FISH HABITAT MAPPING

A review of cephalopod–environment interactions in European Seas

Graham J. Pierce · Vasilis D. Valavanis · Angel Guerra · Patricia Jereb · Lydia Orsi-Relini · Jose M. Bellido · Isidora Katara · Uwe Piatkowski · João Pereira · Eduardo Balguerias · Ignacio Sobrino · Eugenia Lefkaditou · Jianjun Wang · Marina Santurtun · Peter R. Boyle · Lee C. Hastie · Colin D. MacLeod · Jennifer M. Smith · Mafalda Viana · Angel F. González · Alain F. Zuur

Abstract Cephalopods are highly sensitive to environmental conditions and changes at a range of spatial and temporal scales. Relationships documented between cephalopod stock dynamics and environmental conditions are of two main types: those concerning the geographic distribution of abundance, for which the mechanism is often unknown, and those relating to biological processes such as egg survival, growth, recruitment and migration, where mechanisms are sometimes known and in a very few cases demonstrated by experimental evidence. Cephalopods seem to respond to environmental variation both 'actively' (e.g. migrating to areas with more favoured environmental conditions for feeding or spawning) and 'passively' (growth and survival vary according to conditions experienced, passive migration with prevailing currents). Environmental effects on early life stages can affect life history characteristics (growth and maturation rates) as well as distribution and

G. J. Pierce (✉)
Centro Oceanográfico de Vigo, Instituto Español de
Oceanografía, P.O. Box 1552, 36200 Vigo, Spain
e-mail: graham.pierce@vi.ieo.es

G. J. Pierce · I. Katara · J. Wang · P. R. Boyle ·
L. C. Hastie · C. D. MacLeod · J. M. Smith · M. Viana
School of Biological Sciences (Zoology), University of
Aberdeen, Tillydrone Avenue, AB24 2TX Aberdeen, UK

V. D. Valavanis
Marine GIS Laboratory, Institute of Marine Biological
Resources, Hellenic Center for Marine Research, P.O.
Box 2214, 71003 Heraklion Crete, Greece

A. Guerra · A. F. González
ECOBIOMAR, Instituto de Investigaciones Marinas
(CSIC), Eduardo Cabello 6, 36208 Vigo, Spain

P. Jereb
Istituto Centrale per la Ricerca Scientifica e Tecnologica
Applicata al Mare, Via di Casalotti 300, 00166 Rome,
Italy

L. Orsi-Relini
Dipartimento per lo studio del Territorio e delle sue
Risorse, Corso Europa 26, 16132 Genova, Italy

J. M. Bellido
Centro Oceanográfico de Murcia, Instituto Español de
Oceanografía, C/ Varadero 1, Apdo 22, San Pedro del
Pinatar, 30740 Murcia, Spain

U. Piatkowski
Leibniz-Institut fur Meereswissenschaften an der
Universitat Kiel, Düsternbrooker Weg 20, 24105 Kiel,
Germany

J. Pereira
Instituto de Investigaçao das Pescas e do Mar,
Av. de Brasília, 1449-006 Lisbon, Portugal

E. Balguerias
Centro Oceanografico de Canarias, Instituto Español de
Oceanografia, Carretera de San Andrés Apdo 1373, 38120
Santa Cruz de Tenerife, Spain

abundance. Both large-scale atmospheric and oceanic processes and local environmental variation appear to play important roles in species–environment interactions. While oceanographic conditions are of particular significance for mobile pelagic species such as the ommastrephid squids, the less widely ranging demersal and benthic species may be more dependent on other physical habitat characteristics (e.g. substrate and bathymetry). Coastal species may be impacted by variations in water quality and salinity (related to rainfall and river flow). Gaps in current knowledge and future research priorities are discussed. Key research goals include linking distribution and abundance to environmental effects on biological processes, and using such knowledge to provide environmental indicators and to underpin fishery management.

Introduction

The abundance and distribution of the world's commercial cephalopod stocks present wide annual fluctuations, generally attributed to the species' short life cycles, characterized by non-overlapping generations and consequent lack of buffering of the population from the influence of varying environmental conditions on spawning and recruitment success (Boletzky, 1986; Boyle, 1990; Rodhouse, 2001; Piatkowski et al., 2001; Rocha et al., 2001; Guerra,

I. Sobrino
Unidad de Cádiz, Instituto Español de Oceanografía, Campus Universitario de Puerto Real, Institutos de Investigación—CACYTMAR, C/ República Saharaui, s/n, 11510 Puerto Real, Cádiz, Spain

E. Lefkaditou
Institute of Marine Biological Resources, Hellenic Centre for Marine Research, Aghios Kosmas, 16777 Helliniko, Athens, Greece

M. Santurtun
Department of Fisheries Resources, AZTI Foundation, Txatxarramendi ugartea, 48395 Sukarrieta, Spain

A. F. Zuur
Highland Statistics Ltd, 6 Laverock Road, AB41 6FN Newburgh, UK

2004; Boyle & Rodhouse, 2005). Experimental and modelling work on the influence of temperature on hatching dates, hatching success and paralarval survival and growth provide insights into possible mechanisms (Forsythe, 1993; Jackson, 2004), highlighting sensitivity to water temperature. Recent studies suggests that increased temperature may also have a negative impact on cephalopods due to a progressive transition of routine mantle metabolism to an anaerobic mode of energy production (Portner, 1994; Melzner et al., 2006). Consistent with these findings, in European waters, cephalopods appear to be highly influenced by environmental variation at all stages of their life history (e.g. Guerra & Rocha, 1994; Pierce et al., 1994; Balguerias et al., 2000; González et al., 2005; Otero, 2006; Guerra, 2006b).

The sensitivity of cephalopod species to environmental fluctuations is a potentially important factor to take into account in stock assessments and fishery management measures. It also suggests that cephalopods could act as indicators of environmental change and ecosystem conditions. As an important ecosystem component, cephalopods and their fluctuations influence the population dynamics of both higher predators and their own prey. It is generally agreed that the world's climate is currently experiencing unprecedented anthropogenically-induced directional change. Possible effects of climate change on the world's oceans include reduced salinity (due to ice melting), increased temperatures, increases in acidity due to absorption of carbon dioxide, shifts in current systems, changing patterns of upwelling and other cyclical phenomena and increased numbers of storms (see Robinson et al., 2005 for a recent review). The short generation time, plasticity of life history and high environmental sensitivity of cephalopods could prove to be a double-edged sword in the context of fishery exploitation, as already noted by Caddy & Rodhouse (1998). On the one hand, cephalopods may be more strongly and more rapidly affected than many longer-lived species by external drivers such as climate change, yet they may ultimately be quicker to recover from extreme environmental variations and better able to adapt to changing conditions.

Caddy (1983) and Rowell et al. (1985) were probably the first authors to suggest relationships between cephalopod distribution and abundance and the environment, although they did not give much consideration to the nature of such links. In the early

1990s, some authors started to describe relationships between temperature and distribution or abundance for various squid species, initially in South Africa (e.g. Augustyn, 1990, 1991; Sauer et al., 1991; Roberts & Sauer, 1994) and later in Europe (e.g. Rasero, 1994; Pierce et al., 1998; Waluda & Pierce, 1998).

The importance of oceanographic conditions as determinants of cephalopod distribution and abundance has been highlighted in particular in relation to studies on the pelagic squid family Ommastrephidae. Thus, Bakun & Csirke (1998) examined the physical processes affecting different aspects of the life-cycle of the genus *Illex* (enrichment, concentrating food and paralarvae, transporting eggs and juveniles and facilitating adult spawning migrations). Anderson & Rodhouse (2001) noted the importance of understanding the links between oceanographic variability and cephalopod life cycles, and the relative spatial and temporal scales at which different processes take place, giving examples related to the Ommastrephid squids *Dosidicus gigas* in the eastern Pacific, and *Martialia gigas* and *Illex argentinus* from the southwest Atlantic. Semmens et al. (2007) focussed on the pivotal role of movement, during all phases of cephalopod life history, in determining abundance and distribution, and the important effects of environmental parameters, such as sea temperature and oceanographic processes in influencing those movements, especially in oceanic squids.

Relatively recently, the role of global oceanographic phenomena, such as El Niño and La Niña, in determining the distribution and abundance of cephalopod species has become apparent (e.g. González et al., 1997; Waluda et al., 2006; Waluda & Rodhouse, 2006; Rodhouse et al., 2006; Chen et al., 2007). Such large-scale phenomena may be cyclic or occasional and are sometimes linked to dramatic fishery collapses (e.g. Peruvian anchovy). Understanding the role of such events is crucial to understanding the nature of relationships between cephalopods and the environment.

Here, we review and synthesize published literature on cephalopod–environment interactions and categorize cephalopod responses to environmental changes and processes, with particular focus on European Seas. In addition, we briefly review the various techniques, particularly in statistical modelling, used to identify and quantify such relationships and consider how recent advances in methodology may help to shape future research. The main part of the review is structured geographically, with the aim of highlighting differences between contrasting marine environments and different large marine ecosystems. The review focusses on European and adjacent seas (Fig. 1), which we have divided into four broad areas: the NE Atlantic (including the North Sea, the English Channel and the Bay of Biscay), the Iberian Peninsula (Galician and Portuguese waters and the Gulf of Cadiz), the Saharan

Fig. 1 Major oceanic processes affecting cephalopod geographic distribution in European waters (NAO: North Atlantic Oscillation, G.S.: Gulf Stream, C.C.: Canary Current, I.P.C.: Iberian Poleward Current, A.C.: Algerian Current). Areas: N.S.: North Sea, E.C.: English Channel, B.B.: Bay of Biscay, G.W.: Galician Waters, G.C.: Gulf of Cadiz, S.B.: Saharan Bank, W.M., C.M., E.M.: Western, Central, Eastern Mediterranean, A.S.: Aegean Sea
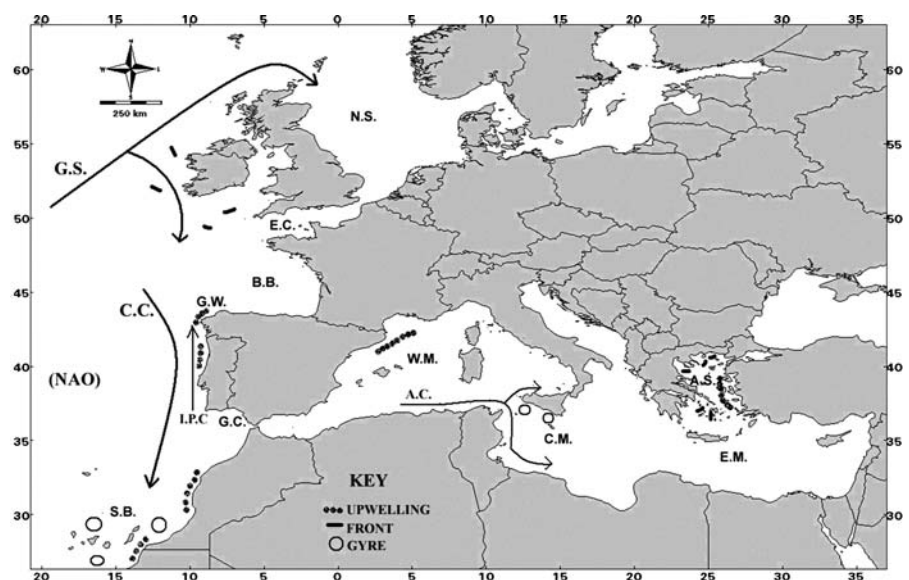
Bank and the Mediterranean Sea (Western/Central/Eastern Mediterranean). We also provide a brief account of studies from the rest of the Atlantic Ocean and adjoining regions.

Physical and oceanographic general characteristics of the study area

Recent reviews on the physical oceanographic conditions in European and adjacent seas of these areas include those by Van Aken & Becker (1996) for the NE Atlantic, Relvas et al. (2007) for the Iberian Peninsula, Lafuente & Ruiz (2007) for the Gulf of Cadiz, Barton et al. (2004) for the Saharan Bank and Millot (2005) for the Mediterranean Sea.

The northern part of the study area (NE Atlantic) is influenced by variations of the Gulf Stream/North Atlantic current that, seasonally, delivers Atlantic water into the North Sea and the English Channel. The southern part of the area (Iberian Peninsula and Saharan Bank) is influenced by seasonal upwelling and gyre formation. The northwestern part of Iberian Peninsula (Galicia) constitutes the northern boundary of the Iberian-Canary current upwelling system, which has been intensively studied from the oceanographic perspective, including physical oceanography, biogeochemical cycles and plankton ecology and productivity (reviewed by Aristegui et al., 2006). The Mediterranean Sea has a highly complex system of water mass circulation, mainly influenced by the Algerian Current (western basin) and Libyo-Egyptian Current (eastern basin), which generate anticyclonic eddies and gyres.

Biological processes (e.g. recruitment and migration) in European Seas and the northwestern African coast are influenced by the North Atlantic Oscillation (NAO) and other atmospheric and ocean processes (e.g. the East Atlantic/Western Russian pattern, the Polar/Eurasian pattern, the East Atlantic jet and the Mediterranean Oscillation) that create seasonal and annual changes in temperature distribution and precipitation levels and corresponding river run-off regimes. Continental shelf regions of varying extent from the coast, and with widely different bottom sediment types and biological assemblages, characterize the whole study area; these support different benthic cephalopod communities and a variety of ocean processes that affect pelagic communities.

Hypotheses, data and methods

Types of questions asked

Studies on cephalopod–environment interactions are usually shaped by the type, resolution and scale of data available. Studies using post-recruit distribution and abundance are, implicitly, examining the cumulative effects of environmental conditions over the entire life history, whereas other studies may focus on particular stages and specific effects (e.g. the influence of temperature on embryonic development). These latter studies should ultimately provide a more detailed and mechanistic understanding of the broader post-recruitment cephalopod–environment relationships. Thus, studies may be divided into those focussing on the geographical distribution of abundance and those relating to specific biological processes such as spawning, embryonic development, hatching, growth, recruitment, maturation and migration, while recognizing that environmental effects on different life-cycle stages and processes are likely to result in changes in abundance and distribution.

Critical stages of cephalopod life cycle include spawning, hatching, early growth, recruitment to the population and to the fishery, and movements to and from the spawning grounds. The majority of studies focus on spatial and temporal patterns in distribution and abundance of the post-recruit stages of commercially exploited species. However, in principle, models of spatiotemporal variation can be fitted to data on distribution, abundance and life history parameters at all life stages, and indeed relationships may be more critical at the earlier stages. In many cephalopods, the paralarval (post-hatching) period tends to be the least well known but there have been several laboratory studies of environmental effects on eggs and paralarvae (Villanueva, 1995; Gowland, 2002; Craig & Overnell, 2003), modelling studies based on laboratory data (Forsythe, 1993) and also studies in the wild focussed on the influence of oceanographic regimes in the distribution and abundance of paralarvae (Rocha et al., 1999; Vecchione, 1999; González et al., 2005; Otero, 2006). It is also important to be aware of possible indirect environmental effects, e.g. operating through environmental effects on the predators, prey competitors or parasites of cephalopods (Otero et al., 2008). Pascual et al. (2007) review relationships between oceanographic

processes and parasite recruitment in fish and cephalopods. They conclude that variability in recruitment of parasite communities tends to be associated with major current systems and that instability in water masses (e.g. due to turbulent mixing in upwelling systems) is associated with instability of trophic interactions over time, which in turn leads to less well-developed parasite communities.

Sources of data on cephalopods

Data on cephalopods may arise from fisheries (landings, by-catch and discard records), trawl surveys (e.g. catch per unit effort (CPUE) and length–frequency distributions in survey trawl hauls), predator stomach contents and tagging or direct observation; obviously, all these sources have associated limitations and biases. Relevant considerations include availability, coverage and resolution (in time and space), and accuracy and precision of the data.

Cephalopod species of no commercial interest tend to be less well documented, with distribution often inferred from indirect evidence such as occurrence in predator stomachs (e.g. Clarke et al., 1980). Even most commercially exploited species are less well studied than many fish, because they are non-target species in large-scale fisheries and/or are targeted by little-monitored artisanal fisheries, or simply because finfish catches are more economically important and attract most funding for routine data collection and research. Although this picture is changing in European waters as many traditional finfish species have been overexploited and fleets are seeking new target species such as cephalopods, many European countries do not regularly record cephalopod catches during fisheries surveys. Survey CPUE is generally regarded as measuring relative abundance in cephalopods, since gear selectivity is poorly known or unknown for most species in most gears (see, however, Bravo de Laguna & Balguerias, 1993; Hastie, 1996).

Commercial landings data are subject to the usual issues of under- and mis-reporting, and cephalopod landings are rarely identified to species, e.g. squid landings are usually classified as 'long-finned' (loliginid) or 'short-finned' (ommastrephid). Where market sampling occurs (e.g. for loliginid squid in Spain, Portugal and Greece), the typical monthly sampling regime is rather coarse for application to such short-lived species (Lourenço & Pereira, 2006).

Life history data tend to be recorded only on a project basis with no long-term and established monitoring taking place in European waters.

Some alternative methodologies and models have been used to estimate catch and CPUE in small-scale fisheries. Among these, Gomez-Muñoz (1990) developed a simple model to estimate catch and CPUE in multispecies small-scale fisheries. This model has been applied in small-scale fisheries for squid and octopus and to larger scale fisheries for monkfish in NW Spain (Simon et al., 1996; Rocha et al., 2004; Otero et al., 2005) and to the fishery for squid in Scottish waters (Young et al., 2006a). In multispecies fisheries, this model can estimate catches of individual species for a specific gear (Rocha et al., 2004).

Environmental variables analyzed

Most cephalopods are benthic, demersal or vertically migrating pelagic species that spend relatively little time in surface waters, except planktonic paralarvae (Jereb & Roper, 2005). However, the ready availability of remotely-sensed ocean surface data, plus the known sensitivity of cephalopod growth to temperature and the presumed importance of primary productivity have led to many studies focussing on the influence of sea surface temperature (SST) and chlorophyll (Chl-a) on cephalopod distribution and abundance. Spatial patterns in these variables may also be used to infer the locations of ocean surface features (thermal fronts, gyres and upwelling), the high productivity of which may be exploited by cephalopods (Jereb et al., 2001; Valavanis et al., 2004; Wang et al., 2004). Surface conditions may also, implicitly or explicitly, be assumed to provide indirect information on sub-surface conditions, although such assumptions are risky without knowledge of local oceanographic conditions (e.g. concerning the degree of mixing of the water column or the existence of sub-surface currents).

Some studies also use sea surface salinity (SSS), e.g. as a proxy for water mass identity or sea surface height (SSH, also expressed as sea level anomaly, SLA) (Valavanis et al., 2002). Where survey environmental data (e.g. conductivity, temperature and depth (CTD) data) are available, studies may also consider sea bottom temperature (SBT) and salinity (SBS) or the temperature and salinity profile of the whole water column (Wang et al., 2003). However, in general, effects of sub-surface oceanographic

conditions on cephalopod distribution and abundance remain poorly known.

Other relevant and readily available data include sea depth (bathymetry), since the distribution of most demersal and benthic species seem to be restricted to certain depth ranges. Loliginid squid may undertake inshore–offshore migrations, so that depth could be a useful predictor of location for particular life stages (e.g. Arkhipkin et al., 2000). Sea bed morphology (e.g. slope, aspect in relation to the direction of prevailing currents and depth variability or 'bumpiness') may also be important. In addition, several studies have analyzed surveyed meteorological (wind and Ekman transport data), thermohaline (CTD data) and chemistry (e.g. dissolved oxygen and nitrate, ammonium and phosphate concentration) variables (e.g. Cushing, 1975; Bakun & Csirke, 1998; Otero, 2006). Studies on *Loligo reynaudii* off South Africa highlight the importance of turbidity and dissolved oxygen in determining the location of spawning areas (e.g. Augustyn et al., 1994).

The known migratory routes of some oceanic squids (e.g. *Illex argentinus* in the southwest Atlantic, Rodhouse et al., 1994a, b, 1995; Waluda et al., 2002) suggest that measures of current direction and strength may be important predictor variables, albeit difficult to incorporate into spatial models. For demersal species, sea bed substrate is another important potential explanatory variable (e.g. for species that attach their eggs to the substratum), although these data are usually only available for coastal areas. The degree to which the substrate has been disturbed by trawling activity may also be important (De Alteris et al., 1998).

Lastly, for analyses of interannual variation in abundance, many studies have used large-scale ocean climate indicators such as the NAO Index. The NAO is the best readily available general index of oceanographic conditions in the NE Atlantic and is related to the strength of the Gulf Stream (Hurrell, 1995; Jones et al., 1997).

Methods of analysis

As there is no buffering effect of older age classes, environmental effects on the extant generation are a crucial feature of cephalopod population dynamics. Indeed, in terms of classical population dynamics, the stock-recruitment relationship (if one exists) and pre-spawning mortality may be the only relevant intrinsic

population parameters (see Pierce & Guerra 1994; Pierce et al., 2006). This has led to a tendency to focus on empirical models of distribution and abundance rather than models rooted in classical population dynamics, such as those used in estimating the abundance of exploited teleost fish populations (e.g. Rochet, 2000). However, in other respects, the approaches to modelling cephalopod habitat requirements are in principle no different from those for other taxa: see, for example, Redfern et al. (2006) for a review of methods applied to data on marine mammals, and Valavanis et al. (2008, this volume), for a review of methods used in essential fish habitat modelling).

Models of cephalopod distribution, abundance and life history parameters can be classified in various ways, e.g. in relation to the species or life-stage to which they refer, whether they address temporal (diurnal, seasonal and interannual) or spatial variation (or some combination thereof), and according to the scale and resolution of the data available or the study area.

Some of the earliest empirical models of abundance (Fogarty, 1989) rely on simple uni-factorial linear regression or correlation. However, advances in statistical modelling have facilitated increasingly sophisticated approaches, taking account of the effects of multiple explanatory variables and their interactions (e.g. multiple linear regression, also ordination and classification methods such as redundancy analysis and regression trees), non-normality in the response variables (e.g. Generalized Linear Models—GLM), non-linearity and heteroscedasticity in the response to variation in explanatory variables (e.g. Generalized Additive Models—GAM), time-lagged effects and temporal autocorrelation (e.g. Auto-Regressive Integrated Moving Average (AR-IMA) and other time-series techniques) and spatial autocorrelation (e.g. Generalized Additive Mixed Models—GAMM). Generic methodologies such as geostatistics, Geographic Information Systems (GIS), bootstrapping, artificial neural networks (ANN) and Bayesian models have also been applied as part of the modelling process (e.g. Georgakarakos et al., 2006).

The objectives of model fitting have been diverse. Often, the underlying purpose is some form of fishery forecasting, with the stated aim of extrapolating model results to either future years or to unexploited areas. However, models based on contemporaneous

environmental conditions are of little use for forecasting, while the short life-cycle of cephalopods restricts the importance of time-lagged environmental effects, although Waluda et al. (1999) showed that SST anomalies associated with El Niño may be linked to recruitment of the ommastrephid squid *Illex argentinus* between 2 and 5 years later. In addition, often no explicit predictions are made since the entire data set is used for model fitting. Indeed, because of this, most published models remain hypotheses generated rather than hypotheses tested (although the development of cross-validation routines for model fitting partially answers this criticism). Other studies focus on individual species habitat requirements or the influence of particular environmental variables on particular life history events or stages (spawning, embryonic increment, hatching, growth, recruitment, maturation and migration). A particular recent focus in fisheries has been on the identification of critical habitats of various life-stages of exploited species, so-called Essential Fish Habitat (EFH), a concept that is readily extended to cephalopods (e.g. articles in this volume).

As indicated above, a particular concern for empirical models, although it could equally be applied to mechanistic models, is that they require adequate testing. Where this has not been done, it is worth keeping in mind the cautionary words of Solow (2001) about the 'fleeting nature of temporal relationships identified between short-time series', a comment that could equally be generalized to spatial extrapolation of studies based on small areas. Finally, even where a correlative relationship is established and can be shown to generate useful predictions, this does not indicate a direct causal link and further study of the underlying mechanism is desirable.

We cite several studies which infer environmental relationships from observed patterns of occurrence without the benefit of any formal statistical analysis. While careful observation of patterns in distribution and abundance is invaluable in defining testable hypotheses, particular caution is needed when interpreting seasonal patterns of distribution or seasonal migrations, since they will inevitably be correlated with seasonal patterns in some environmental variables. An indirect causal link is of course likely (since timing of breeding in many animal taxa is selected to ensure that the young experience favourable environmental conditions and a good food supply).

Review of studies on a regional basis

NE Atlantic (including North Sea, English Channel and Bay of Biscay)

The oceanography of the northeastern Atlantic is strongly affected by the Gulf Stream/North Atlantic Current, which delivers Atlantic water into coastal seas such as the North Sea and English Channel and helps to maintain temperatures at levels higher than at equivalent latitudes elsewhere in the world, and by the NAO, the cycles of which generate substantial variation in temperature and precipitation over the area.

The best documented cephalopods in the NE Atlantic are probably the two *Loligo* species, *L. vulgaris* and *L. forbesi*. Around Scotland, *L. vulgaris* is relatively rare and fishery catches can generally be assumed to be almost exclusively *L. forbesi*. Further south, both species co-exist, although *L. vulgaris* increasingly dominates with decreasing latitude: it has been speculated that the balance between the two species is environmentally mediated (see Chen et al., 2006). These species appear to be patchily distributed in space and time. Many studies of life history, distribution and abundance have pointed to the complexity of population structure in UK, e.g., the existence of summer and winter breeders, as first proposed by Holme (1974). Nevertheless, throughout continental shelf waters, *L. forbesi* seems to comprise a single stock (Shaw et al., 1999) so that the substantial variations in life history parameters reported by numerous authors may be largely environmentally driven.

Making use of spatial and statistical tools, Bellido (2002) reported differences in spatial patterns of distribution of *L. forbesi* between seasons, and between the east and west coasts of Scotland. The separate analysis of data from these two areas revealed intra-annual variability in *L. forbesi* abundance, as later confirmed by Pierce & Boyle (2003) and Pierce et al. (2005a, b), and suggested a possible spatial migration from the west to the east in seasons of high abundance (see also Waluda & Pierce, 1998). Bellido (2002) suggests that the western area represents the main 'reservoir' of squid abundance, with a more or less stable spatial structure, while the east area is occupied seasonally (with a widespread coverage in seasons of high abundance) by a population made up of small, fast moving

aggregations in which it is more difficult to see a clear spatial structure.

Information on detailed habitat preferences and ontogenetic migrations in *L. forbesi* can be inferred from anecdotal evidence provided by fishermen. Thus, in the Moray Firth (Northeast Scotland), fishermen have commented that early in the season (summer), catches are best close inshore around 10-m depth over hard ground. As the season progresses, and the squid increase in size, the squid and the fishery gradually move further offshore to sandy/muddy bottoms in waters of around 55-m depth. Better catches have also been reported in areas that experience stronger tidal currents (Young et al., 2006b).

Interannual variation in abundance of *Loligo* is related to SST, as well as a signal from the previous year's abundance (Pierce & Boyle, 2003). Similarly, *Loligo* landings from the English Channel are related to SST during the previous winter (Robin & Denis, 1999) and there is also evidence that recruitment of the English Channel *L. forbesi* stock is density-dependent (Challier et al., 2005).

The spatial distribution of *Loligo* spp. abundance in the North Sea in winter tends to be positively correlated with both SBT and SST, i.e. higher abundance is seen in areas with higher temperature, while abundance in summer is negatively spatially correlated with SST (Waluda & Pierce, 1998; Pierce et al., 2001). Analysis of survey abundance data from the North Sea in February suggests that squid avoid waters with SBT <7°C (Pierce et al., 1998). Bellido et al. (2001) found evidence that peaks of abundance in Scottish waters occur in the temperature range 8–13°C.

In the Bay of Biscay (ICES Div. VIII a,b,d), *Loligo* spp. catches appeared to be higher in months with lower SST while the spatial distribution of the catches for those cooler higher-catch months is associated with the coolest waters or with the frontal zones (Santurtun et al., 2004).

Both *L. forbesi* and *L. vulgaris* perform seasonal migrations in waters off south-west England. During the winter, *L. forbesi* adults spawn and die, and their eggs hatch in the western English Channel and the new cohort migrates east towards southern North Sea until the following winter (Holme, 1974; Sims et al., 2001). Sims et al. (2001) reported that *L. forbesi* movement in the English Channel is temperature-dependent, migrations occurring earlier in years when water temperatures were generally higher.

The relationships between abundance, movements and SST may be linked to larger-scale climatic variation, as shown by links with the NAO (Sims et al., 2001; Pierce & Boyle, 2003), and thus to Gulf Stream inflow into northeast Atlantic coastal waters. However, signals of both SST and NAO can be detected in the interannual variation of *Loligo* abundance, i.e. local scale variation and large-scale phenomena both play a role (Zuur & Pierce, 2004).

In Scotland, *L. forbesi* exhibits a clear annual abundance peak around October–December as the winter breeding season approaches (Bellido et al., 2001). Nevertheless, analysis by Pierce et al. (2005b) suggested that environmental conditions affect the timing of breeding and the size at maturity, and that (as revealed by changes over three decades in the seasonal pattern of fishery landings) the winter breeding peak may not always have been the dominant one. High autumn/winter temperatures (high winter NAO values) are associated with high squid abundance and precocious maturation and also tend to favour high abundance in the following year, along with increased body weight at length and a decrease in the proportion of animals breeding in December. High abundance in summer, conversely, leads to a fall of body weight at length in the following year. Thus, there may be alternation of precocious and slow maturation, and/or summer and winter breeding, driven by a combination of environmental conditions and intraspecific competition (Pierce et al., 2005b). Sensitivity to environmental triggers is however at least partially under intrinsic control, allowing maturation to begin one to two months earlier in males than in females, as highlighted in analysis by Smith et al. (2005). Boyle et al. (1995) suggested various scenarios under which variation in environmental conditions might affect the duration of the life-cycle and timing of breeding in *L. forbesi*.

The English Channel cuttlefish (*Sepia officinalis*) provides one of the highest cephalopod fishery yields in the NE Atlantic (Royer et al., 2006), spawning in spring on both north (English) and south (French) coasts (Dunn, 1999). Cuttlefish in the English Channel and French Atlantic coast expand their distribution during the spawning season. The centre of high abundance, as identified from fishery data, is located further north in warm years and further south in cooler years (Wang et al., 2003). While local environmental changes, e.g. in SST, affect the

location of peaks in abundance, the authors never-theless note that it is hard to determine if this reflects any causal link.

There have been few studies on environmental relationships for other cephalopods in the NE Atlantic, although Hastie et al. (1994) noted that the high abundance of *Todaropsis eblanae* in the North Sea in 1990 appeared to be related to a positive salinity anomaly (these are generally associated with higher temperatures and stronger inflow of Atlantic water). De Heij & Baayen (2005) discuss the occurrence of various cephalopods in the central and southern North Sea in relation to environmental conditions, although their observations are not supported by any formal statistical analysis. They suggest that the central and southern North Sea is generally unsuitable habitat for cephalopods due to the shallow water. They note that the occurrence of individual species is restricted by water temperature or salinity requirements, as inferred from their seasonal migration patterns. Deep waters in the central and southern North Sea are cooler in summer and warmer in winter, while the reverse is the case in shallow waters and they argue that this explains the seasonal migration of the small loliginid squid *Alloteuthis subulata*, which is sug-gested to prefer relatively warm waters. Differences in the distribution of sepiids and sepiolids are related to differences in salinity tolerance. Thus, *Rossia macrosoma* is restricted to the northern part of the North Sea, because it requires high salinities, while *S. officinalis* and *Sepiola atlantica* both tolerate low salinities. The authors note that incidental findings of unusual cephalopod species in the North Sea (e.g. *Onychoteuthis banksii*) are likely to be the result of passive transport in the north Atlantic current.

The relationship between broad-scale distribution and sea depth is evident in various deep-water benthic and bentho-pelagic cephalopods in the northeast Atlantic. At shallower depths (150–500 m), sepiolids are the most abundant group, with *S. atlantica*, *Sepietta oweniana* and *Rondeletiola minor* restricted to waters <300 m and *Rossia macrosoma* (205–515 m) and *Neorossia caroli* (400–1,535 m) extending into deeper water. Among the incirrate octopods, *Eledone cirrhosa* occurs at depths of up to 500 m, while the genera *Benthoctopus* and *Bathypolypus* occur between 250 and 2,700 m and *Graneledone verrucosa* was caught at depths of 1,785–2,095 m. Cirrate octopods dominate cephalopod catches from the deepest areas, with species including *Opisthoteuthis massyae* (877–1,398 m), *O. grimaldii* (2,165–2,287 m), *Stauroteuthis syrtensis* (1,425–3,100 m), *Cirroteuthis muelleri* (700–4,854 m), *Cirrothauma murrayi* (2,430–4,850 m) and *Grimpoteuthis* spp. (1,775–4,877 m) (Collins et al., 2001).

Relationships between distribution/abundance patterns and environmental factors in North European squid and cuttlefish are relatively well known but most studies do not consider spatial or temporal autocorrelation (e.g. Bellido et al., 2001; Zuur & Pierce, 2004; Pierce et al., 1998, 2005a, b). Bellido (2002) reported that squid abundance in Scotland is correlated over distances between 135 and 405 nautical miles, meaning a spatial correlation of over 5 to 14 ICES rectangles (one ICES rectangle is $1 \times 0.5°$). In the past few years, new statistical approaches to study inter-actions with the environment have emerged (e.g. mixed models, which can take into account temporal autocorrelation), and reanalysis of some of the pub-lished data sets would be useful to confirm whether the relationships previously described persist once auto-correlation is taken into account.

Atlantic waters off Iberian Peninsula (Northern Spain, Portugal and Gulf of Cadiz)

The Iberian Atlantic coast is characterized by a relatively limited continental shelf. The oceanography of the region is dominated by the seasonal upwelling/relaxation pulses of Eastern North Atlantic Central Water (ENACW), linked to the Canary Current and the NAO. The upwelling results in nutrient enrich-ment and supports a high local biodiversity with at least 78 species of cephalopods recorded in Galician waters (Guerra, 1992). In 'relaxed' ENACW periods, the Iberian Poleward Current (IPC) dominates the area, creating appropriate conditions for the transfer of subtropical cephalopod species into northern regions (Guerra et al., 2002).

The upwelling pulses are associated with negative NAO index values and increase the productivity levels of the area, creating favourable conditions for increased paralarval survival in *Octopus vulgaris* (Otero et al., 2005). This influences the artisanal fishery for *O. vulgaris*, which is one of the main small-scale fisheries in the Galician region. This resource shows wide year-to-year fluctuations. Otero et al. (2008) have shown that the wind stress structure, 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 the adult catches. In the Ria de Vigo and the adjacent shelf, upwelling generates a succession of wind stress/relaxation cycles with a periodicity of 10 to 20 days. The associated short-term variation in water chemistry affects paralarval abundance and biomass (Otero, 2006). The decrease in nitrate, ammonium and chlorophyll during the relaxation phase of upwelling events can explain up to 88% of variation in paralarval abundance. During the relaxation phase, nutrient salts are consumed by primary producers to generate biogenic matter, which is retained in the system and transferred through the food web.

Spawning of *O. vulgaris* in this area extends from December to September with a single peak in spring months (Otero et al., 2007). For eggs laid at this peak, the embryonic phase is associated with low bottom temperatures and lasts around 4 months. Thus, the peak of early hatched paralarvae of *O. vulgaris* occurs at the end of the upwelling season, suggesting that the reproductive strategy is tightly linked to the seasonal dynamics of the major local environmental process (Otero, 2006).

Spawning and/or hatching during the upwelling period, as found in *O. vulgaris* in Galician waters, is a common reproductive strategy within other coastal upwelling ecosystems. Factors such as the formation of retention areas due to coastal topography, and the concomitant maintenance of higher productivity levels, play an important role in the determination of the frequency of spawning events, which can vary between different parts of the same upwelling system. *Octopus vulgaris* on the northwestern Portuguese coast displays two spawning peaks, one in March and another in July. This spawning pattern is similar to that found off NW Africa, in the Arguin bank and the South Senegalese coast (Demarcq & Faure 2000), but unlike that found to the north along the Galician coast (Otero, 2006) or to the south on the southwestern Portuguese coast (Pereira et al., unpublished data), all of which areas are within the Canary Current upwelling system.

Studies undertaken in Galician waters show that *O. vulgaris* and *Loligo vulgaris* paralarvae are markedly smaller than those collected in the wild in other areas and under rearing conditions at higher temperatures

(Villanueva, 1995, 2000; Sakaguchi et al., 1999). These size differences are explicable since temperature influences cephalopod growth rate throughout the life cycle. Hatchlings emerging at warmer temperatures have also experienced warmer incubation temperatures during embryonic development, and so hatch at larger sizes (Forsythe, 1993; Pecl et al., 2004). Another reason that could explain the differences in size would be the stress produced during the towing of the net when the animals were captured. However, studies on *L. vulgaris* paralarvae from the Mediterranean hatched in captivity, which were subjected to the same actions involving their capture, revealed that the paralarvae did not shrink substantially after these stressing activities (A. F. Gonzalez, unpublished data).

A positive correlation was observed between the upwelling index and *T. eblanae* abundance in Galician waters over 13 years (1973–1976, 1980–1986 and 1988–1989), suggesting that food availability (abundance of appropriate zooplankton prey, which is strongly related with primary production) during the planktonic phase of the species (paralarvae) is critical for the survival of hatchlings, and consistently, for the success of recruitment (Rasero, 1994).

The NAO index is positively correlated with *O. vulgaris* landings in the Algarve region (Erzini, 2005). Paralarvae of *O. vulgaris* are more abundant during summer (off the west coast) and autumn (off the south coast), while those of ommastrephid squids are abundant during autumn. Highest numbers for both groups are observed over a bathymetric range of 50 to 150 m in SST between 17 and 20°C (Moreno & Pereira, 1998).

Loliginid distribution along the Portuguese continental shelf is limited within SST 13–20°C, with higher catches between 13 and 16°C (Moreno & Sousa-Reis, 1995). A greater number of egg masses of *L. vulgaris* is observed on the south coast of Portugal when higher levels of zooplankton abundance (due to upwelling) are recorded (Villa et al., 1997). Loliginid early life stages are mainly concentrated around the 80–90-m isobath in winter and spring and at 60 m during summer and autumn, while they show a seasonal pattern of higher abundance during winter and spring along the northern Portuguese coast (Cunha et al., 1995). Loliginid and Sepiolid paralarvae are mostly found during winter and spring, in waters with SST less than 16°C and over a bathymetric range of 50 to 100 m (Moreno &

Pereira, 1998). Off the Portuguese coast, higher SST during the first three months of life of the squid *L. vulgaris* was shown to favour somatic development before maturation, with putative effects on fecundity and, indirectly, on abundance (Moreno et al., 2007).

Sepia officinalis tolerates temperatures up to 30°C and the species is found in the lagoon system of the Ria Formosa (South Portugal), where the temperature reaches 27 ± 3°C in summer (Domingues et al., 2002, 2006). Depth tolerance in this species changes over the life cycle: larger cuttlefish implode between 150 and 200 m, whereas advanced embryonic specimens and newly hatched animals implode between 50 and 100 m (Guerra, 2006a).

Recent studies suggest that the distribution of some species around the Iberian Peninsula may be changing, possibly as a consequence of slow environmental trends. The musky octopus (*Eledone moschata*) was considered to be a Mediterranean species (Mangold, 1983) with a low or occasional occurrence in the Gulf of Cadiz (Guerra, 1992; Silva et al., 2004) and southern Portuguese coast, as confirmed by early anecdotal accounts and regular species monitoring surveys of Instituto de Investigacao das Pescas e do Mar (IPIMAR) from the early 1980s. Throughout the 1990s and the beginning of the 2000s, however, it became increasingly abundant and widespread to the north, and is currently well established with breeding populations found as far north as Lisbon (Lourenço et al., unpublished data). The same environmental change seems to have had the opposite consequence for *L. forbesi*, a more northerly species, which has contracted its former distribution to northern waters, becoming scarce or absent in western Iberian shores in the same period of time (Chen et al., 2006).

The analysis of the isotope composition of calcareous structures of marine organisms has proved useful in providing bio-ecological data. Analyses undertaken on the carbon- and oxygen-isotope composition of cuttlebone aragonite of wild and cultivated specimens of *S. officinalis* from NW Spain showed that the seasonal temperature changes inferred from isotope ratios were consistent with changes in the temperature of ambient sea water. The maximum life span of 2 years and variable growth rates among and within individuals can be inferred from isotopic signatures (Bettencourt & Guerra, 1999).

The Gulf of Cadiz is characterized by river discharges that affect SST distribution. Thus, rainfall levels (in turn affected by NAO) play an important role in determining cephalopod abundance. Here, octopus abundance is highly correlated with levels of rainfall prior to the fishing season, river discharges in December and SST in May and June (Sobrino et al., 2002).

Saharan Bank

The oceanography of the Saharan Bank, a highly productive ecosystem, is dominated by strong upwelling activity and gyre formation. Generally, these features increase the productivity levels in the area and create a variable SST distribution, although the intensity of these processes depends on depth. Cephalopod species in the area include *Loligo vulgaris*, *Octopus vulgaris* and *Sepia officinalis*, all of which are or have been important fishery resources and *Todarodes sagittatus*.

There are relatively few studies on the environmental relationships of cephalopods in this region. Balguerias et al. (2000) evaluated the history of fisheries in the area and the apparent replacement of finfish (due to overexploitation of the resource) by *O. vulgaris* and *S. officinalis* since the 1960s. They suggested that changes in the faunistic composition of the communities were caused by a combination of factors, including economic initiatives as well as oceanographic variation and competition for food.

In the Saharan Bank area, two distinct octopus stocks (north and south Saharan Bank) have been described. Annual abundance variability is related to depth and SST, with abundance reaching a maximum in October–November when SST is highest (Balguerias et al., 2002). Transient productive gyres of the Saharan Bank seem to trap octopus paralarvae, positively affecting their survival (Balguerias et al., 2000, 2002). Faraj & Bez (2007) showed that there are clear distinctions between the spatial distribution patterns of the spawning and recruitment phases of the Dakhla stock of *O. vulgaris* in relation to bathymetry: juveniles are more coastal, less spatially dispersed, patchier, and more anisotropically distributed.

In the Saharan Bank region, *Todarodes sagittatus* reaches maturity at younger ages and smaller sizes than in the Mediterranean (further north), while the latter attain larger sizes as a result of maintaining fast growth over a longer period and delaying maturation. Greater growth rates in juveniles from the Saharan

Bank could be explained by higher temperatures in this area than in the Mediterranean (Quetglas & Morales-Nin, 2004).

The common cuttlefish is not very tolerant of low oxygen concentrations. Low oxygen concentrations can account for the absence or low abundance of *S. officinalis* (Guerra, 2006a). The existence of cuttlefish fisheries in the upwelling areas off the NW African coast and the Northern Benguela current suggests continuous eutrophic scenarios in shallow waters in the cores of the southern upwelling cells (Guerra & Sanchez, 1985). This is where low oxygen concentrations are common, and they appear to be the most important limiting factor for the development of cuttlefish populations.

Mediterranean Sea

In this warm, oligotrophic body of water, the hydrological circulation is dominated by the continuous transformation of the Atlantic Water (AW) into Mediterranean Water (MW), and the formation of dense water masses, which sink offshore in specific northern zones of the western and eastern basins (see Millot & Taupier-Letage, 2004; Millot, 2005 for reviews). In particular, the highly unstable southern portions of the two main water gyres circulating in the western and eastern basin, also named the Algerian and Libyo-Egyptian Currents, meander and generate anticyclonic eddies and water masses at very different depths, resulting in rather complex circulating systems. River flows and discharge and wind systems represent additional important driving forces in the Mediterranean water circulation. Bottom diversity and the existence of widely contrasting bathymetries along the whole Mediterranean Sea contribute to make this a very interesting area to study cephalopod distribution and abundance in relation to environmental conditions.

Along the Iberian Mediterranean coast three main cephalopod communities are defined (González & Sanchez, 2002): the shelf community (<150 m), the middle slope community (>480 m) and a group of cephalopods that are widely distributed on the lower continental shelf-upper slope (150–480 m). In the Balearic Sea, there are two main cephalopod assemblages that are associated with the continental shelf (50–100 m) and the upper slope (600–800 m) respectively, separated by a wide transitional zone

(100–600 m) (Quetglas et al., 2000). Depth and shelf shape are among the factors affecting the spatial distribution and abundance of *Eledone cirrhosa* in the Aegean Sea, Western Mediterranean (French and Spanish waters) and coastal waters off Sardinia (Lefkaditou et al., 2000).

Known teleconnection patterns such as the East Atlantic/Western Russian pattern, NAO, the Polar/Eurasian pattern, the East Pacific/North Pacific, the East Atlantic jet and the Mediterranean Oscillation all affect chlorophyll concentration in the Mediterranean, especially in coastal areas, areas of upwelling and regions with a gyre formation (Katara et al., 2008, this volume). In the Ligurian Sea, *E. cirrhosa* abundance, recorded during late spring-summer surveys, was positively related to the winter NAO index (Orsi Relini et al., 2006). In addition, river discharges and bathymetry play important roles in determining the distribution of cephalopods. In the Gulf of Lions and the Gulf of Roses-Cape Creus (France), *E. cirrhosa*, *L. vulgaris* and *S. officinalis* landings are positively correlated with run-off of the local Rhone and Muga rivers (Lloret et al., 2001).

In the Central Mediterranean between southern Sardinia and northern Tunisia off northwestern Sicily, the flow of the AW splits: one stream continues westwards and northwards, along the southwestern Tyrrhenian Sea, while the other flows southwards, through the Sicilian channel, towards the eastern Mediterranean basin. This central portion of the western Mediterranean is characterized by complex water circulation (e.g. Atzeni et al., 1997; Millot, 2005) with upwelling events and cyclonic meanders that are maintained both by the coastal topography and the intermediate flow of waters that goes from the eastern to the western basin, also named Mid-Mediterranean Jet (MMJ) (Rio et al., 2007). Jereb et al. (2005) investigated cephalopod abundance and distribution in Sardinian waters and showed a correlation between *I. coindetii* recruitment and environmental variation off the western Sardinian coast. A temporal shifting of the Algerian current, and consequently of the frontal zone off the western Sardinian coasts, during 1996 and 1998 was probably responsible for the unusually high pulse of recruitment observed for *I. coindetii* during 1997 (Cuccu et al., 2008). Anomalous SST values were observed corresponding to a shift in the Algerian Current, confirming the potential for using SST as an indirect

indicator of biological conditions for squids (see also Dawe et al., 2000, 2001).

A similar correlation was hypothesized for *I. coindetii* in the Strait of Sicily (Jereb et al., 2001). In this area, two cyclonic meanders create a Western Sector with colder waters (16.9–20°C), an Eastern Sector with warmer waters (20–23.2°C), and a permanent upwelling along the southern Sicilian coasts (e.g. Piccioni et al., 1998; Mazzola et al., 2000). Here, the shift of the frontal zone resulting from the two opposing water masses of the western and eastern side was probably responsible for an unusual pulse of recruitment, and consequently, for the unusually high concentration of juveniles (Jereb et al., 2001).

In the Eastern Mediterranean, the area that supports the most important cephalopod fisheries (*L. vulgaris*, *I. coindetii*, *S. officinalis*, *O. vulgaris*, and *Eledone* spp.) is the North Aegean Sea (Lefkaditou et al., 2007). Here, environmental conditions and oceanic processes affect species recruitment timing, seasonal abundance and migration. In general, the positive correlation between loliginid landings and SST concerns nutrient-rich areas (North Aegean), while in oligotrophic areas (Central/South Aegean), higher production is attributed to the occurrence of seasonal, randomly distributed marine productivity hotspots, areas of below-average SST and above average chlorophyll concentration (Georgakarakos et al., 2002).

In Greek waters, it has been shown that SST may be used to forecast loliginid landings, but is inadequate to predict landings of ommastrephids, which occur in deep pelagic zones (Georgakarakos et al., 2006). Nevertheless, Arvanitidis et al. (2002) highlighted the importance of SST and Chl-*a* concentration in determining biological indices of *I. coindetii* in the Eastern Mediterranean. Analysis of bottom trawl data for the ommastrephid squid *Todarodes sagittatus* from the Western Mediterranean showed significant correlations between hatching success and temperature at 50-m depth (Quetglas & Morales-Nin, 2004). Mediterranean squids have wider embryonic increments in their statoliths than Atlantic squids due to higher water temperatures in the Mediterranean (Villanueva et al., 2003). In the early life stages, there is superior growth performance for *I. coindetii* and *I. illecebrosus* specimens hatched in warm conditions relative to specimens hatched in colder conditions (Ragonese et al., 2002).

In the North Aegean, Cyclades Plateau and Ionian Sea fishing grounds, the spatial distribution of *L. vulgaris* and *I. coindetii* CPUE was found to be positively correlated with the distribution of marine productivity hotspots (Valavanis et al., 2004) as well as with the distribution of mesoscale thermal fronts (Valavanis et al., 2005). Suitable habitat areas for *I. coindetii* are characterized by SST of 13 to 29°C, surface chlorophyll-a concentrations of 0.30 to 15.60 mg/m^3 and SSS values of 36.12 to 38.51‰ (Valavanis et al., 2002).

Movements of *L. vulgaris* into inshore fishing grounds are mainly related to seasonal variability of temperature in the NE Aegean Sea, whereas in coastal areas occupied by water masses of lower salinity, variation in CPUE of this species is also related to rainfall variability (Lefkaditou et al., 1998a). Recruitment timing and duration as well as the resulting seasonal demographic structure and abundance of *E. moschata* are associated with temporary upwelling and shelf topography in the insular area of the Southern Aegean Sea, which affect the productivity levels of this area that is generally characterized by oligotrophic waters (Lefkaditou et al., 1998b).

The reproductive strategies of cephalopod species that are found throughout the Mediterranean are seen to vary depending on the location of each population, suggesting a strong influence of environmental factors on significant biological traits such as the size and number of eggs produced by females (Laptikhovsky et al., 2008). Specimens found in the Western Mediterranean tend to be more similar to those found in adjacent areas of the Atlantic, whereas those found in the Eastern Mediterranean display adaptations which seem to bring the characteristics of the reproductive strategies of different species in the area closer to each other.

Cephalopod–environment relationships in other areas

The SW Atlantic is a well-studied area due to the important fisheries for *Illex argentinus* and *Loligo gahi*. Many studies reveal links between the environment and the distribution and abundance of those cephalopods (e.g. Bakun & Csirke, 1998; Semmens et al., 2007).

Annual recruitment success in *I. argentinus* is related to SST in the region where the animals hatch, in particular to the proportion of the hatching grounds occupied by 'frontal' waters and favourable SST conditions (González et al., 1997; Waluda et al., 1999, 2001a). Waluda et al. (2001b) showed that the distribution of *I. argentinus* around the Falkland Islands was associated with areas of thermal gradients, commonly seen at the interface of Falkland Current and Patagonian shelf waters.

Sacau et al. (2005) described the spatio-temporal pattern of abundance of *I. argentinus*, demonstrating that higher catches and higher proportions of mature squid were related to warmer and deeper water. Waluda et al. (2008) studied the spatial dynamics of the *I. argentinus* fishery by tracking the powerful incandescent lights of the jigging vessels used to attract squid, noting that SST during June and July of 2003 and 2004 (the egg-hatching period) was 0.4 and 0.9°C warmer than average, respectively, which may have partially contributed to the reduced fishery yield during 2004 and 2005.

Hatfield (2000) showed that *L. gahi* hatched in the summer, i.e. at higher temperatures, were significantly larger than squid of the same age but hatched in the winter months. Agnew et al. (2000) showed a negative correlation between SST and the strength of the recruitment of *L. gahi*, with a delay of 6 months. Arkhipkin et al. (2004) studied the effects of the Falkland current inflows on the ontogenetic migrations of *L. gahi* and showed that stronger flows of the Falkland current onto the western part of the southern Falkland Shelf induce stronger outflows of warmer and less saline shelf waters, and correspondingly greater offshore movements of squid. Arkhipkin et al. (2006) identified the role of the Falkland current in the dispersal of *L. gahi* along the Patagonian shelf. They reported a good correspondence between the inshore movements of the current in May–July with the squid abundance in the following September–October. Inter-specific competition between *I. argentinus* and *L. gahi* is highly plausible as Arkhipkin & Middleton (2002) reported inverse patterns of abundance of these two species in Falkland waters.

In South African waters, the chokka squid *Loligo reynaudii* (formerly *Loligo vulgaris reynaudii*) has long been the focus of a directed fishery and associated studies (e.g. Augustyn, 1990, 1991; Sauer et al., 1991; Roberts & Sauer, 1994). Olyott et al. (2006) studied

spatio-temporal patterns in maturation of this species off the coast of South Africa, relating maturity cycles to environmental conditions, finding that squid matured smaller in winter/spring than in summer/autumn and that squid in the east Agulhas Bank matured at a smaller size than squid in the west. Mqoqi et al. (2007) studied the influence of abiotic factors (depth, region, temperature, salinity and oxygen) on the abundance of the cuttlefish *Sepia australis* along the coast of South Africa, suggesting that abundance increases in areas with high temperature anomalies and along increasing bathymetry gradients.

Collins & Rodhouse (2006) reviewed the Southern Ocean cephalopod fauna, reporting the main biological and oceanographic factors related to those species. Rodhouse et al. (1994a, b, 1996) described some environmental relationships with cephalopod distribution and abundance, particularly related to the ommastrephid squid *Martialia hyadesi*. The appearance of *M. hyadesi* in the Falkland Islands fishery has been related to SST anomalies (Gonzalez et al., 1997). Teleconnections probably exist between these anomalies, El Niño Southern Oscillation (ENSO) events in the Pacific and sub-decadal oceanographic instability in the Antarctic. However, it is not clear at what stage in the life cycle of *M. hyadesi* these oceanographic events exert their effect. These authors proposed two alternative, but not mutually exclusive, hypotheses. Warm events prior to the appearance of *M. hyadesi* may favour reproductive success of the parent generation, giving rise to a strong recruitment, or alternatively this cool water species may extend its range to the edge of the Patagonian Shelf early in the development of cold oceanographic events. In either case, oceanographic effects are probably mediated via effects on the squids' prey. Rodhouse et al. (1996) described the mesoscale oceanography of the Antarctic Polar Front and how it affects cephalopod distribution and abundance.

Conclusion and future concerns

Numerous studies reviewed here have underlined the high sensitivity of cephalopod species to local, regional and large-scale environmental conditions and changes. Clearly, spatiotemporal environmental variations strongly affect the biological processes and characteristics of cephalopods during their short life

cycle. Cephalopods seem to respond to environmental variation both 'actively' (migrating to areas with more favoured environmental conditions) and 'passively' (using optimum environmental conditions to reach certain life stages at different growth rates between different generations).

In many demersal and benthic species, distribution range is related to bathymetry and 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 squids, inshore–offshore migrations are seen within the range of occurrence. The pelagic species, such as ommastrephid squids, tend to be highly migratory, and are likely to be strongly affected by changes in current systems (O'Dor, 1992) and large-scale oceanographic phenomena (e.g. El Niño). Coastal species may be impacted 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, has been shown to be 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 can often be shown to be related to the seasonal cycle of environmental conditions, raising the issue that climatic change may result in a mismatch between the timing of critical life stages and optimum environmental conditions (Bakun & Csirke, 1998).

Besides the importance of environmental parameters in modulating the abundance of adult cephalopod resources, more attention should be given to the early stages of development, especially in those species with a planktonic stage. This part of most cephalopod life cycles is highly influenced by physical and chemical oceanographic factors, which when combined with the variation of prey abundance will lead to large variations in growth and mortality rates. There is evidently considerable plasticity in life-cycles, and consequently, changes in SST and productivity can affect the life-cycle in unexpected ways. For example, higher temperatures in early life will strongly affect growth rates. In some species, the animals may consequently reach a larger adult size and perhaps achieve greater reproductive success

due to a positive relationship between adult body size and fecundity and/or egg size. For example, fecundity in female *Loligo forbesi* increases with body size (Boyle et al., 1995). However, in other species, faster early growth may paradoxically lead to more rapid maturation at a smaller adult body size. In addition, the timing of migration may be altered.

It is not clear for most species whether there is any density dependence in recruitment or spawning success. There is generally high variability in annual abundance of many cephalopods, suggesting that environmental effects on abundance at the population level tend to be transient: there is little evidence that consistently high or low abundance can be sustained over a substantial number of years. Cephalopods are intrinsically unpredictable fishery resources and links between abundance and environmental conditions often become clear only after the fact, although there clearly is scope to use conditions experienced by hatchlings as a means for forecasting fishery success when that generation matures. Based on this general perspective, future research should include a thorough examination and explanation of the environmental 'teleconnection' processes in European Seas (e.g. from NAO and Gulf Stream to local environmental variation) as well as an in-depth overview of the individual and population level responses of cephalopods to a combination of changing environmental habitat descriptors. We can also learn much about cephalopod habitat use from the experience of fishermen and much more use could be made of such 'anecdotal' sources of information, if only to suggest hypotheses that can be tested by future scientific studies.

The ability of environmental fishery models to forecast recruitment suggest that in the future it may be possible to set the level of fishing effort in some cephalopod fisheries (mainly targeted squid species) on the basis of scientifically predicted levels of abundance in advance of recruitment of the individuals into the fishery (Boyle & Rodhouse, 2005). For example, Agnew et al. (2002) have developed an approach that may allow for an increased catch while at the same time reducing the possibility of overexploiting the fishery.

Some questions that should be addressed in future research include:

1. Which environmental factors have the most important effects on individual life history and

population parameters of different cephalopod species, what are the mechanisms underlying these effects and how do they link to patterns of distribution and abundance?

2. To what extent do we need to revise our understanding of cephalopod–environment relationships as new data (e.g., on oceanographic phenomena, especially sub-surface phenomena) and analytical techniques (e.g. accounting for spatial and temporal autocorrelation) become available?

3. Are these effects observed consistently through time, in different areas and when other aspects of environmental conditions change, and can they be used in stock assessment and/or fishery forecasting for cephalopods?

4. What are the specific teleconnection mechanisms, between large scale meteo-oceanic phenomena and local environmental variation, that are relevant to cephalopods?

5. Can cephalopod populations be used as indicators of climate change?

Topics of this nature may be useful objectives for new research initiatives to facilitate our understanding of what determines the distribution of cephalopod habitats in an ever changing marine environment, to identify certain species as important environmental change indicators and to improve current stock assessment methods. Research contributions of this type will help to underpin any new management effort under both the ecosystem-based and precautionary approaches.

References

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

Agnew, D. J., S. Hill & J. R. Beddington, 2000. Predicting the recruitment strength of an annual squid stock: *Loligo gahi* around the Falkland Islands. Canadian Journal of Fisheries and Aquatic Sciences 57: 2479–2487.

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

Aristegui, J., X. A. Alvarez-Salgado, E. D. Barton, F. G. Figueiras, S. Hernandez-Leon, C. Roy & A. M. P. Santos, 2006. Oceanography and fisheries of the Canary Current/Iberian region of the eastern North Atlantic. In Robinson, A. R. & K. H. Brink (eds), The sea. Harvard University Press, Cambridge, MA: 877–931.

Arkhipkin, A. I., P. Jereb & S. Ragonese, 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., V. V. Laptikhovsky, A. M. Sirota & R. Grzebielec, 2006. The role of the Falkland Current in the dispersal of the squid *Loligo gahi* along the Patagonian Shelf. Estuarine, Coastal and Shelf Science 67: 198–204.

Arkhipkin, A. I. & D. A. J. Middleton, 2002. Inverse patterns in abundance of *Illex argentinus* and *Loligo gahi* in Falkland waters: possible interspecific competition between squid? Fisheries Research 59: 181–196.

Arkhipkin, A. I., D. A. J. Middleton, A. M. Sirota & R. Grzebielec, 2004. The effect of Falkland Current inflows on offshore ontogenetic migrations of the squid *Loligo gahi* on the southern shelf of the Falkland Islands. Estuarine, Coastal and Shelf Science 60: 11–22.

Arvanitidis, C., D. Koutsoubas, J.-P. Robin, J. Pereira, A. Moreno, M. Cunha, V. D. Valavanis & A. Eleftheriou, 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.

Atzeni, A., A. Balzano & G. Lai, 1997. Sulle correnti del Golfo di Cagliari: dipendenza dalle correnti del Mediterraneo e simulazione numerica dei regimi stagionali. Quaderni di ricerca del Dipartimento di Ingegneria del Territorio. Sezione di Ingegneria Idraulica: 27–79.

Augustyn, C. J., 1990. Biological studies on the Chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. South African Journal of Marine Science 9: 11–26.

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

Augustyn, C. J., M. R. Lipinski, W. H. H. Sauer, M. J. Roberts & B. A. Mitchell-Innes, 1994. Chokka squid on the Agulhas Bank: life history and ecology. South African Journal of Marine Science 90: 143–153.

Bakun, A. & J. Csirke, 1998. Environmental processes and recruitment variability. In Rodhouse, P. G., E. G. Dawe & R. K. O'Dor (eds), Squid Recruitment Dynamics. The Genus *Illex* as a Model. The Commercial *Illex* Species. Influences on Variability, Vol. 376. FAO Fisheries Technology Paper: 273.

Balguerias, E., C. Hernandez-Gonzalez & C. Perales-Raya, 2002. On the identity of *Octopus vulgaris* Cuvier, 1797 stocks in the Saharan Bank (Northwest Africa) and their spatiotemporal variations in abundance in relation to some

environmental factors. Bulletin of Marine Science 71: 147–163.

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

Barton, E., J. Aristegui, P. Tett & E. Navarro-Perez, 2004. Variability in the Canary Islands area of filament-eddy exchanges. Progress in Oceanography 62: 71–94.

Bellido, J. M., 2002. Use of geographic information systems, spatial and environment-based models to study ecology and fishery of the veined squid (*Loligo forbesi* Steenstrup 1856) in Scottish waters. PhD Thesis. University of Aberdeen, United Kingdom: 183.

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

Bettencourt, V. & A. Guerra, 1999. Carbon- and oxygen-isotope composition of the cuttlebone of *Sepia officinalis*: a tool for predicting ecological information? Marine Biology 133: 651–657.

Boletzky, S. V., 1986. Reproductive strategies in cephalopods: variations and flexibility of life-history. Advances in Invertebrate Reproduction 4: 379–389.

Boyle, P. R., 1990. Cephalopod biology in the fisheries context. Fisheries Research 8: 303–321.

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

Boyle, P. R. & P. G. Rodhouse, 2005. Cephalopods. Ecology and Fisheries, Blackwell Science Ltd, Oxford.

Bravo de Laguna, J. & G. E. Balguerias, 1993. La pesqueria sahariana de cefalopodos: una breve revision. Boletin del Instituto Espanol de Oceanografia 9: 203–213.

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

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

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

Chen, C. S., G. J. Pierce, J. Wang, J. P. Robin, J. C. Poulard, J. Pereira, A. F. Zuur, P. R. Boyle, N. Bailey, D. J. Beare, P. Jereb, S. Ragonese, A. Mannini & L. Orsi-Relini, 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., X. H. Zhao & Y. Chen, 2007. Influence of El Nino/La Nina 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.

Clarke, M. R., N. MacLeod, H. P. Castello & M. C. Pinedo, 1980. Cephalopod remains from the stomach of a sperm whale stranded at Rio Grande do Sul in Brazil. Marine Biology 59: 235–239.

Collins, M. A. & P. G. K. Rodhouse, 2006. Southern ocean cephalopods. Advances in Marine Biology 50: 191–265.

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

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

Cuccu, D., P. Jereb, S. Ragonese, N. Giovannini, S. Colella & A. Cau, 2008. On the abundance and spatial distribution of *Illex coindetii* and *Eledone moschata* in the Sardinian Seas (central-western Mediterranean)—A preliminary and qualitative investigation with special attention to some environmental constraints. Bollettino Malacologico 54: 15–25.

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

Cushing, D. H., 1975. Marine Ecology and Fisheries. Cambridge University Press, Cambridge: 271.

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

Dawe, E. G., L. C. Hendrickson, E. B. Colbourne, M. A. Showell, D. D. Jones & D. A. Methven, 2001. Squids as potential indicators species of environmental or ecosystem change in the Northwest Atlantic Ocean. ICES CM 2001/K:07.

De Alteris, J., L. Skrobe & C. Lipsky, 1998. Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society Symposium Series 22: 224–237.

De Heij, A. & R. P. Baayen, 2005. Seasonal distribution of cephalopod species living in the central and southern North Sea. Basteria 69: 91–119.

Demarcq, H. & V. Faure, 2000. Coastal upwelling and associated retention indices derived from satellite SST. Application to *Octopus vulgaris* recruitment. Oceanologica Acta 23: 391–408.

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

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

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.

Erzini, K., 2005. Trends in NE Atlantic landings (southern Portugal): identifying the relative importance of fisheries and environmental variables. Fisheries Oceanography 14: 195–209.

Faraj, A. & N. Bez, 2007. Spatial considerations for the Dakhla stock of *Octopus vulgaris*: indicators, patterns, and

fisheries interactions. ICES Journal of Marine Science 64: 1820–1828.

Fogarty, M. J., 1989. Forecasting yield and abundance of exploited invertebrates. In Caddy, J. F. (ed.), Marine Invertebrate Fisheries: Their Assessment and Management. Wiley: 701–724.

Forsythe, J. W., 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In Okutani, T., R. K. O'Dor & T. Kubodera (eds), Recent Advances in Cephalopod Fisheries Biology. Tokai University Press, Tokyo: 133–143.

Georgakarakos, S., J. Haralabus, V. D. Valavanis, C. Arvanitidis & D. Koutsoubas, 2002. Prediction of fishery exploitation stocks of Loliginid and Ommastrephid squids in Greek waters (Eastern Mediterranean) using uni- and multivariate time series analysis techniques. Bulletin of Marine Science 71: 269–288.

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

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

González, A. F., J. Otero, A. Guerra, R. Prego, F. J. Rocha & A. W. Dale, 2005. Temporal variation of cephalopod paralarvae in a wind-driven upwelling area (Ria of Vigo, NW Spain). Journal of Plankton Research 27: 271–277.

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

González, M. & P. Sanchez, 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. Scientia Marina 66: 199–208.

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

Guerra, A., 1992. Mollusca, cephalopoda. In: Ramos, M. A., J. Alba, X. Bellés, J. Gosálbez, A. Guerra, E. Macpherson, F. Martín, J. Serrano & J. Templado (eds), Fauna Ibérica, Vol. 1. Museo Nacional de Ciencias Naturales, CSIC, Madrid: 327 pp.

Guerra, A., 2004. Relaciones entre la oceanografia y los recursos marinos renovables. Revista de la Real Academia de Ciencias Exactas. Fisicas y Naturales 98: 77–88.

Guerra, A., 2006a. Ecology of Sepia officinalis. Vie et Milieu. Life and Environment 56: 97–107.

Guerra, A., 2006b. Estrategia evolutiva de los cefalopodos. Investigacion y Ciencia 355: 50–59.

Guerra, A., A. F. González & F. Rocha, 2002. Appearance of the common paper nautilus Argonauta argo related to the increase of the sea surface temperature in the north-eastern Atlantic. Journal of Marine Biological Association of U.K. 82: 855–858.

Guerra, A. & F. Rocha, 1994. The life history of Loligo vulgaris and Loligo forbesi (Cephalopoda: Loliginidae) in Galician waters (NW Spain). Fisheries Research 21: 43–69.

Guerra, A. & P. Sanchez, 1985. Comparacion de las pesquerias de cefalopodos de dos areas de afloramiento de la costa occidental africana. Simposio Internacional sobre Afloramientos. Instituto de Investigaciones Pesqueras, Barcelona II: 749–760.

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

Hatfield, E. M. C., 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, Loligo gahi (Cephalopoda: Loliginidae). Fisheries Research 47: 27–40.

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

Hurrell, J. W., 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676–679.

Jackson, G. D., 2004. Cephalopod growth: historical context and future directions. Marine and Freshwater Research 55: 327–330.

Jereb, P., D. Cuccu, D. Giordano, P. Maiorano & S. Ragonese, 2005. Using historical series of trawl surveys data to investigate cephalopods: a new method of exploratory analysis. Biologia Marina Mediterranea 12: 526–530.

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

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

Jones, P. D., T. Jonsson & D. Wheeler, 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and Southwest Iceland. International Journal of Climatolology 17: 1433–1450.

Katara, I., J. Illian, G. J. Pierce, B. Scott & J. Wang, 2008. Atmospheric forcing on chlorophyll concentration in the Mediterranean. Hydrobiologia (this volume).

Lafuente, J. G. & J. Ruiz, 2007. The Gulf of Cadiz pelagic ecosystem: a review. Progress in Oceanography 74: 228–251.

Laptikhovsky, V., J. Pereira, A. Salman, A. Arkhipov & A. Costa, 2008. A habitat-dependence in cephalopod and pelagophil fish reproductive strategies in the Mediterranean Sea. Bollettino Malacologico (in press).

Lefkaditou, E., P. Sanchez, A. Tsangridis & A. Adamidou, 1998a. 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., A. Siapatis & C. Papaconstantinou, 1998b. Seasonal and spatial changes in the abundance and

distribution of *Eledone moschata* (Cephalopoda: Octopoda), in the South Aegean Sea (Eastern Mediterranean). ICES CM 1998/M:44.

Lefkaditou, E., A. Souplet, N. Peristeraki, M. Gonzalez, S. Kavadas, P. Vidoris, D. Cuccu & C. Papaconstantinou, 2000. Preliminary investigation of factors affecting the spatial distribution and abundance of *Eledone cirrhosa* (Cephalopoda: Octopoda) in the Mediterranean Sea. In Bertrand, J. A. & G. Relini (eds), Demersal Resources in the Mediterranean. Actes de Colloques 26, Ifremer, Plouzane: 208–218.

Lefkaditou E., G. Verriopoulos & V. Valavanis, 2007. Research on cephalopod resources in Hellas. In Papaconstantinou, C., A. Zenetos, V. Vassilopoulou & G. Tserpes (eds), State of Hellenic Fisheries. Hellenic Centre for Marine Research, Athens: 440–451.

Lloret, J., J. Lleonart, I. Sole & J. M. Fromentin, 2001. Fluctuations of landings and environmental conditions in the North-Western Mediterranean Sea. Fisheries Oceanography 10: 33–50.

Lourenço, S. & J. Pereira, 2006. Estimating standardised landings per unit effort for an octopus mixed components fishery. Fisheries Research 78: 89–95.

Mangold, K., 1983. *Eledone moschata*. In Boyle, P. R. (ed.), Cephalopod Life Cycles. Species Accounts. Academic Press, New York: 387–400.

Mazzola, S., A. Garcia & J. G. Lafuente, 2000. Distribution, Biology and Biomass Estimates of the Sicilian Channel Anchovy. Final Report. Commission of the European Communities. Directorate General for Fisheries (DG-XIV), Mimeo:152.

Melzner, F., C. Bock & H.-O. Portner, 2006. Critical temperatures in the cephalopod *Sepia officinalis* investigated using in vivo 31P NMR spectroscopy. Journal of Experimental Biology 209: 891–906.

Millot, C., 2005. Circulation in the Mediterranean Sea: evidences, databases and unanswered questions. Scientia marina 69: 5–21.

Millot, C. & I. Taupier-Letage, 2004. Circulation in the Mediterranean Sea. The Handbook of Environmental Chemistry. The Natural Environment and the Biological Cycles 1: 1–30.

Moreno, A., M. Azevedo, J. Pereira & G. J. Pierce, 2007. Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. Marine Biology Research 3: 49–59.

Moreno, A. & J. M. F. Pereira, 1998. Cephalopod paralarval distribution in Iberian Atlantic waters. ICES CM 1998/M:42.

Moreno, A. & C. Sousa-Reis, 1995. Seasonal distribution of loliginid early young stages in the Portuguese continental shelf. ICES CM 1995/K:32.

Mqoqi, M., M. R. Lipinski & A. G. V. Salvanes, 2007. The ecology of *Sepia australis* (Cephalopoda: Sepiidae) along the south coast of South Africa. ICES Journal of Marine Science 64: 945–955.

O'Dor, R. K., 1992. Big squid in big currents. South African Journal of Marine Science 12: 225–235.

Olyott, L. J. H., W. H. H. Sauer & A. J. Booth, 2006. Spatiotemporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa. ICES Journal of Marine Science 63: 1649–1664.

Orsi Relini, L., A. Mannini, F. Fiorentino, G. Palandri & G. Relini, 2006. Biology and fishery of *E. cirrhosa* in the Ligurian Sea. Fisheries Research 78: 72–88.

Otero, J., 2006. Ecologia del pulpo comun (*Octopus vulgaris* Cuvier, 1797) en un area de afloramiento costero (Galicia, NE Atlántico). PhD Thesis, University of Vigo, Spain.

Otero, J., X. A. Alvarez-Salgado, A. F. Gonzalez, A. Miranda, S. B. Groom, J. M. Cabanas, G. Casas, B. Wheatley & A. Guerra, 2008. Bottom-up and top-down controls of common octopus (*Octopus vulgaris*) in a wind-driven upwelling ecosystem (Galicia, NE Atlantic). Marine Ecology Progress Series. doi:10.3354/meps07437.

Otero, J., A. F. Gonzalez, M. P. Sieiro & A. Guerra, 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. Fisheries Research 85: 122–129.

Otero, J., F. Rocha, A. F. Gonzalez, J. Gracia & A. Guerra, 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.

Pascual, S., A. F. Gonzalez & A. Guerra, 2007. Parasite recruitment and oceanographic regime: evidence suggesting a relationship on a global scale. Biological Reviews 82: 257–263.

Pecl, G. T., M. A. Steer & K. E. Hodgson, 2004. The role of hatchling size in generating the intrinsic size-at-age variability of cephalopods: extending the Forsythe Hypothesis. Marine and Freshwater Research 55: 387–394.

Piatkowski, U., G. J. Pierce & M. Morais da Cunha, 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fisheries Research 52: 5–10.

Piccioni, A., M. Gabriele, E. Salusti & E. Zambianchi, 1988. Wind-induced upwellings off the southern coast of Sicily. Oceanologica Acta 11: 309–314.

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

Pierce, G. J., P. R. Boyle, L. C. Hastie & M. B. Santos, 1994. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. Fisheries Research 21: 149–164.

Pierce, G. J. & A. Guerra, 1994. Stock assessment methods used for cephalopod fisheries. Fisheries Research 21: 255–286.

Pierce, G. J., M. B. Santos, C. D. MacLeod, J. Wang, V. D. Valavanis & A. F. Zuur, 2006. Modelling environmental influences on squid life history, distribution, and abundance. Proceedings of the GLOBEC-CLIOTOP Working Group 3 and the Pelagic Fisheries Research Program (PFRP) Workshop. Nov. 14–17, 2006, University of Hawaii, Honolulu.

Pierce, G. J., G. Stowasser, C. D. MacLeod, T. Valinassab, M. B. Santos & J. Wang 2005a. Mapping and modelling spawning habitat for the squid *Loligo forbesi*. In The Third International Symposium on GIS/Spatial Analyses in Fishery and Aquatic Sciences, 22–26, 2005, Shanghai, China.

Pierce, G. J., J. Wang, J. M. Bellido, C. M. Waluda, J. P. Robin, V. Denis, D. Koutsoubas, V. D. Valavanis & P. R. Boyle, 1998. Relationships between cephalopod abundance and environmental conditions in the Northeast Atlantic and Mediterranean as revealed by GIS. ICES CM 1998/M:20.

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

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

Portner, H. O., 1994. Coordination of metabolism, acid-base regulation and haemocyanin function in cephalopods. In Portner, H. O., R. K. O'Dor & D. L. Macmillan (eds), Physiology of Cephalopod Molluscs: Lifestyle and Performance Adaptations. Gordon & Breach, Basel: 131–148.

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

Quetglas, A. & B. Morales-Nin, 2004. Age and growth of the Ommastrephid squid Todarodes sagittatus from the western Mediterranean Sea. Journal of the Marine Biological Association of the UK 84: 421–426.

Ragonese, S., P. Jereb & E. Dawe, 2002. A comparison of growth performance across the squid genus Illex (Cephalopoda, Ommastrephidae) based on modelling weight-at-length and age data. Journal of Shellfish Research 21: 851–860.

Rasero, M., 1994. Relationship between cephalopod abundance and upwelling: the case of Todaropsis eblanae (Cephalopoda: Ommastrephidae) in Galician waters (NW Spain). ICES CM 1994/K:40.

Redfern, J. V., M. C. Ferguson, E. A. Becker, K. D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M. F. Baumgartner, K. A. Forney, L. T. Ballance, P. Fauchald, P. Halpin, T. Hamazaki, A. J. Pershing, S. S. Qian, A. Read, S. B. Reilly, L. F. Torres & F. Werner, 2006. Techniques for cetacean habitat modelling. Marine Ecology Progress Series 310: 271–295.

Relvas, P., E. D. Barton, J. Dubert, P. B. Oliveira, A. Peliz, J. C. B. da Silva & A. M. P. Santos, 2007. Physical oceanography of the western Iberia ecosystem: Latest views and challenges. Progress in Oceanography 74: 149–173.

Rio, M. H., P. M. Poulain, A. Pascual, E. Mauri, G. Larnicol & R. Santoleri, 2007. A mean dynamic topography of the Mediterranean Sea computed from altimetric data, in-situ measurements and a general circulation model. Journal of Marine Systems 65: 484–508.

Roberts, M. J. & W. H. H. Sauer, 1994. Environment: the key to understanding the South African chokka squid (Loligo vulgaris reynaudii) life-cycle and fishery? Antarctic Science 6: 249–258.

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

Robinson, R. A., J. A. Learmonth, A. M. Hutson, C. D. Macleod, T. H. Sparks, D. I. Leech, G. J. Pierce, M. M. Rehfisch & H. Q. P. Crick, 2005. Climate Change and Migratory Species: A Report for DEFRA on Research Contract CR0302. BTO Research Report 414, British Trust for Ornithology.

Rochet, M.-J., 2000. A comparative approach to life-history strategies and tactics among four orders of teleost fish. ICES Journal of Marine Science 57: 228–239.

Rocha, F., J. Gracia, A. F. Gonzalez, C. M. Jardon & A. Guerra, 2004. Reliability of a model based on a short fishery statistics survey: application to the Northeast Atlantic monkfish fishery. ICES Journal of Marine Science 61: 25–34.

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

Rocha, F., A. Guerra, R. Prego & U. Piatkowski, 1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). Journal of Plankton Research 21: 21–33.

Rocha, F., J. Otero, R. Outeiral, A. F. Gonzalez, J. Gracia & A. Guerra, 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., J. Barton, E. M. C. Hatfield & C. Symon, 1995. Illex argentinus: life cycle, population structure and fishery. ICES Marine Science Symposium 199: 425–432.

Rodhouse, P. G., U. Piatkowski & C. C. Lu, 1994a. Southern ocean cephalopods: life cycles and populations. Antarctic Science 6: 135–290.

Rodhouse, P. G., P. A. Prince, P. N. Trathan, E. M. C. Hatfield, J. L. Watkins, D. G. Bone, E. J. Murphy & M. G. White, 1996. Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions. Marine Ecology Progress Series 136: 37–50.

Rodhouse, P. G., K. Robinson, S. B. Gajdatsy, H. I. Daly & M. J. S. Ashmore, 1994b. Growth, Age structure and Environmental history in the cephalopod Martialia hyadesi (Teuthoidea, Ommastrephidae) at the Antarctic Polar Frontal zone and on the Patagonian Shelf Edge. Antarctic Science 6: 259–267.

Rodhouse, P. G., C. M. Waluda, E. Morales-Bojorquez & A. Hernandez-Herrera, 2006. Fishery biology of the Humboldt squid, Dosidicus gigas, in the Eastern Pacific Ocean. Fisheries Research 79: 13–15.

Rowell, T. W., J. H. Young, J. C. Poulard & J. P. Robin, 1985. Changes in the distribution and biological characteristics of Illex illecebrosus on the Scotian shelf, 1980–83. NAFO Scientific Council Studies 9: 11–26.

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

Sacau, M., G. J. Pierce, J. Wang, A. I. Arkhipkin, J. Portela, P. Brickle, M. B. Santos & X. Cardoso, 2005. The spatiotemporal pattern of Argentine shortfin squid Illex argentinus abundance in the southwest Atlantic. Aquatic Living Resource 18: 361–372.

Sakaguchi, H., T. Hamano & A. Nakazono, 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.

Santurtun, M., Y. Sagarminaga, P. Lucio, I. Galparsoro, J. Quincoces & A. Iriondo, 2004. Interannual trends in catches of squid (*Loligo* spp.) in the Bay of Biscay (ICES Div. VIIIa, b, d) during 2000 in relation to oceanographic features. ICES CM 2004/CC.

Sauer, W. H. H., W. S. Goschen & A. S. Koorts, 1991. A preliminary investigation of the effect of sea temperature fluctuations and wind direction on catches of Chokka squid *Loligo vulgaris reynaudii* off the Eastern Cape, South Africa. South African Journal of Marine Science 11: 467–473.

Semmens, J. M., G. T. Pecl, B. M. Gillanders, C. M. Waluda, E. K. Shea, D. Jouffre, T. Ichii, K. Zumholz, O. N. Katugin, S. C. Leporati & P. W. Shaw, 2007. Approaches to resolving cephalopod movement and migration patterns. Reviews in Fish Biology and Fisheries 17: 401–423.

Shaw, P. W., G. J. Pierce & P. R. Boyle, 1999. Subtle population structuring within a highly vagile marine invertebrate, the Veined Squid *Loligo forbesi*, demonstrated with microsatellite DNA markers. Molecular Ecology 8: 407–417.

Silva, L., F. Ramos & I. Sobrino, 2004. Reproductive biology of *Eledone moschata* (Cephalopoda: Octopodidae) in the Gulf of Cádiz (south-western Spain, ICES Division IXa). Journal of the Marine Biological Association of the United Kingdom 84: 1221–1226.

Simon, F., F. Rocha & A. Guerra, 1996. 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., M. J. Genner, A. J. Southward & S. J. Hawkins, 2001. Timing of squid migration reflects North Atlantic climate variability. Proceedings of the Royal Society of London 268(1485): 2607–2611.

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

Sobrino, I., L. Silva, J. M. Bellido & F. Ramos, 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cadiz. Bulletin of Marine Science 71: 851–866.

Solow, A. R., 2001. Observation error and the detection of delayed density dependence. Ecology 82: 3263–3264.

Valavanis, V. D., S. Georgakarakos, A. Kapantagakis, A. Palialexis & I. Katara, 2004. A GIS environmental modelling approach to essential fish habitat designation. Ecological Modelling 178: 417–427.

Valavanis, V. D., S. Georgakarakos, D. Koutsoubas, C. Arvanitidis & J. Haralabous, 2002. Development of a marine information system for Cephalopod fisheries in the Greek Seas (Eastern Mediterranean). Bulletin of Marine Science 71: 867–882.

Valavanis, V. D., I. Katara & A. Palialexis, 2005. Marine GIS: identification of mesoscale oceanic thermal fronts. International Journal of Geographical Information Science 19: 1131–1147.

Valavanis, V. D., G. J. Pierce, A. F. Zuur, A. Palialexis, A. Saveliev, I. Katara & J. Wang, 2008. Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. Hydrobiologia (this volume).

Van Aken, H. M. & G. Becker, 1996. Hydrography and through-flow in the north-eastern North Atlantic Ocean: the NANSEN project. Progress in Oceanography 38: 297–346.

Vecchione, M., 1999. Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987. Fishery Bulletin 97: 1025–1030.

Villa, H., J. Quintela, M. L. Coelho, J. D. Icely & J. P. Andrade, 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 plancktonic *Octopus vulgaris* from hatching to settlement. Canadian Journal of Fisheries and Aquatic Sciences 52: 2639–2650.

Villanueva, R., 2000. Effect of temperature on statolith growth of the European squid *Loligo vulgaris* during early life. Marine Biology 136: 449–460.

Villanueva, R., A. Arkhipkin, P. Jereb, E. Lefkaditou, M. R. Lipinski, C. Perales-Raya, J. Riba & F. Rocha, 2003. Embryonic life of the Loliginid squid *Loligo vulgaris*: comparison between statoliths of Atlantic and Mediterranean populations. Marine Ecology Progress Series 253: 197–208.

Waluda, C. M., H. J. Griffiths & P. G. Rodhouse, 2008. Remotely sensed spatial dynamics of the *Illex argentinus* fishery Southwest Atlantic. Fisheries Research 91: 196–202.

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

Waluda, C. M. & P. G. Rodhouse, 2006. Remotely sensed mesoscale oceanography of the Central Eastern Pacific and recruitment variability in *Dosidicus gigas*. Marine Ecology Progress Series 310: 25–32.

Waluda, C. M, P. G. Rodhouse, G. P. Podestá, P. N. Trathan & G. J. Pierce. 2001a. Oceanography of *Illex argentinus* (Cephalopoda: Ommastrephidae) hatching and influences on recruitment variability. Marine Biology 139: 671–679.

Waluda, C. M., P. G. Rodhouse, P. N. Trathan & G. J. Pierce, 2001b. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. Fisheries Oceanography 10: 207–216.

Waluda, C. M., P. N. Trathan, C. D. Elvidge, V. R. Hobson & P. G. Rodhouse, 2002. Throwing light on straddling stocks of *Illex argentinus*: assessing fishing intensity with satellite imagery. Canadian Journal of Fisheries and Aquatic Science 59: 592–596.

Waluda, C. M., P. N. Trathan & P. G. Rodhouse, 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., C. Yamashiro & P. G. Rodhouse, 2006. Influence of the ENSO cycle on the light-fishery for

Dosidicus gigas in the Peru Current: an analysis of remotely sensed data. Fisheries Research 79: 56–63.

Wang, J., G. J. Pierce, P. R. Boyle, V. Denis, J. P. Robin & J. M. Bellido, 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.

Wang, J., G. J. Pierce, M. B. Santos & P. R. Boyle, 2004. Integration of GIS, remote sensing and statistical technologies for analysing and modelling cephalopod resources dynamics in the Northeast Atlantic waters. Littoral 2004, Seventh International Conference Delivering Sustainable Coasts: Connecting Science and Policy. Sep. 20–22, 2004. Aberdeen, Scotland, UK.

Young, I. A., G. J. Pierce, J. Murphy, H. I. Daly & N. Bailey, 2006a. Application of the Gomez- Muñoz model to estimate catch and effort in squid fisheries in Scotland. Fisheries Research 78: 26–38.

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

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