánchez
Author: Sections 3.1, 4, 5
Institut de Ciències del Mar, (CSIC)
Passeig Marítim de la Barceloneta 37-49
08003 Barcelona
Spain
pilar@icm.csic.es

Maria Begoña Santos
Author: Section 6
Instituto Español de Oceanografía, Centro Oceanográfico de Vigo
Apdo. 1552
36200 Vigo
Spain
m.b.santos@vi.ieo.es

Marina Santurtún
Author: Sections 5, 6
AZTI-Tecnalia, Marine Research Division
Txatxarramendi Ugartea z/g
48395 Sukarrieta
Spain
msanturtun@azti.es

Sonia Seixas
Author: Sections 3.1, 3.4, 6
Universidade Aberta
Rua Escola Politécnica 147
1269-001 Lisbon
Portugal
soniabseixas@gmail.com
and
Institute of Marine Research,
CIC,
University of Coimbra,
3000 Coimbra,
Portugal

Ignacio Sobrino
Author: Sections 3.1, 4, 5
Instituto Español de Oceanografía, Centro Oceanográfico de Cadiz
Muelle Pesquero de Cadiz
Apdo. 2609
11006 Cadiz
Spain
ignacio.sobrino@cd.ieo.es

Roger Villanueva
Author: Sections 3.1, 4, 6
Institut de Ciències del Mar, (CSIC)
Passeig Marítim de la Barceloneta 37-49
08003 Barcelona
Spain
roger@icm.csic.es

Authors

Nick Bailey
Section 4
Marine Scotland, Marine Laboratory
PO Box 101
375 Victoria Road, Aberdeen
AB11 9DB
UK
n.bailey@marlab.ac.uk

Paola Belcari
Sections 3.1, 6
Dipartimento Scienze Uomo e Ambiente
Via Derna 1
56125 Pisa
Italy
p.belcari@ucl.ac.uk

Peter Boyle
Section 1
Deceased

Laurence Challier
Section 6
UMR-IFREMER Physiologie et Ecophysiologie des Mollusques Marins, I.B.F.A.
Université de Caën Basse-Normandie
Esplanade de la Paix
14032 Caën Cedex
France
c/o jean-paul.robin@unicaen.fr

Yves Cherel
Section 6
CEBC – CNRS
BP 14
79360 Villiers-en-Bois
France
cherel@cebc.cnrs.fr

Lee C. Hastie
Sections 3.1, 4
University of Aberdeen, Oceanlab
Main Street, Newburgh
Aberdeenshire
AB41 6AA
UK
l.c.hastie@abdn.ac.uk

Ane Iriondo
Section 5
AZTI-Tecnalia, Marine Research Division
Txatxarramendi Ugartea z/g
48395 Sukarrieta
Spain
airiondo@suk.azti.es

Noussithé Koueta
Sections 4, 6
UMR-IFREMER Physiologie et Ecophysiologie des Mollusques Marins, I.B.F.A.
Université de Caën Basse-Normandie
Esplanade de la Paix
14032 Caën Cedex
France
noussithe.koueta@unicaen.fr

Véronique Legrand
Section 5
Comité Régional de Pêches Maritimes et des Elevages Marins de Basse-Normandie
9 quai du Général Lawton Collins
B.P. 445, 50104 Cherbourg
France
vlegrand.crpbn@wanadoo.fr

Pia Orr
Section 5
Fisheries Group, Imperial College London
Silwood Park Campus
Buckhurst Road, Ascot
Berkshire SL5 7PY
UK
p.orr@imperial.ac.uk

Santiago Pascual
Sections 3.1, 3.4
Instituto de Investigaciones Marinas (CSIC)
Eduardo Cabello 6
36208 Vigo
Spain
spascual@iim.csic.es

Adam Payne
Section 5
Fisheries Group, Imperial College London
Silwood Park Campus
Buckhurst Road, Ascot
Berkshire SL5 7PY
UK
adam.payne@erm.com

Cristina Pita
Section 6
Business School, Department of Economics, University of Aberdeen
Edward Wright Building
Dunbar Street
Aberdeen AB24 3QY, Scotland
UK
c.pita@abdn.ac.uk

Jean-Paul Robin
Sections 4, 5, 6
UMR-IFREMER Physiologie et Ecophysiologie des Mollusques Marins, I.B.F.A.
Université de Caën Basse-Normandie
Esplanade de la Paix
14032 Caën Cedex
France
jean-paul.robin@unicaen.fr

Beatriz Roel
Section 6
Cefas Lowestoft Laboratory
Pakefield Road
Lowestoft
Suffolk
NR33 0HT

UK
beatriz.roel@cefas.co.uk

Paolo Sartor
Section 3.1
Centro Interuniversitario di Biologia Marina ed ecologia applicata "G. Bacci"
Viale Nazario Sauro
4–57128 Livorno
Italy
psartor@cibm.it

Paul W. Shaw
Sections 3.2, 6
School of Biological Sciences, Royal Holloway University of London
Egham
Surrey
TW20 0EX
UK
p.shaw@rhul.ac.uk

Jennifer Smith
Section 6
University of Aberdeen, Oceanlab
Main Street, Newburgh
Aberdeenshire
AB41 6AA
UK
jennifer.smith@abdn.ac.uk

Gabrielle Stowasser
Section 6
British Antarctic Survey
High Cross
Madingley Road
Cambridge
CB3 0ET
UK
gsto@bas.ac.uk

Manuel Garcia Tasende
Sections 3.1, 5
Unidade Técnica de Pesca de Baixura (UTPB), Servizo de Planificación
Dirección Xeral de Ordenación e Xestión dos Recursos Mariños
Consellería do Mar
Xunta de Galicia
Rúa Valiño 63-65
San Lázaro
15703 Santiago de Compostela
Spain
manuel.garcia.tasende@xunta.es

Vasilis Valavanis
Section 6
Institute of Marine Biological Resources, Hellenic Centre for Marine Research
Gournes Pediados
PO Box 2214
71003 Heraklion
Crete
Greece
vasilis@her.hcmr.gr

Jianjun Wang
Section 6
School of Biological Sciences
University of Aberdeen
Zoology building
Tillydrone Avenue
Aberdeen AB24 2TZ, UK
j.wang@abdn.ac.uk

Sansanee Wangvoralak
Section 6
University of Aberdeen, Oceanlab
Main Street, Newburgh
Aberdeenshire
AB41 6AA
UK
s.wangvoralak@abdn.ac.uk

Manuela Weis
Section 6
Instituto Español de Oceanografía, Centro Oceanográfico de Vigo
Apdo. 1552
36200 Vigo
Spain
Heliantus@web.de

Iain G. Young
Section 4
School of Biological Sciences
University of Aberdeen
Zoology building
Tillydrone Avenue
Aberdeen AB24 2TZ, UK
IAGYoung@aol.com

Karsten Zumholz
Section 6
INRB/L-IPIMAR, Instituto Nacional de Recursos Biológicos
Av. Brasilia, s/n
1400-038 Lisboa
Portugal
kzumholz@ifm-geomar.de

List of abbreviations

AA	administrative authorization
AEP	average engine power
CRPM	Regional Fisheries Council
DCR	the European Community’s Data Collection Regulation
DML	minimum landing size
EAFM	ecosystem approach to fisheries management
EFH	essential fish habitat
ENSOI	*El Nino* Southern Oscillation
EnviEFH	Environmental Approach to Essential Fish Habitat Designation (an EC-funded project)
GIS	geographic information system
IBD	isolation-by-distance
IBTS	International Bottom Trawl Survey
ICZN	International Commission on Zoological Nomenclature
ML	mantle length
NAO	North Atlantic Oscillation
PAH	polycyclic aromatic hydrocarbons
PCB	polychlorinated biphenyl
POC	persistent organic compound
POP	persistent organic pollutant
RO	regional order
SST	sea surface temperature
WGCEPH	ICES Working Group on Cephalopod Fisheries and Life History