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Resolving climate impacts on fish stocks

Editors

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Contents

Foreword

Climate change will affect fishery resources and challenge managers to develop sustainable exploitation strategies. Knowledge of the effects of climate on fishery resources is still fragmentary. This report presents an overview of the literature on the impact of climate change and variability on fish and shellfish populations in the Northeast Atlantic and the Mediterranean and Black seas, with a focus on the processes that govern the response of fish and shellfish to climate change. The work was part of a research project carried out by nine European research institutes and funded by the Sixth Framework Programme (FP6) of the European Union (RECLAIM, Contract 044133) and the national programmes. Results have been used in various ICES working groups and study groups and are now collated in this *ICES Cooperative Research Report*, which is structured in five parts.

Part 1 comprises five sections on general issues:

i) introduction to the report, including a conceptual framework for the study of climate effects on fish (Section 1);
ii) classification system (ecotypology) and species list of Northeast Atlantic fish species (Section 2);
iii) ecophysiology of fish (Section 3);
iv) discussion of the uncertainties in biophysical modelling (Section 4);
v) review of approaches to disentangle the effect of climate change from the other anthropogenic effects (such as fishing and eutrophication (Section 5).

Part 2 comprises five sections:

i) observed variation in ocean climate and biota: ocean climate and the IPCC forecast on climate change (Section 6);
ii) phytoplankton and zooplankton (Section 7);
iii) ecosystem functioning in the Northeast Atlantic (Section 8);
iv) ecosystem functioning in the Mediterranean and Black seas (Section 9);
v) review of changes in the distribution of fish (Section 10).

Part 3 comprises sections on eleven fish and two shellfish species that represent different commercially important resources, ecosystem components (pelagics, demersals), and different trophic roles ("wasp-waist", apex predators) within Northeast Atlantic ecosystems (Sections 11–23). The aim of the individual sections is to evaluate the effect of climate on individual species that integrate the effects on different life-history stages.

Part 4 summarizes the key findings and formulates hypotheses for future research (Section 24).

Part 5 comprises four annexes comprising species lists and ecotypological data for fish species in the North Sea, the Baltic, and the Irish Sea, and European seas (eastern North Atlantic).

1 General introduction and conceptual framework

Adriaan D. Rijnsdorp

1.1 Introduction

Evidence is accumulating that the increase in CO_2 is affecting the global climate, with far-reaching implications for biological processes and ecosystem services (IPCC, 2001). Marine capture fisheries yield ca. 85 million tonnes year^{-1} and provide an economic basis for many communities, with a total value of US$50 billion. The sustainability of the fisheries is being jeopardized by overfishing (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Jørgensen *et al.*, 2007), but climate change may also affect the productivity of fishery resources (Brander, 2005; Harley *et al.*, 2006; Lehodey *et al.*, 2006).

The general concern about global warming and its effects has triggered a rapidly increasing body of scientific literature, in which ecological time-series are correlated with environmental indicators (Drinkwater, 2005; Weijerman *et al.*, 2005; Brunel and Boucher, 2007). Recent studies suggest that there is evidence for a northward shift in the distributional range of fish species (Quéro *et al.*, 1998; Hiscock *et al.*, 2001; Beare *et al.*, 2004; Perry *et al.*, 2005) and changes in the productivity of commercially exploited stocks (O'Brien *et al.*, 2000; Brander, 2005), but the mechanisms underlying these changes remain uncertain. Hence, it is largely unknown whether the observed distributional shifts are caused by a relocation of the spawning and feeding grounds, a change in the local survival of fish, or immigration into new habitats.

The study of the effect of climate change on fish populations is complicated, because climate change will affect a multitude of environmental factors that may impact various biological processes at different levels of organization. Even if the effect of an environmental factor, for instance on the physiology of an organism, is known, it will be difficult to evaluate the contribution at the population or ecosystem level (MacKenzie and Köster, 2004). Likewise, in the case of a northward shift in distribution of a species that matches an increase in temperature, it is difficult to establish a causal relationship because the change may be caused equally by fishing activities (Daan *et al.*, 2005; Daan, 2006).

There are several approaches to the study of the effect of climate change on fish populations and the development of a basis for scenario studies. Statistical analysis of available time-series can reveal changes in distribution and abundance of fish species that correlate with environmental variables (Murawski, 1993; Beaugrand, 2003; Köster *et al.*, 2005; Weijerman *et al.*, 2005). Process-oriented field studies can address specific working hypotheses using dedicated field-sampling programmes. Experimental analysis can reveal the response of organisms to environmental factors, which can then be used to interpret the response in the ecosystem (Pörtner and Knust, 2007). Finally, modelling studies can be used to explore the biological or ecological response to the climate-induced changes in environmental factors (Pörtner *et al.*, 2001; Drinkwater, 2005; Gallego *et al.*, 2007). A special branch of the latter is the temperature–envelope approach, in which the effect of climate change on the distribution of suitable habitat is studied (Drinkwater, 2005; Cheung *et al.*, 2009).

Global concern may lead to a bias in reports that demonstrate significant correlations between ecological processes and climate indicators. Therefore, to assess the potential impact of climate change on the productivity and distribution of fishery resources, a bottom–up approach, based on first principles, should be adopted. In this study, we develop a conceptual framework to generate (quantitative) hypotheses about the responses of fish and shellfish populations to climate change/variability (Figure 1.1). Abiotic factors that are expected to be affected most by climate change and available biophysical models are reviewed. The climate effects are then assessed on the level of biotic factors (lower trophic levels), the physiology of the species, the level of population dynamics, and the level of ecosystem dynamics.

It is noted that fish and shellfish have complicated life cycles. Successive life-history stages (eggs, larvae, juveniles, and adults) increase in individual size by a factor of up to 10^5, have specific habitat requirements, live in separate habitats, and occupy different trophic levels. This implies that climate change may affect fish populations differently at the various life-history stages. For a full understanding of the possible effects, it is of paramount importance to follow an integrated approach, comprising all life-history stages and the connectivity between successive habitats. This framework can be used to formulate research questions and working hypotheses on the effects of climate change on population abundance and distribution.

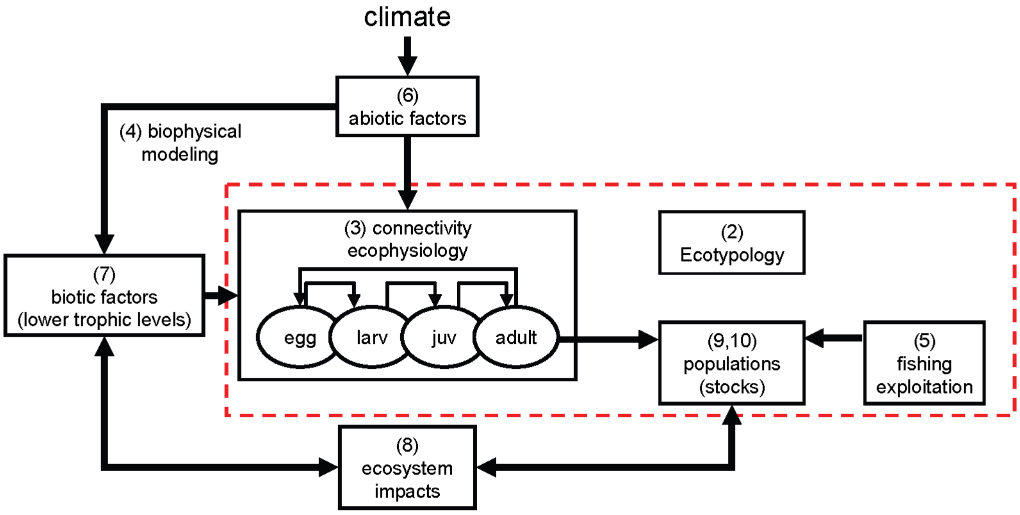


Figure 1.1. Conceptual framework for the study of climate effects on fish and shellfish populations. The numbers refer to individual sections. The box outlined in red dashes includes elements reviewed in the sections on individual species.

1.2 Ecotypology

Climate models indicate that the impact of climate change will differ between geographic areas. The impact will also differ between fish species. Species inhabiting areas most affected by climate change are likely to be more affected. Further, species with narrow habitat requirements or low dispersal will be more sensitive to climate change, whereas species with wide tolerance ranges or high dispersal capabilities will be less sensitive. Reproductive rate, growth rate, and longevity will affect the speed with which a species may respond to climate change. Based on these criteria, ecotypes can be defined as groups of species that share relevant ecological characteristics, such as biogeographic affinities, feeding guild, reproductive mode, and habitat preferences. These ecotypes may then be used as a basis to extrapolate the findings from case studies of particular species of fish to other fish species of the same ecotype. It is recognized that the ecotypology concept is flexible and needs to be defined in each study, based on the specific research question. The annexes in Part 5 present this ecotype concept and include lists of all fish species recorded in the North Sea, the Baltic, and the Irish Sea, as well as a list for the Northeast Atlantic as a whole, with information on their biogeographic affinity, reproductive mode, habitat, feeding guild, trophic level, and maximum body size that can be used to classify ecotypes.

1.3 Ecophysiology

Key factors affecting the physiology of marine organisms are temperature, salinity, oxygen, and pH. Organisms can only survive within a certain range of environmental conditions (tolerance range). Temperature determines the rate of physiological processes. Salinity affects the energy cost of osmoregulation, may influence the buoyancy of pelagic stages, and plays a role in the motility of spermatozoa of organisms with external fertilization. Acidification affects the building of external skeletons by organisms such as corals and some plankton (Orr *et al.*, 2005), but is probably less important in fish.

The ecophysiological framework of Fry (1971) offers a powerful approach to the classification of abiotic factors and their effect on the physiology of an organism. Tolerance ranges will differ among species because of local adaptation, but within species, tolerance ranges may also differ between life-history stages. Fish may increase their tolerance range by acclimation to specific environmental conditions (Pörtner *et al.*, 2005). As an example, bigeye tuna (*Thunnus obesus*) may regulate body temperature in order to allow hunting in cool waters below the thermocline (Holland *et al.*, 1992). Another route to increased plasticity is through behaviour. Species may optimize their ambient temperature environment by short-term migrations between warm- and cold-water bodies.

There is some evidence that early life-history stages, such as eggs and larvae, have narrower tolerance ranges than juveniles or adults (Irvin, 1974), and that the optimum temperature decreases with body size (Imsland *et al.*, 1996; Lafrance *et al.*, 2005). In Section 3, the ecophysiological concepts are presented, and the literature on fish is reviewed, with particular focus on the effect of increasing temperature.

1.4 Modelling tools

If the habitat requirements of a fish species are known and information is available on the changes in habitat expected as a result of climate change, habitat models may provide a first approach to the exploration of the possible consequences of climate change on the distribution of fish (Drinkwater, 2005; Cheung *et al.*, 2009).

Biophysical models are a powerful tool in the study of the effects of physical processes and climate change on ecological processes. In Section 4, the biophysical models reviewed have been developed for areas in the North Atlantic using different approaches and applying different levels of complexity. For the purpose of our study, spatially resolved models of the hydrodynamics of the Northeast Atlantic are needed that can capture the key processes affecting ecological processes (nutrients–phytoplankton–zooplankton–detritus, or NPZD).

Because fish populations are affected by a number of environmental drivers, it can be difficult to interpret observed changes in population in terms of response to climate change or variability. Section 5 presents approaches to disentangle the response to climate from responses to other anthropogenic activities.

1.5 Climate variability and climate change

Historically, climate has varied on decadal and multidecadal time-scales. On a geological time-scale, large changes in climate have occurred, for example, between the glacial and interglacial eras. Decadal-scale oscillations in the pressure fields over the North Atlantic (North Atlantic Oscillation (NAO): Hurrell, 1995), the South Pacific (*El Niño* Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO): Bond and Harrison, 2000) have major impacts on fish populations and ecosystem functioning (Francis *et al.*, 1998). Recently, multidecadal variations (e.g. Atlantic Multidecadal Oscillation (AMO)) have been reported in ecosystem properties (Chavez *et al.*, 2003; Johannessen *et al.*, 2004; Sutton and Hodson, 2005).

Global warming will affect a multitude of atmospheric and oceanographic processes (IPCC, 2001, 2007). The most important changes in ocean climate that may affect fish populations are increasing temperature, melting of sea ice, changes in ocean circulation, increase in storm surges, changes in precipitation and evaporation, changes in river run-off, and acidification. Climate-induced changes in cloud cover may influence the UV-B radiation that can affect organisms living in intertidal habitats or in the upper layers of the ocean.

Models play an indispensable role in climate research, and various scenarios of climate change have been developed (IPCC, 2001, 2007). Climate models indicate that changes will differ on a regional scale and will be greatest at high latitudes. In northern European seas, daily ocean monitoring since the 1860s demonstrates that summer temperatures since 1985 increased at nearly triple the global warming rate (Enghoff *et al.*, 2007). A review of the climate variability of the various ecosystems in the North Atlantic and the Mediterranean and Black seas is given in Section 6.

1.6 Lower trophic levels

Primary and secondary production is highly variable in space and time, although typical seasonal patterns occur that are related to the balance between daylength, radiation, availability of nutrients, and temperature. Climate change will affect primary production through the effect on the availability of nutrients caused, for instance, by upwelling or stratification depth. Phytoplankton species composition and, hence, trophic processes are affected by the ratio in which different nutrients are available (Philippart *et al.*, 2000) and by temperature regime (Hare *et al.*, 2007). Temperature will positively influence growth rate. It has been demonstrated that sea-surface warming in the Northeast Atlantic is accompanied by increasing phytoplankton abundance in cooler regions and decreasing phytoplankton abundance in warmer regions. Increased CO_2 levels in the atmosphere will lead to higher CO_2 levels in the ocean, which may promote primary production (Schipper *et al.*, 2004). These changes will propagate up the foodweb to copepod herbivores and zooplankton carnivores (Richardson and Schoeman, 2004). Changes in temperature conditions and ocean currents will also directly affect zooplankton production and species composition, as illustrated by the shift in dominance of *Calanus finmarchicus* to *C. helgolandicus* in the Northeast Atlantic (Beaugrand *et al.*, 2002). Higher CO_2 levels and the resulting reduction in pH may negatively affect organisms, particularly those that build calcareous skeletons, such as corals and coccolithophores (Riebesell *et al.*, 2000). A review of the impact of climate change on primary and secondary production in the North Atlantic is given in Section 7.

1.7 Population dynamics

Like other animal populations, marine fish and shellfish populations are believed to be regulated by density-dependent processes that may be related to increased mortality at high density, caused by predation, starvation, or reduced reproduction (Rothschild, 1986; Lorenzen and Enberg, 2002). Density-independent processes, particularly during early life stages, induce random variations in survival and give rise to wide fluctuations in recruitment.

Fish species are characterized by a complex life cycle comprising the egg, larval, juvenile, and adult stages, during which they increase in size over several orders of magnitude (Rothschild, 1986). The increase in body size coincides with an increase in trophic position (Jennings *et al.*, 2002a) and has further important implications for the spatial dynamics and the risk of predation or starvation. The various life-history stages have different habitat requirements and may be spatially segregated; for example, in many demersal species, the eggs and larvae occupy a pelagic habitat whereas the juveniles and adults occupy a benthic habitat. In several fish species, the juvenile and adult stages may live in different habitats, as the early demersal stages settle in restricted nursery grounds (Gibson, 1994). Also, in pelagic fish, juveniles and adults tend to be spatially separated. A population can only survive if the life cycle can be closed successfully (Sinclair, 1988); hence, it is not only the survival through the successive life-history stages that is important, but also the connectivity between life-history habitats. For pelagic species such as herring (*Clupea harengus*) and for demersal species spawning on banks, the retention of eggs and larvae is a dominant feature (Iles, 1984; Sinclair, 1988; Smith and Morse, 1985), whereas, for flatfish, the nursery grounds appear to be crucially important (Rijnsdorp *et al.*, 1992; Gibson, 1994; van der Veer *et al.*, 2000). Survival of early life-history stages depends on the timing of spawning in relation to the peak of larval food abundance (Cushing, 1990; Pope *et al.*, 1994; Platt *et al.*, 2003).

Habitat connectivity is determined by the transport of early life-history stages (eggs and/or larvae) from spawning to nursery areas and the successful completion of the migration cycle of adult fish between spawning and feeding habitats (Harden Jones, 1968). The pelagic egg and larval stage of marine fish species deserves special attention, because of their limited capabilities to actively select an appropriate habitat. Spawning, therefore, occurs in areas characterized by specific hydrographic conditions that are expected to retain the early pelagic stages and, moreover, are close enough to suitable nursery areas for the juveniles (Sinclair, 1988). Larval transport is generally passive, although larvae may influence their transport through active vertical migrations. In coastal waters, fish larvae may migrate to nursery grounds using selective tidal-stream transport (Boehlert and Mundy, 1988; Rijnsdorp *et al.*, 1985).

A consequence of the complex life cycle of fish species is that population abundance may be determined by the availability of suitable habitat for one (or more) specific life-history stages. As the life cycle is embedded in a specific landscape, the life stage most critical in determining overall population abundance may differ between populations. The abundance of herring populations appears to be determined by the size of larval retention areas (Sinclair, 1988). In Atlantic cod (*Gadus morhua*), population abundance in the Baltic is determined by available spawning habitat affecting the survival of eggs (Sparholt, 1996; MacKenzie *et al.*, 2000). It is not known whether or not this bottleneck also applies to other cod stocks that spawn in more stable oceanic conditions. Flatfish abundance, across both species and populations of the same species, appears to be related to available nursery habitat (Rijnsdorp *et al.*, 1992; Gibson, 1994; Le Pape *et al.*, 2003).

Fishing is known to have a major effect on the abundance of fish populations. Fishing acts as a top–down control that increases the mortality of fish above the retention size, reducing the biomass and the age and size structure of the population, which may lead to increased variability of population abundance (Anderson *et al.*, 2008). This may make populations more sensitive to the effects of climate change, and there is evidence of such increased sensitivity in the commercially important northeastern Arctic cod stock (Ottersen *et al.*, 2006).

Based on the population dynamic considerations above, climate change is expected to have the greatest impact on the following: (i) size and location of suitable habitat; (ii) retention of eggs and larvae; (iii) match in timing of the fish larvae and their food; (iv) connectivity between habitats of successive life stages; (v) growth; and (vi) predation mortality. As life-history stages require different habitats, the key processes in population regulation will be species- and area-specific, because the complex life cycle is embedded in a specific geographic landscape.

Climate change will undoubtedly affect the quality of suitable spawning and nursery areas. If the (eco-)physiological characteristics of the successive life-history stages are known, the envelopes of suitable abiotic conditions can be derived to overlay habitat suitability maps of successive life stages as a basis for estimating climate effects. Whether or not an area is suitable for spawning depends on the retention of eggs and larvae, as well as on the timing of egg production in relation to production of larval food. Climate change may affect the occurrence and stability of retention areas through its effect on ocean currents and the strength and frequency of storm surges. An increase in temperature may affect the probability of a mismatch between the production of larval fish and the production of the food that they require, if there is a difference between the temperature responses of the two. In addition, the survival of fish larvae may be affected by a climate-induced change in the timing of stratification.

The connectivity between habitats may be influenced by changes in ocean currents, melting of sea ice, and changes in river-discharge patterns. In particular, the impact on egg and larval transport is expected to be more marked than that on migration cycles of adult fish. Climate may influence growth rate, either directly, by affecting physiological rates, or indirectly, by affecting food availability. Finally, climate change may affect the timing of predators, disease agents, and competitors. For instance, temperature affects the timing of the migration cycle of brown shrimp (*Crangon crangon*) in coastal waters. After a cold winter, the return migration to shallow estuarine waters is delayed, lowering the predation mortality rate on shrimp by 0-group plaice (*Pleuronectes platessa*).

Changes in the distribution of fish species are reviewed in Section 10. A review of the impact of climate on a selection of commercially important species is presented in Sections 11–23.

1.8 Ecosystem dynamics

Marine ecosystems are generally considered to be regulated by bottom–up processes (Aebischer *et al.*, 1990; Ware and Thomson, 2005), although it was recently suggested that this generalization needs modification, because latitude, species diversity, and exploitation rate also play a role (Frank *et al.*, 2007). In high-latitude ecosystems, which are generally species-poor, and in intensively exploited systems, top–down control appears to predominate (Worm and Myers, 2003; Frank *et al.*, 2005). The effect of climate change on ecosystem dynamics will differ between bottom–up and top–down regulated systems. In bottom–up regulated systems, the production and distribution of fish and shellfish will be affected by climate-induced changes in primary and secondary production. In top–down regulated systems, the indirect effect will be through the climate effect on predators. Ecosystem regulation may change from bottom–up to top–down, and vice versa, in response to changes in the environment (Hunt *et al.*, 2002).

Size structure is an important property of marine ecosystems, affecting ecosystem processes, such as the transfer of energy through the foodweb. Physiological efficiencies and predator–prey relationships are strongly size dependent. The fact that climate change may change the size structure of phytoplankton and zooplankton populations may have important implications for the survival chances of fish larvae. Another property of ecosystems affected by climate change is the production cycle, which may result in the match or mismatch between the production cycles of fish larvae and their food. Seasonality also affects the availability of food for early juvenile and later stages. Food shortages occur in certain seasons, and fish build up energy reserves to survive these periods. Temperature, if it affects the timing and duration of these periods, will also affect growth rates and survival probabilities. As many ecological relationships are non-linear, climate-induced changes in these relationships may result in changes in alternative stable states, known as "regime shifts". Ecosystems characterized by low species diversity and top–down control may be more sensitive to regime shifts.

A review of the impact of climate on the structure and functioning of ecosystems is presented in Section 8. Section 9 comprises a review of the changes in the ecosystems of the Mediterranean and Black seas.

1.9 Discussion and conclusions

Environmental modifications caused by climate change are expected to result in evolutionary alterations in traits under selection. In the realm of terrestrial ecology, climate-induced evolutionary changes have been reported (Parmesan, 2006; Bradshaw and Holzapfel, 2001). In the marine realm, evolutionary changes are currently being heatedly debated in the context of fisheries, because of accumulating evidence that fishing may lead to genetic changes over decadal time-scales corresponding to a few generations (Law, 2000; Conover and Munch, 2002; Jørgensen *et al.*, 2007). Key questions for further research in the domain of ecophysiology, population dynamics, ecosystem dynamics, and evolutionary dynamics are listed in Table 1.1.

In the study of the impact of climate change on the productivity and distribution of fish populations, a variety of complementary modelling approaches will be needed. These models will allow the exploration of system dynamics in dependence of model assumptions and allow the interpretation of the role of processes underlying changes in empirical datasets. Three classes of models will be of particular importance.

i) Using ecophysiological characteristics as a basis, habitat–envelope models can be developed that predict the envelope of suitable environmental conditions. Combined with spatially resolved physical models, these can be used to construct habitat suitability maps for successive life-history stages. A problem yet to be solved is how to estimate the connectivity of habitats based on the transport of eggs and larvae and the migration cycles of adult fish. These models can be used to evaluate the implications of climate-change scenarios on habitat suitability and the possibility of life-cycle closure. In a next step, the abiotic habitat suitability models can be extended to include biotic variables, such as food and predators. The predictive power of this approach will depend on the role of top–down or bottom–up processes operating in the area of interest.

ii) Three-dimensional biophysical models will be useful for exploring the impact of climate change on primary and secondary production. One of the major challenges will be to extend these models to include benthic productivity.

iii) Population dynamics models comprising successive life-history stages, in relation to food and predators, will be important for exploring the interaction between climate change and exploitation.

Table 1.1. Key questions to address in future research.

Ecophysiology	Are there general patterns in the response to temperature (and other environmental variables) among organisms in relation to their biogeographic affinity? Are there differences in the responses to temperature of bacteria, phytoplankton, zooplankton, fish, and shellfish?
Population dynamics	Are some life-history stages more sensitive to climate change than others? Are species with narrow habitat requirements more sensitive to climate change than species with broad habitat requirements? Is the response to climate change affected by longevity and intrinsic population growth rate? How do fisheries affect the sensitivity of populations to climate change?
Ecosystem dynamics	Are ecosystems that are controlled by top–down processes more sensitive to climate change than ecosystems controlled by bottom–up processes? Do the physiological relationships with temperature observed among species and size classes have a predictable effect on their role in the ecosystem?
Evolutionary dynamics	How quickly can species adapt to changes in environmental variables, particularly temperature? How does the evolutionary response of species interact with ecosystem dynamics?

2 Ecotypes

Jim R. Ellis, Georg H. Engelhard, and John K. Pinnegar

2.1 Introduction

Cushing and Dickson (1976) suggested that the biological response to climate change would involve the appearance of new "indicator" species and new (resident) populations, as well as increases/decreases in fish stocks and more fundamental structural changes in the ecosystem and fish assemblage. The scientific community has seen an increased interest in the reporting of new distribution records and range extensions of marine fish (e.g. Arvedlund, 2009), although it is often argued that it is inappropriate to use records of such "vagrants" to examine climatic effects. For example, the reporting of such finds can depend on how proactive fishers or fish biologists are in collecting material and collating records, and this will be highly variable, both spatially and temporally. Hence, most studies examining the impacts of climatic factors (e.g. water temperature or the NAO index) on fish have examined particular fish species that are relatively common (see Sections 11 – 23). However, it will also be necessary to examine whether or not there are such climate-induced changes in the wider fish assemblage.

Predicting the potential effects of climate change on fish assemblages (including their structure, diversity, and function) can be complicated, because there will probably be wide differences in the responses of the various species in a fish fauna to climate change. Such understanding may, however, be facilitated by classifying the many fish species into a smaller set of "ecotypes", that is, groups of species that demonstrate similarities in particular biological characteristics and, therefore, may respond in similar ways to environmental change. Several aspects of fish life history and demography can be used to establish the range of ecotypes that may be considered within the overall fish community of an area, including biogeographic affinity, reproductive mode, body size, trophic niche, and habitat. This section summarizes these aspects and how they can be applied to European fish, with more detail for North Sea and Irish Sea fish. Although there have been several multispecies studies incorporating aspects of the biogeography of European fish (e.g. Yang, 1982a; Perry *et al.*, 2005), they can vary in their allocation of fish to biogeographic groups. Hence, there is a need for an agreed and standardized approach to the allocation of fish, for example, to biogeographic or trophic guilds.

There are many taxonomic accounts covering the fish of northwest Europe, including the works of early ichthyologists, such as Yarrell (1836), Couch (1864), Day (1880–1884), Moreau (1881–1891), Jenkins (1925), Lozano Rey (1928, 1947, 1952a, 1952b, 1960), Nobre (1935), Redeke (1941), Poll (1947), Tortonese (1956, 1970, 1975), and Wheeler (1969, 1978, 1992). More recent accounts include Bauchot and Pras (1980), Whitehead *et al.* (1984–1986), Lythgoe and Lythgoe (1991), Muus *et al.* (1998), Quéro *et al.* (2003), and Louisy (2006), while some of the more widely occurring Atlantic fish species are included in Carpenter (2002).

In terms of the North Sea (ICES Subarea IV), the fish fauna has been studied for more than 100 years, and accounts range from the early report by Garstang (1905) and regional and national overviews of the fish fauna (e.g. Redeke, 1941; Poll, 1947) to the more contemporary studies of Yang (1982a, 1982b, 1982c), Daan *et al.* (1990), Knijn *et al.* (1993), Greenstreet and Hall (1996), Rice and Gislason (1996), Rogers *et al.* (1998a, 1998b), Greenstreet *et al.* (1999), Jennings *et al.* (1999a, 2001b, 2002a), and Callaway *et* *al.* (2002). Yang (1982b) recorded 224 species, which he classified as either dominant (18 species), abundant (8 species), moderately abundant (16 species), frequent (31 species), rare (92 species), or vagrants (59 species). From a biogeographic standpoint, Yang (1982a) classified North Sea fish as northern Boreal (66 species), southern Lusitanian (110 species), and Atlantic (48 species). Since Yang (1982a), several additional species of fish have been reported from the North Sea, including white pomfret (*Pampus argenteus*; Davis and Wheeler, 1985) and pelagic stingray (*Pteroplatytrygon violacea*; Ellis, 2007). In total, approximately 250 marine fish species have been recorded (or may be present) in the wider North Sea area (Yang 1982a, 1982b; Fricke, 1999; Carl *et al.*, 2004; ICES, 2004d; Table 1 in Wheeler *et al.*, 2004). It should be recognized that many of these are southern, northern, or oceanic vagrants. A taxonomic list of North Sea fish species and associated ecotypes is provided in Annex 1. Table 2.1 provides examples of the ecotypes of some North Sea fish.

Several of the marine fish recorded from the North Sea have also been reported from the Baltic Sea, Skagerrak, and Kattegat, although the fully marine species tend to be restricted to the western parts of this region, with more euryhaline species extending farther into the Baltic Sea. Additionally, parts of the Baltic Sea have fish communities that include freshwater and brackish-water species. A list of Baltic Sea fish species with their associated ecotypes is provided in Annex 2.

The fish of the Irish Sea (ICES Division VIIa) have been studied less than those in the North Sea (see Ellis *et al.*, 2002, for an overview), although there has been a long history of ichthyological studies (e.g. Herdman and Dawson, 1902; Nash, 1990). The ichthyofauna of this area and the ecotypes of the fish are summarized in Annex 3.

Although other parts of the Celtic Sea ecoregion and the Biscay–Iberian ecoregions have been subject to detailed ichthyological studies, the proximity of these areas to the wider Atlantic (including the continental slope and deep water) means that detailed regional inventories of the ichthyofauna are more problematic to compile. The taxonomic list of European marine fish species provided in Annex 4 is adapted from the European Register of Marine Species (Costello *et al.*, 2001; with revisions by Costello *et al.*, 2004) and includes preliminary information on the ecotypes.

Given that these lists contain many deep-water and oceanic species, and other taxa whose taxonomy and biology are poorly known, these ecotypes should be considered preliminary and, as such, may be subject to modification during the course of the RECLAIM project and in future studies. In terms of how a fish species may respond to changing environmental conditions (e.g. climate) and/or human impacts (e.g. overfishing), other aspects of fish ecology (e.g. generation times, location and utilization of nursery grounds) are also important, but because such information is not accurately known for many European fish, these have not been included. Nevertheless, analyses targeted at more specific regions and fish assemblages can usefully incorporate such information.

Table 2.1. Examples of ecotypes of North Sea fish.

(A) Atlantic species

		PISCIVORES: THRESHER SHARK, SWORDFISH
Oceanic (occasional or periodic vagrants)	Epipelagic	Planktivores: Saurey pike, sunfish
		Scavenger: pilotfish
	Mesopelagic	Piscivores: Deal fish, Ray's bream
		Planktivores: oarfish, louver
Slope	Bathydemersal	Large piscivores: six-gill shark, kitefin shark
		Large benthivores: rabbitfish

		PISCIVORES: THRESHER SHARK, SWORDFISH
	Benthopelagic	Piscivores: black scabbardfish
		Planktivore: blue whiting
	Bathypelagic	Planktivore: pearlside
Shelf	Demersal	Scavenger: hagfish
	Benthopelagic	Benthivore: pufferfish
	Pelagic	Planktivore: basking shark
		Piscivores: porbeagle, mackerel
Coastal	Demersal	Bentho-piscivore: European eel

(B) Boreal species

		BENTHIVORES: SAILFIN RAY, ROUND SKATE
Slope	Demersal	Piscivores: Norwegian skate, ling, halibut
	Benthopelagic	Piscivore: Greenland shark
		Planktivore: greater argentine
	Pelagic	Plankto-piscivore: redfish
Shelf	Demersal	Piscivores: starry ray, saithe
		Ectoparasite: sea lamprey
		Bentho-piscivores: bullrout, long-rough dab
		Benthivores: haddock, pogge, Norwegian goby, witch
	Reef-associated	Benthivores: Guillet's goby, diminutive goby
	Benthopelagic	Piscivore: spurdog
		Bentho-piscivores: Norway pout, lumpsucker
		Plankto-piscivore: jellycat
		Planktivores: herring, lesser sandeel
	Pelagic	Piscivore: sea trout
		Planktivore (vagrant): capelin
Coastal	Demersal	Piscivore/ectoparasite: river lamprey
		Benthivore: three-spined stickleback
		Planktivore: whitefish
	(Bentho) Pelagic	Piscivore: char
		Benthivore: smelt

(C) Lusitanian species

		PISCIVORE: LONG-NOSE SKATE
Slope	Demersal	Bentho-piscivore: black-mouth dogfish
		Planktivore: boarfish
	Pelagic	Planktivore: silvery pout
Shelf	Demersal	Piscivores: angel shark, cuckoo ray, whiting, turbot
		Bentho-piscivores: thornback ray, greater forkbeard, lesser weeverfish
		Benthivores: smoothhounds, grey gurnard, dragonets, plaice, sole
	Reef-associated	Piscivores: greater spotted dogfish, conger eel
		Benthivores: tompot blenny, triggerfish
	Benthopelagic	Piscivores: tope, John dory, bass
		Benthivore: eagle ray
		Planktivore: lesser argentine
		Herbivore: saupe
	Pelagic	Piscivores: garfish, horse mackerel
		Planktivores: sprat, shads, crystal goby
Coastal	Demersal	Benthivores: rock goby, flounder
		Planktivores: sea-horse, greater pipefish
	Reef-associated	Piscivore: moray eel
		Bentho-piscivore: cuckoo wrasse
		Benthivore: ballan wrasse
	(Bentho) Pelagic	Benthivore: sand smelt
		Omnivore: bogue
		Detritivores: grey mullets

2.2 Biogeographic affinity

There have been several reviews of the biogeography (or zoogeography) of various marine taxa, including the works of Ekman (1953), Briggs (1974), and Longhurst (1998), and these and other works have been reviewed recently by Dinter (2001). Early marine zoologists, such as Edward Forbes, identified four major provinces: Arctic, Boreal, Celtic, and Lusitanian (western Iberian). Some later scientists reduced these provinces to three by combining the Boreal and Celtic provinces into the "Eastern Atlantic Boreal Region" (Dinter, 2001). In contrast, others made further subdivisions, identifying Arctic, Boreal–Arctic, Boreal, Boreal–Lusitanian, Lusitanian–Boreal, and Lusitanian biogeographic zones (e.g. Hiscock, 1998). Although such delineation is appropriate to fish assemblages on the continental shelf, such provinces may be less appropriate to individual species, because the Boreal–Lusitanian and Lusitanian–Boreal provinces are essentially based on varying proportions of species of Lusitanian and Boreal affinities.

With regard to North and Irish Sea fish, we have followed Yang's (1982a) three biogeographic categories: Boreal, Lusitanian, and Atlantic (see below). We differ from Yang (1982a) in considering the spurdog (*Squalus acanthias*) and roundhead rattail (*Coryphaenoides rupestris*) to be Boreal (not Atlantic) species, and the pollack (*Pollachius pollachius*) and Norwegian goby (*Pomatoschistus norvegicus*) to be Boreal (not Lusitanian) species. For a wider analysis of European fish, further biogeographic categories are required for Arctic, Mediterranean, Black Sea, Macaronesian, and African species.

It should be noted that the biogeographic affinities used in the present study are meant to provide information on broad zoogeographic distribution in the Northeast Atlantic. Therefore, widely distributed species that may be circumglobal in nature are attributed to the biogeographic province most suitable for the European population(s).

Arctic fish are those species restricted to the northernmost parts of the ICES/OSPAR areas, with southern limits off north Norway and Iceland. Families of marine fish well represented in the Arctic include skates (Rajidae), whitefish (Salmonidae), cod (Gadidae), sculpins (Cottidae), poachers (Agonidae), lumpfish (Cyclopteridae), sea snails (Liparidae), and eelpouts (Zoarcidae); these families also include several Boreal forms.

Boreal fish are considered northern taxa and include both Boreal species (which extend northwards to the Norwegian Sea and Icelandic waters) and Boreal–Arctic species (which extend into Arctic waters and possibly even into the cold waters of the Northwest Atlantic). These species generally have the southern limit of their distribution around the British Isles or west of Brittany.

Lusitanian fish are those southern species that tend to be abundant from the Iberian Peninsula (including the Mediterranean Sea) to as far north as the British Isles. They may have their northern limits in the southern or central North Sea (although many of these species extend to higher latitudes on the western seaboard of the British Isles, and so can also occur in the northwestern North Sea). Many of these species have distributions extending into the Mediterranean Sea and off the coast of northwest Africa.

Mediterranean fish are those species that are broadly endemic to the Mediterranean Basin (although their distributions may extend slightly into Moroccan or Portuguese waters); therefore, their distributions do not usually extend as far as the

Biscay–Iberian ecoregion. Although several species of Mediterranean fish also occur in the Black Sea, those fish that are mostly endemic to the Black Sea are listed as Sarmatic (following Ekman, 1953).

Macaronesian fish are those species (or subspecies) that tend to be restricted to Atlantic islands (Azores, Madeira, Canary Islands), although some specimens of these species may have been occasionally recorded from African coastal waters.

African fish are considered those species that have a northerly distribution in the southern or western Mediterranean, but are more typically encountered off northwest Africa. This region would equate with the Mauritanian province of some biogeographic studies (e.g. Ekman, 1953) or the Eastern Canary Coastal and Guinea Current Coastal provinces of Longhurst (1998). Certain sea breams (Sparidae) are particularly characteristic of this ecotype.

Atlantic fish are those (often pelagic or deep-water) species that are widespread in the North Atlantic and include many of the deeper-water species that may be widely distributed along the continental slope. Some Atlantic fish, which occur on both sides of the Atlantic, but are limited to the more tropical parts of the Northeast Atlantic, have been noted as Atlantic (African) for the present overview.

Marine fish that are not native to European waters include some salmonids that have been introduced from the Northwest Pacific and Lessepsian migrants that have entered the Mediterranean through the Suez Canal (i.e. Indo–Pacific species), although there have been reports of Indo–Pacific species elsewhere in European seas (e.g. *Pampus argenteus* in the North Sea). The opening of the Suez Canal in 1869 connected the Red Sea with the eastern Mediterranean. It removed the geographic barrier between these seas, and many organisms originally inhabiting the Red Sea have now penetrated deep into the Mediterranean. Inventories of Lessepsian migrants need to be updated regularly. For example, *Fistularia commersonii, Oxyurichthys petersi, Upeneus pori, Callionymus filamentosus, Etrumeus teres, Lagocephalus suezensis, Petroscirtes ancylodon, Sphyraena flavicauda,* and *Tylerius spinosissimus* have all been recorded from the eastern Mediterranean in recent years (Corsini *et al.*, 2005; Akyol *et al.*, 2006; Pais *et al.*, 2007), and may need to be added to the list of European fish. Some Lessepsian migrants are now spreading westwards throughout the Mediterranean and, in certain places, have displaced native species. The eastern Mediterranean is now regarded by many researchers as a subprovince of the Red Sea system (Corsini *et al.*, 2006).

There are also examples of translocations of native Black Sea and Caspian fish species to the Baltic via the Danube canal and river systems, e.g. the round goby (*Neogobius melanostomus*). The round goby is now the dominant fish species in most of the shallow waters of the Gulf of Gdańsk (Sapota, 2004). The species has also been introduced into the North American Great Lakes. The potential for non-native species to establish themselves depends on the prevailing environmental (climatic) conditions, as well as shipping routes and global transportation networks.

2.3 Reproductive strategy

The ways in which fish respond to climate change is influenced largely by their reproductive strategy. Broadcast spawners, for example, shed large numbers of eggs into the water column, where the survival and growth of the early life-history stages will depend on environmental conditions (e.g. temperature, predator–prey interactions). In contrast, for live-bearing fish species that only produce a small number of pups, recruitment may depend more on the size of the maternal stock than on environmental conditions. Fish exhibit a wide range of reproductive strategies, many of which have been categorized by Balon (1984).

In general, most species of fish occurring in the temperate waters of the Northeast Atlantic are broadcast spawners (see above). Some species, e.g. anglerfish (*Lophius piscatorius*) and related species, also produce planktonic eggs, but these are laid in gelatinous masses (rafts).

Many fish, however, are demersal egg-layers, depositing their eggs on the seabed (e.g. on broken shells, maerl, gravel, kelp holdfasts, rocks). Several families of European fish lay their eggs demersally, including hagfish (Myxinidae), catshark (Scyliorhinidae), skate (Rajidae), chimaera (Chimaeridae), smelt (Osmeridae), herring (Clupeidae), clingfish (Gobiesocidae), sculpin (Cottidae and Psychrolutidae), pogge (Agonidae), lumpsucker (Cyclopteridae), sea snail (Liparidae), sandeel (Ammodytidae), wolffish (Anarhichadidae), butterfish (Pholidae), prickleback (Stichaeidae), some eelpout (Zoarcidae), blenny (Blenniidae), goby (Gobiidae), and triggerfish (Balistidae).

Some demersal egg-layers, e.g. herring (*Clupea harengus*), do not provide any parental care, whereas the adults of other species, e.g. wolffish (*Anarhichas lupus*), may protect the developing eggs. A small group of species lay eggs with sticky filaments that adhere to vegetation or other floating objects; this group includes sand smelt (Atherinidae), garfish (Belonidae), half-beak (Hemiramphidae), and flying fish (Exocoetidae).

Several fish exhibit parental care, such as the "brooders", which protect their eggs and recently hatched young in a brood pouch, e.g. in sea horses and pipefish (Syngnathidae), or brood them in the mouth, as in cardinal fish (Apogonidae). Other fish build nests in which to protect the young, a strategy seen in stickleback (Gasterosteidae), black sea bream (Sparidae, *Spondyliosoma cantharus*), some wrasses (Labridae), and damselfish (Pomacentridae).

Several European fish are anadromous, migrating into freshwater ecosystems to deposit their eggs; these fish include lamprey (Petromyzontidae), sturgeon (Acipenseridae), shad (Clupeidae, *Alosa* spp.), and various salmonids (Salmonidae). In contrast, catadromous species, typified by the European eel (*Anguilla anguilla*), live in freshwater and spawn in the marine ecosystem. The reproductive biology of the European eel and other eels, e.g. European conger eel (*Conger conger*), are poorly known, although the leptocephalus larvae have been described.

Viviparity occurs in a variety of fish taxa. Among teleosts, it occurs in redfish (*Sebastes* spp.), eelpout, or viviparous blenny (*Zoarces viviparus*), and viviparous brotula (Bythitidae), whose females give birth to larvae. In these instances, the developing embryos are nourished exclusively by nutrients contained in the eggs, a form of reproduction sometimes referred to as "ovoviviparity". This mode of reproduction is also seen in some elasmobranchs, e.g. spurdog (*Squalus acanthias*) and other squaliform sharks, although it is often referred to as "aplacental viviparity".

Other, more advanced modes of viviparity occur in the elasmobranchs. These range from: (i) the supply of nutrients to developing embryos by uterine villi and trophonemata, e.g. stingray (*Dasyatis pastinaca*); (ii) oophagy, in which the mother continues to produce oocytes, which are eaten by the developing embryos, e.g. porbeagle (*Lamna nasus*); to (iii) placental connections supplying nutrients, e.g. blue shark (*Prionace glauca*).

2.4 Maximum body length

Size is known to be an informative life-history parameter that is often correlated with vulnerability. For species for which aging has been undertaken, growth models can be used to estimate L_∞, although imprecise age estimation, low sample size, or restricted size distribution of studied material can lead to under- or overestimation of L_∞. The maximum observed length (L_{max}) is the better known for a greater range of taxa (although poor species identification can be a problem). Most fish species are measured in terms of total length (L_T), although for species with long, thin, fragile caudal fins, other dimensions (e.g. standard length, fork length, or disc width) may be more appropriate. For the purposes of the present study, most of the maximum size information is from FishBase or Whitehead *et al.* (1984–1986), with minor amendments made for some of the more common shelf-living species, for which there is extensive length–frequency information from fishery-independent groundfish surveys.

2.5 Trophic guilds and trophic level

Feeding behaviours and foraging strategies/tactics have been documented for some fish species occurring in European seas, though they are not well defined for many species. Feeding habits (diets) of most of the larger shelf species are relatively well known (see Section 10 in ICES, 2005e, and references therein) although factors that affect feeding habits, including temporal variation (diurnal–seasonal), ontogenetic changes, and spatial patterns in food availability, have only been examined for some of the more abundant species.

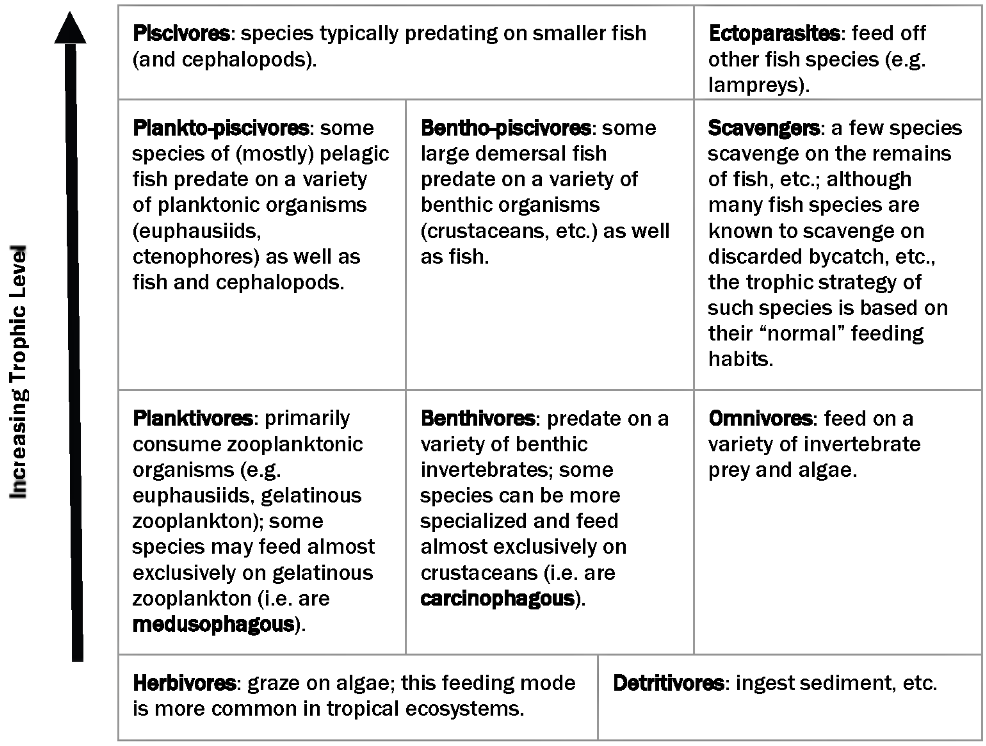
It should also be noted that the feeding habits of some small benthic fish and most deep-water fish are poorly known. Additionally, many of the fish species occurring in deeper waters often regurgitate their stomach contents when brought to the surface; consequently, little is understood about their diets (Polunin *et al.*, 2001).

Hence, although the diets of many (but certainly not all) shelf-living European fish species have been described, these studies may be limited by spatial and temporal constraints, sample size, the size range studied, and the methods used. Hence, categorizing all fish into defined trophic guilds, as undertaken for other sea areas (e.g. Garrison and Link, 2000; Bulman *et al.*, 2001; Marancik and Hare, 2007) has yet to be attempted in a European context. Ontogenetic changes in fish feeding habits are well documented and, for the purposes of the present study, we have tried to encapsulate the diets of adult fish.

Most European fish are categorized here as (i) piscivores, species in which the adults predate primarily on fish (and cephalopods); (ii) plankto-piscivores, species that predate on a variety of larger zooplankton and fish; (iii) planktivores, species predating primarily on zooplanktonic organisms; (iv) bentho-piscivores, species predating on a variety of larger epifaunal invertebrates and fish; or (v) benthivores, species predating primarily on benthic and epibenthic invertebrates. Although piscivores are listed as the top predatory category, it should be recognized that some of the larger sharks, e.g. tiger shark (*Galeocerdo cuvier*) and white shark (*Carcharodon carcharias*), also consume higher vertebrates (e.g. turtles, seabirds, and marine mammals) as well as fish.

Although these categories are somewhat generic, some fish species are known to have more specialized feeding habits. Some benthivorous species, e.g. smoothhound (*Mustelus* spp.), feed almost exclusively on crustaceans and may be termed carcinophagous. Some planktivorous species specialize in feeding on gelatinous zooplankton and may be termed medusophagous. Adult lampreys are ectoparasites, feeding off a variety of fish and marine mammals. Several species, e.g. hagfish (*Myxine glutinosa*) and pilotfish (*Naucrates ductor*), tend to scavenge, although many demersal fish are known to predate on discarded fish and fish offal, as well as on invertebrates or fish injured or killed by fishing gear. Other fish species may be omnivorous, e.g. bogue (*Boops boops*), which feeds on small invertebrates as well as algal material, detritivorous, e.g. grey mullets (Mugilidae), which typically eat organic material from the sediment and graze algae, or more herbivorous, e.g. saupe (*Sarpa salpa*).

Trophic level can be based on stomach-content analysis, knowledge of natural history, or the relative concentrations of naturally occurring isotopes of nitrogen (the "heavier" form of which tends to become concentrated in the tissues of predators). Although trophic levels, as indicated by isotopes, are available for many of the more common North Sea and Mediterranean fish (Pinnegar *et al.*, 2002, 2003), in order to allow consistency over all taxa, information on trophic level has been taken from FishBase (Froese and Pauly, 2007). Trophic levels of European fish generally range from 2.0–2.5, for species such as bogue, sand smelts (*Atherina* spp.), and grey mullets to 4.5, for piscivorous fish, such as porbeagle, thresher shark (*Alopias vulpinus*), John dory (*Zeus faber*), and swordfish (*Xiphias gladius*). The generalized relationship between trophic categories and trophic level is illustrated in Figure 2.1.



Piscivores: species typically predating on smaller fish (and cephalopods).

Ectoparasites: feed off other fish species (e.g. lampreys).

Plankto-piscivores: some species of (mostly) pelagic fish predate on a variety of planktonic organisms (euphausiids, ctenophores) as well as fish and cephalopods.

Bentho-piscivores: some large demersal fish predate on a variety of benthic organisms (crustaceans, etc.) as well as fish.

Scavengers: a few species scavenge on the remains of fish, etc.; although many fish species are known to scavenge on discarded bycatch, etc., the trophic strategy of such species is based on their "normal" feeding habits.

Planktivores: primarily consume zooplanktonic organisms (e.g. euphausiids, gelatinous zooplankton); some species may feed almost exclusively on gelatinous zooplankton (i.e. are **medusophagous**).

Benthivores: predate on a variety of benthic invertebrates; some species can be more specialized and feed almost exclusively on crustaceans (i.e. are **carcinophagous**).

Omnivores: feed on a variety of invertebrate prey and algae.

Herbivores: graze on algae; this feeding mode is more common in tropical ecosystems.

Detritivores: ingest sediment, etc.

Figure 2.1. Generalized relationship between feeding guilds and trophic level.

2.6 Habitat

Various factors affect the overall distribution and habitats of fish, and water temperature, salinity, water depth, and sedimentary environment are the underlying determinants of broadscale geographic distributions. Other factors, including local predator–prey relationships, water quality, and cover (e.g. physical structures or algal cover) operate on smaller spatial scales.

Given that climatic variability may have a greater influence on coastal and shallow shelf seas than on deeper waters (which typically have more stable environmental conditions), species occurring in shallow areas may be more affected by environmental fluctuations and changes. Additionally, changes in oceanographic circulation, as well as affecting planktonic early life-history stages, may affect the distribution and movement of pelagic fish. In contrast, the distribution of demersal fish can be strongly correlated with the sedimentary environment, as well as with bathymetry, temperature, and salinity. It has been hypothesized that pelagic and demersal species will differ in their responses to climate change, because the former can more easily follow changes in water masses than the latter, which have more geographically fixed habitat requirements (Rijnsdorp *et al.*, 2009).

Although some fish species can be highly selective in their habitat requirements and utilization, others occupy a wide range of habitats. For example, red bandfish (*Cepola rubescens*) are restricted to particular sediment types, where it can form burrows, whereas lesser spotted dogfish (*Scyliorhinus canicula*) can occur on a variety of sediments, ranging from mud to rock. The effects of fine-scale habitat properties (e.g. seabed topography, presence of physical relief) on the fine-scale distribution of fish are poorly known for many species, although groundfish surveys can provide general information for describing broader types of habitat usage by fish, in terms of the sedimentary and bathymetric environments in which they are most abundant.

It should also be noted that fish habitats may vary temporally (ranging from diurnal to seasonal patterns in habitat use), as well as ontogenetically (e.g. in many marine species, juveniles occur in shallower waters than adults do).

For the purposes of this account, we distinguish between "horizontal habitat", which ranges from estuarine and coastal fish to oceanic species, and the somewhat related "vertical habitat", which accounts for their position in the water column.

Coastal. Some species of fish are more prevalent in shallow-water coastal zones, although the population as a whole may extend farther offshore. For example, various pipefish tend to be recorded most often in such shallow-water habitats. This area also includes more specialized habitats, such as the rocky intertidal zone, where species such as blenny (*Lipophrys pholis*) are found almost exclusively. Other species of fish may be restricted to inshore kelp forests or seagrass meadows. Some species of fish may occur almost exclusively in estuaries, for example, flounder (*Platichthys flesus*) and grey mullet (Mugilidae), which are most prevalent in brackish waters. The juveniles of some marine species may inhabit estuarine areas as 0-groups (e.g. sea bass), and estuarine environments are also important for diadromous fish.

Continental shelf (down to 200 m). The majority of commercially important European fish are demersal or small pelagic (neritopelagic) species occurring on the continental shelf. Some are widespread across the entire shelf, whereas others are restricted to either the shallower waters of the inner shelf or the deeper waters of the outer shelf. This broad habitat type accounts for the greatest proportion of fish in enclosed seas (e.g. the North and Irish seas). Although much of the continental shelf is characterized by mud, sand, and gravel, rocky outcrops (as well as wrecks and oilrigs) can have a "reef-associated" fish community.

Continental slope. This habitat is occupied by various demersal, bathydemersal, bentho-pelagic, and pelagic species. Although many outer-shelf species occur on the upper margins of the continental slope, these areas are also inhabited by various deep-water species that are not typically reported from shelf seas, with some referred to as bathydemersal, or bathypelagic, species.

Oceanic. The offshore pelagic ecosystem adjoining the European continental shelf contains myriad fish species, including many whose biology is poorly known. The fish of this ecosystem may be broadly characterized into (i) epipelagic species (e.g. oceanic fish occurring from 0 to 200 m depth); (ii) mesopelagic species (typically occurring from 200 to 1000 m depth); (iii) bathypelagic species, (occurring from 1000 to 4000 m depth), and (iv) abyssopelagic species, occurring at >4000 m depth. Several epi- and mesopelagic species have been reported from shelf seas (including the North Sea), where they may be regarded as occasional vagrants, often carried into shallow water by freak oceanographic features (e.g. Heessen *et al*., 1996).

2.7 Macroecological perspectives

It should also be emphasized that, in the examination of temporal changes in the structure and composition of fish assemblages, relevant "ecological rules" may need to be considered, and several such rules may apply to fish in the Northeast Atlantic.

Polar gigantism (i.e. the attainment of larger body size by species in northern latitudes) has been well documented by zoologists, and Bergmann's Rule (Bergmann, 1847) suggests that the size of a species increases with cooler environmental conditions. Indeed, some of the northern fish species occurring in the North Sea are known to attain larger sizes farther north, e.g. starry skate (*Amblyraja radiata*).

In terms of shelf-dwelling fish species, juveniles tend to occur in shallow inshore waters, with fish moving offshore into deeper waters as they attain a larger size (Heincke's Law; Heincke, 1913). Such patterns are known to occur in various flatfish, e.g. plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), sole (*Solea solea*), as well as in some skate, e.g. thornback ray (*Raja clavata*).

Rapoport's Rule (Rapoport, 1975, 1982; Stevens, 1989) considers latitudinal gradients in species diversity and richness, with a general tendency for biodiversity to be greater at lower latitudes (i.e. towards the tropics). This macro-ecological rule does not apply to all parts of the European continental shelf. For example, the North Sea has a large latitudinal range (ca. 10°), but it should be recognized that temperature and bathymetric regimes are autocorrelated latitude in the North Sea. Furthermore, "southern" fish species may enter the North Sea not only via the English Channel in the south, but also via the Fair Isle Current (running between the Orkney and Shetland isles) and via a route north of the Shetland Isles. Hence, the North Sea does not provide an appropriate ecoregion in which to test Rapoport's Rule.

Abundance–size relationships are evident in various fish species, with the general rule that, as a species increases in abundance, its distribution also increases, and conversely, as a population declines, its distribution contracts. (For further information on abundance–size relationships see Section 3.2 in ICES, 2004d; Section 7 in ICES, 2005e; and Section 3 in ICES, 2006n).

2.8 Maintenance of up-to-date ichthyofaunal inventories

Given the changes that can occur in the distribution of fish and that reports of such changes are often scattered throughout the scientific and natural history literature (see Addendum), there is a continuing requirement for regularly updated ichthyofaunal inventories (e.g. by ICES ecoregion). This is of particular relevance to climate-change issues, because predicted increases in water temperature are expected to result in the increased occurrence of subtropical fish in European seas. Additionally, other human factors (ranging from introductions of non-native species-to-species extirpations through overexploitation and habitat degradation) will also affect the wider fish assemblage. Hence, the ICES scientific community should consider becoming more proactive in the maintenance of such ichthyological information, because it will assist scientists and managers in the evaluation of climate change and wider ecosystem issues, including biodiversity.

Addendum

Since the European Register of Marine Species was compiled and the Annexes for this account collated, there have been new records of marine fish occurring in either the Mediterranean Sea (including the North African coast) or the Atlantic waters of Europe, both in terms of range extensions and through descriptions of new species (see chart below).

SPECIES	FAMILY	SOURCE
Centroscymnus owstoni	Somnosidae	Moura *et al.* (2008)
Neoraja iberica	Rajidae	Stehmann *et al.* (2008)
Cheilopogon furcatus	Exocoetidae	Ben Souissi *et al.* (2005a)
Synaphobranchus affinis	Synaphobranchidae	Almeida and Biscoito (2007)
Synaphobranchus brevidorsalis	Synaphobranchidae	Almeida and Biscoito (2007)
Cephalopholis taeniops	Serranidae	Ben Abdallah *et al.* (2007)
Chloroscombrus chrysurus	Carangidae	Acosta *et al.* (2008)
Acanthurus monroviae	Acanthuridae	Hemida *et al.* (2004)
Chromogobius britoi	Gobiidae	Beldade *et al.* (2006)
Poecilopsetta beanie	Pleuronectidae	Nielsen and Casey (2008)
Elates ransonnetii	Platycephalidae	Mastrototaro *et al.* (2007)
Chilomycterus reticulatus	Diodontidae	Follesa *et al.* (2009)

There continue to be many reports of new Lessepsian migrants in the Mediterranean Sea, and although most of these records are from the southern and eastern parts of the Mediterranean, some species have extended into European waters. Records of new Lessepsian migrants in the wider Mediterranean include *Dasyatis chrysonota, Rhinobatos halavi, Scarus ghobban, Apogon smithi, Nemipterus japonicus, Nemipterus randalli, Decapterus russelli, Omobranchus punctatus, Fistularia commersonii, Upeneus pori, Papillogobius melanobranchus,* and *Hippocampus fuscus* (Golani, 2000, 2004, 2006; Golani and Fine, 2002; Golani and Capape, 2004; Bariche and Saad, 2005; Ben Souissi *et al.*, 2005b, 2007; Golani and Sonin, 2006; Kovacic and Golani, 2007; Gokoglu *et al.*, 2008; Golani *et al.*, 2008).

As noted above, given the changes that can occur in the distribution of fish and that reports of such changes are often scattered throughout the literature, there is a continuing need for regularly updated ichthyofaunal inventories (e.g. by ICES ecoregion) that will allow such signals to be included in analyses of climatic impacts.

3 Ecophysiology

Myron A. Peck and Henk W. van der Veer

3.1 Introduction

The need to better understand and incorporate physiology into projections of climate impacts on marine species has recently been discussed with renewed vigour (Pörtner and Farrell, 2008). The aim of this section is to review basic ecophysiological concepts with regard to how changes in key environmental factors influence the vital rates of marine fish and shellfish. Research on fish at the organismal level (whole organism and bioenergetics studies) and emerging concepts at the cellular level are reviewed. Evidence for variability in physiological tolerance among individuals, populations, and/or species is also presented, because such variability is likely to be an important component of the "adaptive capacity" of fish stocks to changes in climate-driven factors.

Throughout the section, the concept of a balanced energy budget is used as a framework for understanding the changes in growth performance that result from changes in abiotic factors (with a primary emphasis on water temperature). Modelling approaches that directly incorporate physiological mechanisms (larval fish individual-based models (IBMs) and dynamic energy budgets (DEBs)) are highlighted because their use as tools is important to the understanding of the impacts of climate change on individual fish species. The importance of understanding the physiological impacts of multiple factors acting synergistically is also emphasized.

This section provides the supporting information required to understand the overall conceptual framework (Section 1) and the mechanisms behind biogeographic classifications (Section 2), and sheds light on the underlying mechanisms behind changes in distributional ranges (Section 12) and productivity of individual species within specific areas (Sections 13–22).

3.2 Physiological rates and the influence of environmental factors

Climate change and variability act both directly and indirectly on the environment (i.e. the totality of all extrinsic (abiotic and biotic) factors experienced by marine fish and shellfish resources). However, the consequences of these environmental changes on the vital rates of organisms depend largely on intrinsic factors peculiar to each species (e.g. life-history strategy, ecotypology, physiological tolerances). For example, sessile organisms are more likely to respond to environmental changes by adapting their physiology than motile animals, which can respond by adapting their behaviour.

Understanding the extent to which organisms cope with the problems posed (and exploit the opportunities offered) by changes in their particular habitat must include insight into the physiological effects imposed by the environment as well as the ecophysiological responses of an organism at all stages of its life cycle (Willmer *et al.*, 2000).

3.3 Balanced bioenergetics budgets as a framework

Predictions of the intra- and interspecific physiological consequences of climate change and/or variability require a general framework that describes the relationship between prevailing abiotic and biotic environmental conditions and fish performance in terms of vital rates (e.g. rates of survival, growth, and reproduction). At the organismal level, the use of balanced energy budgets to predict various aspects of the field ecology and biology of commercially and recreationally important fish and shellfish (e.g. prey consumption, growth rates) has become common in the last three decades (Brett and Groves, 1979; Hanson *et al.*, 1997). A balanced energy budget was first applied to fish by Winberg (1956, p. 172):

$$Rat = 1.25\,(P + T),\text{ or } C = 1.25\,(G + M), \tag{1}$$

where C = food consumption (Rat = ration; Winberg, 1956), G = growth (P = prirost), M = expenditures for metabolism (T = traty). This balanced energy budget has subsequently been expanded to include specific pathways for energy loss via metabolism:

$$C = G + R + E + F, \tag{2}$$

where C = energy gained from food consumption, G = the energy gained in growth, R = energy lost via respiration, E = energy lost via nitrogenous excretion, and F = the energy lost in egested faecal material. All parameters have common energetic units (e.g. joules d^{-1}).

Further subdivision of parameter rates is often employed. For example, rates of R (and E) can be subdivided to include different levels of energy loss caused by basal (standard) metabolism (R_S), feeding metabolism (specific dynamic action, R_{SDA}), and active (R_A) metabolism (Brett and Groves, 1979). The increase in rates of O_2 consumption during feeding (R_{SDA}) has also been termed "apparent heat increment" (e.g. Blaikie and Kerr, 1996). Growth can be subdivided into gonadal growth (G_G) and somatic growth (G_S). This balanced energy budget is most commonly used to estimate either growth or food consumption after various other parameters have been determined (Hanson *et al.*, 1997). Rates of these parameters are affected by a number of factors, including water temperature, fish body size, and feeding level (Brett and Groves, 1979). Thus, balanced energy budgets provide a means of exploring potential impacts of environmental changes at the level of the individual using physiological principles. However, this approach is limited because the budget does not account for the "history" of the organism, but merely provides a snapshot of the metabolic rates at a particular time. A "dynamic" version of energy budgeting is discussed in Section 3.6.2.

The main physiological factor responsible for differences in environmental (e.g. thermal) tolerance is the rate of energy loss caused by metabolism. Fry (1971) classified environmental factors according to their influence on aerobic metabolism and aerobic scope (the difference between the lowest and highest rates of aerobic respiration; Figure 3.1a and b). Aerobic scope represents the energy available for all life processes after accounting for standard levels (or costs), and Fry's factors act to either increase (unload or release) or decrease (e.g. limit) the aerobic scope. At the most basic level, suitable environments are those in which an organism's metabolic scope is positive and various controlling factors (e.g. temperature, pressure, and pH) determine the range of metabolic scope and, hence, reflect the tolerance range. Other factors interact with the controlling effect of temperature to either increase or decrease the metabolic rate and scope of an organism (Figure 3.1c and d). The result can be a change in the optimal range of temperatures (i.e. the temperatures where metabolic scope is highest).

Fry (1971) separated environmental factors into five categories.

i) Controlling factors, which govern metabolic rate by affecting molecular kinetics (e.g. temperature, pressure, pH).

ii) Lethal factors, which drastically alter lifespan (e.g. intolerable levels of temperature and dissolved O_2).

iii) Limiting factors, which restrict the supply or removal of metabolites (food, water, and respiratory gases) that affect activity and usually operate above or below a threshold.

iv) Masking factors, which modify or prevent the effect of other environmental factors by influencing the channelling of energy (e.g. salinity affecting osmoregulation).

v) Directive factors, which cue some response affecting energy partitioning, typically via hormone induction (photoperiod on reproduction).

The outcome of changes in aerobic scope at different levels of these factors is most easily observed by evaluating the feeding–growth relationship of an organism (Figure 3.2). Over short time-scales, utilization of energy reserves creates some individual flexibility with respect to these tolerance limits. However, over longer periods, tolerance limits to environmental factors dictate the specific habitats that organisms can exploit. To some extent, masking, loading, and limiting factors can modify, and may modulate, these tolerance limits. Acclimatization provides an additional route, allowing organisms to utilize new environmental conditions.

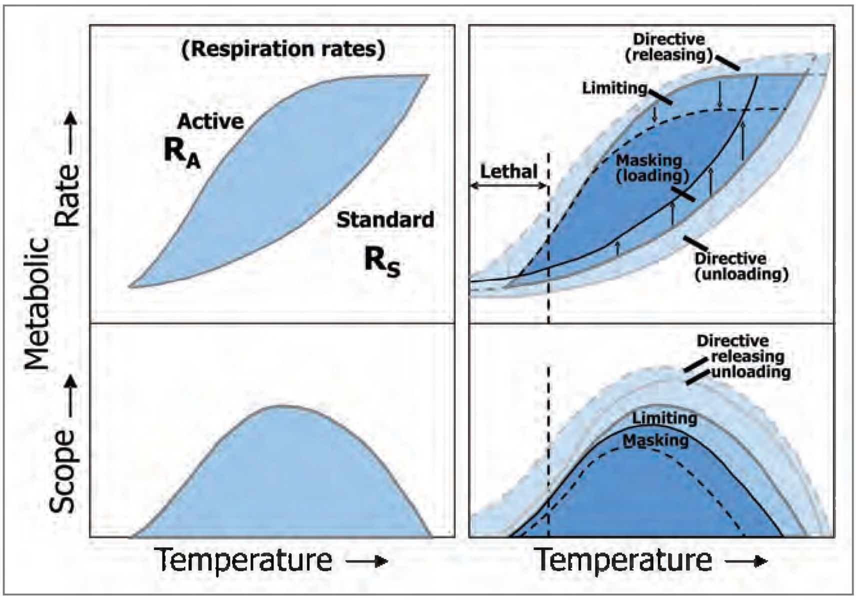


Figure 3.1. Changes in (a) standard metabolic rate (R_S) and active metabolic rate (R_A) with temperature, and (b) metabolic scope (R_A–R_S) vs. temperature. Increases or decreases in (c) metabolic rate and (d) scope caused by the interaction of other environmental factors superimposed on the controlling effect of temperature (based on Fry, 1957).

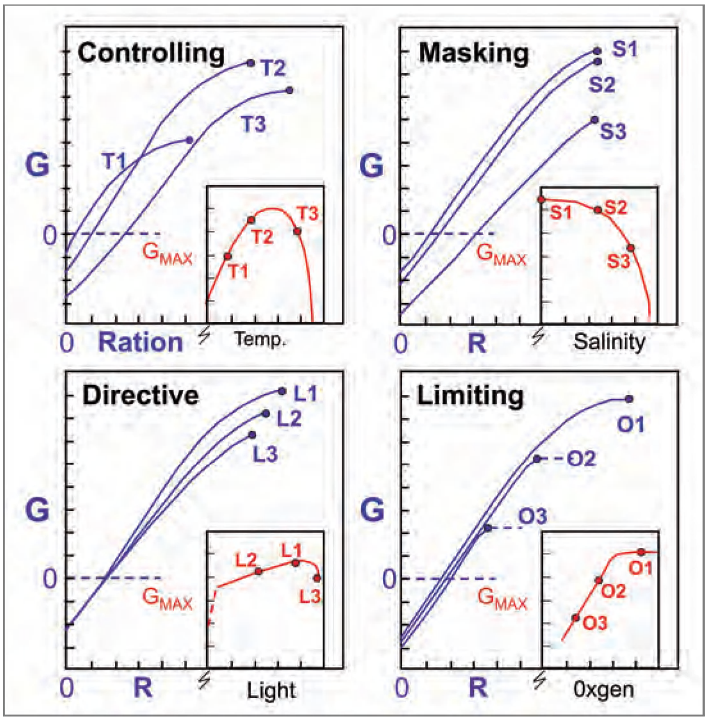


Figure 3.2. Four of the five classes of environmental (abiotic) factors distinguished by Fry (1971) to describe the physiological (organismal level) impacts. The remaining class (lethal factors) is not shown (redrawn from Brett, 1979).

3.4 Temperature tolerance

3.4.1 Whole organism thermal studies

Critical temperature maximum (*CT*MAX), lethal maximum and minimum temperatures (*LT*MAX and *LT*MIN, respectively), and preferred temperature (*PT*) are factors that have been quantified in the laboratory for a variety of organisms, including various species of fish (e.g. Table 4.1 in Tsuchida, 1995). The final *PT* often coincides with optimum temperatures for growth (Brett, 1971; Jobling, 1981), but this depends heavily on the acclimation characteristics of specific populations (e.g. Zakhartsev *et al.*, 2003; Pörtner *et al.*, 2008). In 14 species of marine fish, the relationship between *PT* and *CT*MAX or *LT*MAX was highly significant (Tsuchida, 1995), indicating that temperature tolerance and temperature preference are somehow closely connected. Combining the results from a variety of studies (see Table 4.1 in Tsuchida, 1995) reveals a linear relationship between *PT* and the *LT*MAX (Figure 3.3). Although these studies do not examine underlying physiological mechanisms, their relevance stems from the good correspondence between laboratory-derived measures and limits of thermal distribution in the field (Cech *et al.*, 1990). However, care must be taken not to "oversimplify" estimates of *PT*s gauged from field fish, because these may be modified by other environmental factors. For example, when acclimated to the same temperature, unfed fish (or fish that have been maintained on low-quality food) tend to have lower *PT*s (often by 2–4 °C) than fish that are well fed (Magee *et al.*, 1999; Despatie *et al.*, 2001; Pulgar *et al.*, 2003). This indicates that, from a physiological standpoint, the preferred environment of an individual species will depend on a combination of abiotic and biotic factors, including the availability of suitable prey resources. A second important point is that "realized" temperatures (i.e. the temperatures at which fish are found in the field) may well be suboptimal.

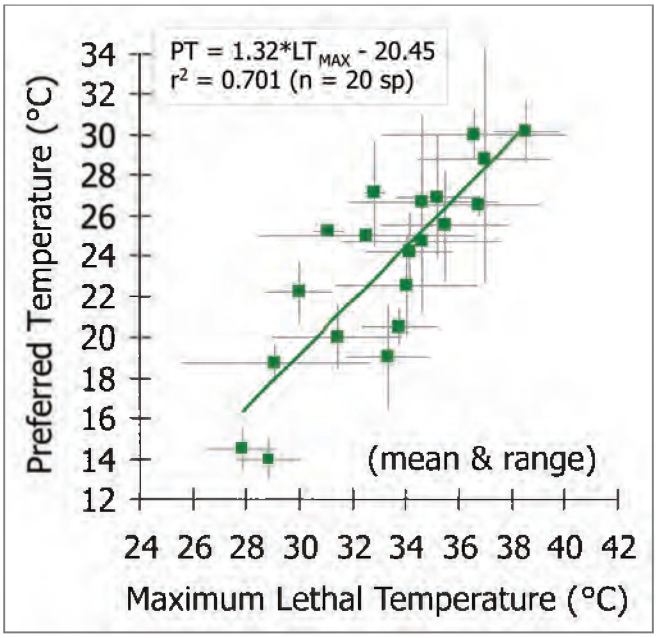


Figure 3.3. Final preferred temperature (*PT*) vs. maximum lethal temperature (*LT*$_{MAX}$) for 20 different species of marine species (compiled from various published data).

There is substantial evidence that the temperature-tolerance range varies with both life stage and body size. Laboratory experiments on growth and development of different life stages suggest that the temperature-tolerance range is often maximal during the juvenile stage (Campos and van der Veer, 2008). It is not clear whether the temperature tolerance of a fish is affected by its body size or its body size is affected by its temperature tolerance. Factors such as fish condition, temperature acclimatization, and duration of exposure all have an impact. In general, there is a lack of information regarding the growth physiology of the late larval/early juvenile stages of many marine fish, which is surprising, given that processes acting during these stages can have important consequences for recruitment strength (Bailey and Houde, 1989; Sogard, 1997).

Under field conditions, the range in stage-specific temperatures at the lower and upper extremes of tolerance is probably the most important factor for the persistence of a species in a given area. In relation to body size, the cold-water tolerance of juvenile Atlantic croaker (*Micropogonias undulates*) was size-dependent, with smaller individuals surviving significantly longer than larger ones (Lankford and Targett, 2001). However, the warm-water tolerance of small tropical reef fish does not seem to be affected by body size. There is a suggestion that the temperatures selected by early life stages (e.g. juveniles) are higher than those selected by older conspecifics (McCauley and Huggins, 1979), Also, the optimal thermal environment in fish (defined as the temperature at which growth rate is maximum) decreases with increasing body size/volume (Kuipers and Fonds, 1978; Fonds *et al.*, 1992; Yamashita *et al.*, 2001), although the strength of this trend will be species-specific.

The shift in optimal temperature with fish size is probably related to two processes.

(i) The supply of oxygen to fuel aerobic metabolism is limited by high temperatures and large body sizes, as discussed for Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*) by Pörtner *et al.* (2001). Additional factors can exacerbate the effects of these size differences. For example, the optimal difference between the sizes of prey and predatory fish was found to be fourfold in Atlantic cod in the North

Sea (Daan *et al.*, 1990). The absence of suitably sized prey places additional costs on foraging, thus reducing the energy available for growth, as observed in both Atlantic cod (Daan, 1973) and turbot (*Psetta maxima*; Wetsteijn, 1981). This means that, apart from differences in the energy costs of finding and handling prey, maximum growth will occur at a lower temperature and the LT_{MAX} will decrease with increasing predator size. The observed relationship between fish size and depth (Heincke's Law; Heincke, 1913) may be a reflection of the decrease in the LT_{MAX} with increasing size.

(ii) In relation to latitude, the greater temperature variation at temperate (mid) latitudes is expected to select for wider physiological tolerance windows in poikilothermic animals, whereas the smaller temperature variation at tropical (low) latitudes is expected to lead to narrower tolerance windows (Dobzhansky, 1950; Stevens, 1989). The climate variability hypothesis of Stevens (1989) formulated such a relationship between climate variation and thermal tolerance windows. A recent comparative study of the lethal thermal limits of temperate and tropical bivalve species support this hypothesis (Compton *et al.*, 2007). However, it is unclear whether or not this hypothesis also applies to fish species. If true, it has far-reaching implications for the extent of geographic ranges and patterns of species richness (Gaston, 2003). Combined analysis of laboratory studies conducted on a variety of marine fish demonstrates a clear change in both the LT_{MAX} (based on 55 species) and the LT_{MIN} (27 species) in relationship with the latitude of the field population (see Figure 3.4). There is a reduction in the difference between the LT_{MAX} and LT_{MIN} that suggests a narrowing of thermal tolerance for populations located at extremely low and extremely high latitudes (i.e. in the tropics and at the poles).

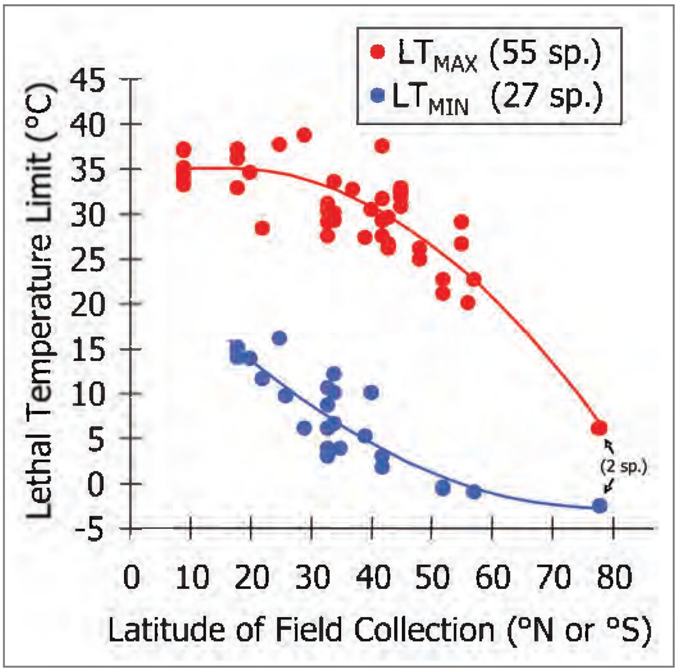


Figure 3.4. Lethal temperature for various fish species vs. latitude of field collection. Both lethal maximum (LT_{MAX}) and lethal minimum (LT_{MIN}) are shown. The regressions suggest a reduction in the differences between LT_{MAX} and LT_{MIN} at extreme latitudes.

3.4.2 Organismal-level bioenergetics

Quantifying the temperature-tolerance range of a species provides an insight into the spatial–temporal window of opportunity for somatic growth and reproduction. Over short time intervals, individuals can survive outside their temperature-tolerance range, but only at the cost of negative growth (i.e. the utilization of energy reserves). Information on the temperature tolerance of a species is based on a number of lines of evidence at the organismal level, including measurements of various energy-budget parameters, e.g. rates of respiration (metabolic scope), as discussed above, as well as rates of food consumption and direct measures of growth rate at different temperatures. In the latter case, tolerable temperatures are simply those where the reaction rate is positive, i.e. the zone of above-zero growth performance (Huey and Kingsolver, 1993).

Within the normal range of temperatures experienced by an organism, coupling the measurements of the rates of maintenance food consumption (C_{MAIN}; i.e. food consumption rates at zero growth) and maximum food consumption (C_{MAX}) at different levels of an environmental factor (most often different temperatures) allows the estimation of the "scope for growth" (SfG; Figure 3.5). Similar to metabolic scope, the SfG is a measure of growth potential that can also be used to provide an estimate of the optimal temperature range (Brett, 1979). In this case, the lower and upper limits of temperature tolerance are established by the outcome of opposing bioenergetic rates of energy loss and energy gain. The general pattern is considered to be an outcome of the steady increase in metabolic energy loss with increasing temperature combined with food ingestion (energy gain), and increases only until an abrupt decline occurs at high temperatures.

Based on the balanced energy budget (Equation (2)), potential growth rate therefore increases steadily with increasing temperature until it reaches a maximum, and is followed by a sharply defined upper boundary. Unfortunately, the physiological literature is lacking in such "bioenergetically based" SfG estimates at different temperatures for many commercially important fish species. Furthermore, possible ontogenetic changes in the effects of temperature on the SfG of most commercially exploited marine fish and shellfish species remain largely unexplored. However, the bioenergetic costs and trade-offs at different temperatures are most clearly demonstrated when growth rate is measured for fish maintained at a variety of different temperatures, as reported by Fonds *et al.* (1992) for plaice (*Pleuronectes platessa*) and European flounder (*Platichthys flesus*).

Measurements of O_2 consumption rates at different acclimation temperatures have also been used to elucidate temperature optima and temperature sensitivity in fish. Optimal temperatures have been determined by establishing the thermal range in which the thermal quotient (Q_{10}; a measure of the change in reaction rates between temperatures differing by 10°C) for O_2 consumption rate starts to decrease with increasing acclimation temperature (Kita *et al.*, 1996). Although the Q_{10} has been widely utilized, the accuracy and the variance of this factor have been questioned by some (e.g. Willmer *et al.*, 2000). Other researchers have chosen to use the Arrhenius relationship, based on the Van't Hoff equation, which usually provides a good explanation for the variation in temperature dependence of metabolic rates across species (Gillooly *et al.*, 2001).

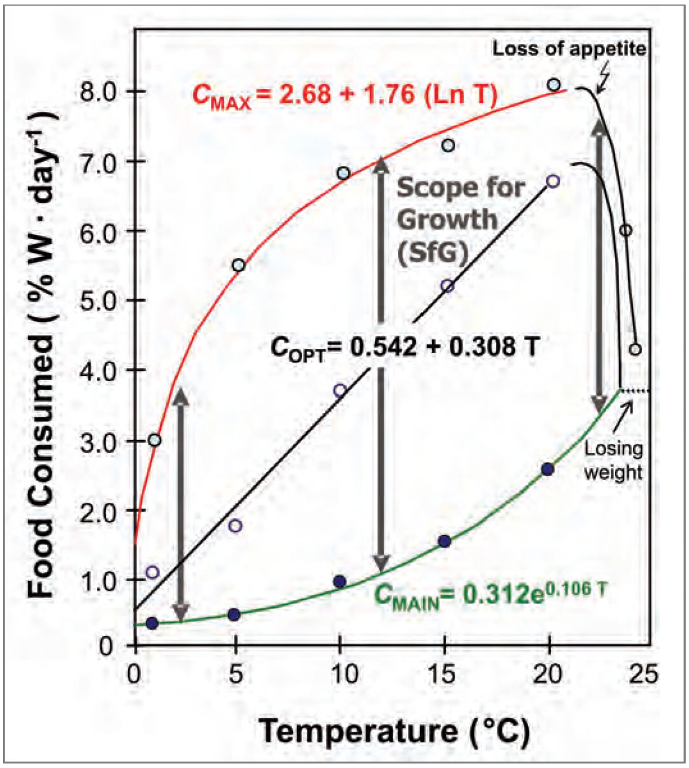


Figure 3.5. Scope for growth (SfG) of sockeye salmon (*Oncorhynchus nerka*) at different temperatures (grey arrows), as determined from measurements of maximal (CMAX) and maintenance (CMAIN, zero growth) rates of feeding at different temperatures. The optimal rations (COPT; i.e. the ration providing the best growth efficiency) are also shown (redrawn from Brett, 1979).

3.4.3 Cellular-level physiological responses

At the cellular level, the physiological underpinning of temperature optima and tolerances has been explained in a variety of ectothermic animals, including fish, using the concept of oxygen-limited thermal tolerance (Pörtner *et al.*, 2001; Pörtner and Knust, 2007; Figure 3.6). This concept provides a physiological basis for the interpretation of observed differences in life-history characteristics among conspecifics inhabiting different environments and for the estimation of the potential impacts of climate variability and/or change on specific populations. According to this model, an optimal range of oxygen availability to tissues characterizes the temperature window of optimum aerobic performance and scope for aerobic activity. Thermal tolerance becomes progressively time-limited once aerobic scope decreases within the range of pejus (pejus = getting worse) temperatures (T_P) that occurs prior to the onset of anaerobic metabolism. Short-term thermal tolerance can be improved by biochemical synthesis of antioxidative defence and heat-shock proteins. At thermal extremes, there is a transition to anaerobic metabolism and protein denaturation. Importantly, the points of transition from optimum to pejus temperature ranges demark the temperature range of maximum aerobic activity and very probably characterize long-term environmental temperature limits or the ecological tolerance range. The potential effects of developmental stage, specifically the pattern of response of the embryonic stages and exogenously feeding larval stages of fish, have not been fully explored, but differences are expected because of the vast changes in the structures responsible for gas exchange that take place during early ontogeny.

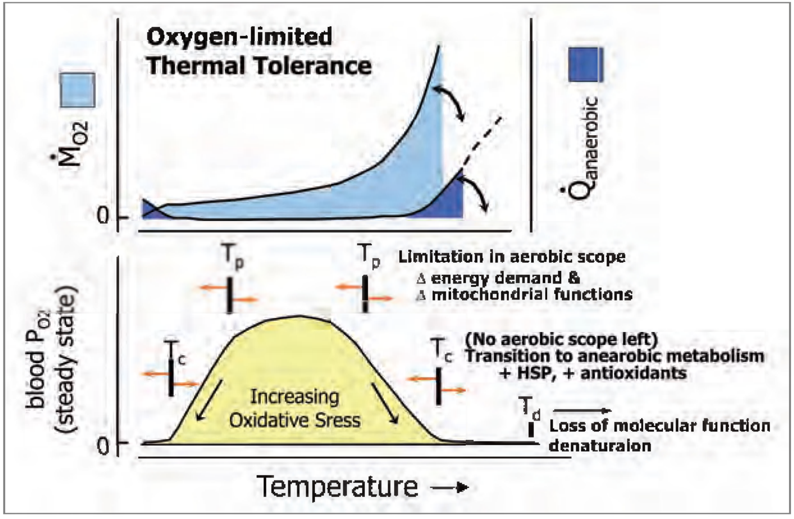


Figure 3.6. Model of oxygen-limited thermal tolerance where pejus temperature (T_p) and critical temperature (T_c) are set by the capability of oxygen supply to meet tissue oxygen demand according to ventilatory and circulatory performance. Heat-shock proteins (HSP) and antioxidative defence may increase the tolerance range at high (and low) thermal extremes by shifting denaturation temperatures (T_d), but are not thought to affect pejus temperatures. (See Figure 5 in Pörtner *et al.*, 2001)

3.5 Variability and plasticity in physiological responses/observed trends

It should be kept in mind that there is considerable variability in physiological tolerances and responses between species, within species (between populations), and among individuals within the same population. In addition to an acute response to temperature, an individual can demonstrate (i) a chronic response, namely acclimatization; and (ii) an evolutionary response, namely adaptation, which is measured in time-scales of generations and ultimately leads to a modification of the physiological performance and response of an organism. As an example of population differences, Svåsand *et al.* (1996) observed significantly higher growth rates and lower condition factors for Norwegian coastal cod compared with Arcto-Norwegian cod when fish from the two populations were reared in the same tank. Latitudinal changes in the thermal tolerance of populations of Atlantic cod, eelpout, and several species of invertebrates have been well documented (Pörtner *et al.*, 2001, 2006, 2008). In terms of growth rate, the phenomenon of countergradient variation (defined by Levins, 1969; reviewed by Conover and Schultz, 1995) provides an example of the plasticity of a species' physiology in response to long-term environmental conditions. The extent to which this phenomenon corresponds to irreversible non-genetic adaptation during early life stages (Kinne, 1962) is not clear.

Common-environment experiments have revealed both countergradient variation in growth rate (maximum growth rates found within and among species at higher latitudes) and a shift to lower temperatures in growth-reaction norms (dome-shaped relationships between growth and temperature) of northern species, indicating adaptation to temperature at the interspecific level (Yamahira and Conover, 2002). Interestingly, most evidence for countergradient variation in growth rate in fish comes from studies conducted on early juvenile life stages (e.g. Yamahira and Takeshi, 2008), which appears logical, given the importance to overall fitness of growth rate during the first year of life (i.e. in terms of overwinter survival at higher latitudes). Interestingly, there appear to be predation-related trade-offs associated with increased growth rates in northern conspecifics. This indicates that, to some extent, the capacity for physiological adaptation to meet growth requirements in changing abiotic conditions may be regulated by both bottom–up (prey supply) and top–down (predation risk) factors.

Plasticity in responses to prevailing environmental conditions exists not only among populations but also among individuals within specific populations. For example, studies conducted on fish species of a variety of different families (Salmonidae, Cyprinidae, Gadidae) suggest that relationships exist between inter-individual differences in rates of metabolism (respiratory and exercise physiology) and somatic growth (Peck *et al.*, 2004; Lankin *et al.*, 2008; and references therein). These studies indicate that impacts of climate change and variability will probably affect the growth physiology and survival of individuals from different populations (and even individuals within the same population) in different ways. Populations from mid-latitudes would be expected to express the greatest plasticity in physiological response compared with populations inhabiting environments that demonstrate less thermal variability, where, for example, stenothermal characteristics may be expressed. The presence of inter-individual variability in growth energetics may be a key element in dictating the adaptive capacity of populations to climate-driven changes in environmental factors.

Through its direct effect on growth rate, temperature also affects other life-history characteristics. For example, many organisms tend to grow more slowly in colder environments but, as adults, are larger than their conspecifics in warmer waters. This widespread phenomenon has been explained using both "Bergmann's Rule" (Bergmann, 1847), which describes the relationship between environmental temperature and body size in endotherms, and the "temperature–size rule", which describes laboratory-derived reaction norms of temperature and body size (e.g. Angilletta and Dunham, 2003). Theoretical considerations of decreasing growth efficiency with increasing temperature were thought to explain these trends in body size and temperature. However, this assertion was not supported empirically and alternative theories have been proposed, for example, that differences reflect changes in overall average food levels (Kooijman, 2000), or that temperature may impose constraints on growth that only arise late during ontogeny (see Angilletta *et al.*, 2004).

The latter theory is supported by the fact that the thermal optima for growth efficiency and growth rate decrease as individuals grow (see Angilletta and Dunham, 2003). For example, the growth response of Atlantic cod to a standard increase in water temperature changes markedly with body size (Figure 3.7). This underscores an important point, namely that physiologically "optimal" environments (as well as tolerances) will probably change during ontogeny. This indicates that understanding the impacts of climate variability on the vital rates of key species will require assessments of a variety of life stages (see Pörtner and Farrell, 2008). Ontogenetic changes in optimum temperature have been observed in a number of fish species, including Atlantic cod, wolffish (*Anarhichas lupus*), common sole (*Solea solea*), and turbot (*Scophthalmus maximus*; Irvin, 1974; McCauley and Huggins, 1979; Cuenco *et al.*, 1985; Imsland *et al.*, 1996, 2005, 2006).

Interestingly, for exploited fish populations coping with climate change (general warming), a strong selection for smaller adult body size may result from the combined effects of two simultaneously acting pressures. The first is a physiologically based decrease in adult body size, compared with conspecifics inhabiting colder waters, often observed for individuals within populations inhabiting areas with higher water temperatures (Pörtner *et al.*, 2001; Angilletta *et al.*, 2004). The second is an exploitation-based reduction in size-at-first-maturity, which has been commonly noted in many fish species (e.g. Jørgensen, 1990; Rijnsdorp, 1993b), and is caused by an evolutionary change in the reaction norm (see review in Dieckman and Heino, 2007). Such a shift results in a decrease in the mean weight-at-age of adult fish.

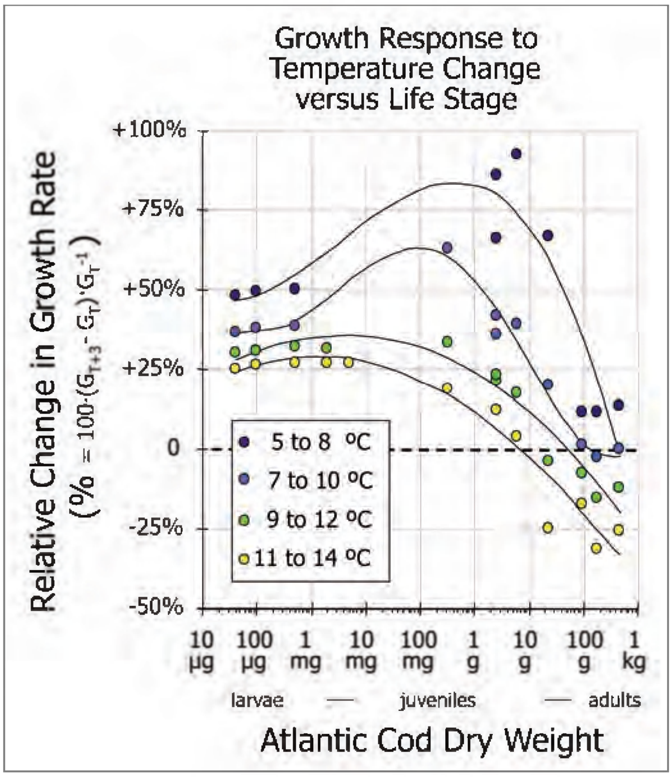


Figure 3.7. Predicted changes in the growth rate of Atlantic cod juveniles and adults after a 3°C increase in temperature from 5, 7, 9, and 11°C. The relationship depicted here (Peck, unpublished) is taken from a combined analysis of data presented by Otterlei *et al.* (1999) and Björnsson *et al.* (2001).

3.6 Physiologically based models and estimating climate impacts

3.6.1 Mechanistic individual-based models

In order to estimate the impacts of direct and indirect effects of climate change on the vital rates of marine fish and shellfish, a number of the currently employed modelling approaches are based on physiological (bioenergetics) principles. Although most balanced bioenergetics budgets have been applied to juvenile and adult stages of fish, recent mechanistic IBMs for larval fish include temperature-dependent growth and foraging subroutines based on balanced energy budgets (e.g. Lough *et al.*, 2005; Peck and Daewel, 2007; Kristiansen *et al.*, 2009). These models have been constructed using time-steps in the order of 1–2 h to 1 d and, therefore, are more dynamic (e.g. individuals can lose and gain mass in a more realistic manner). As vital rates of organisms are influenced not only by the direct effects of climate (e.g. on temperature and advection via water currents), models predicting climate impacts on local prey fields have also been developed, some of which have been coupled to IBMs (a short review is provided by Daewel, 2008). Such "coupled models" are powerful tools for assessing the theoretical "bottom–up" impacts of differences in climate forcing on key species from a physiological standpoint. In future, the utilization of IBMs (for eggs and larvae), coupled with bioenergetics models (for juveniles and adults), will provide the best opportunity to examine and compare temporally and spatially resolved environmental impacts that encompass the physiology of all life stages of the same species.

3.6.2 Dynamic energy budgets

Dynamic energy budgets (DEBs) offer another framework (Kooijman, 1993, 2000; Nisbet *et al.*, 2000) for assessing the physiological consequences of climate variability and change. In contrast to balanced energy budgets, DEBs take into account the "history" of the fish by incorporating values for stored energy reserves as an independent energy source and sink. The DEB approach quantifies rates of energy flow through an individual and the allocation of energy to growth and reproduction in relation to environmental conditions and food intake. Only seven parameters are needed to describe fully the energy flow through an organism. The elegance of DEB models is that a common model structure is employed, which allows interspecific comparisons to be made simply by comparing parameter estimates. The DEB model approach has been successfully applied to the analysis of the impact of toxic components in mussels (van Haren and Kooijman, 1993), the comparison of life-history strategies of marine flatfish species (van der Veer *et al.*, 2001), and simulations of growth and reproduction in oysters (Bacher and Gangnery, 2006; Pouvreau *et al.*, 2006).

According to the DEB theory, food conditions determine the maximum size that a species can obtain and, therefore, differences among populations reflect differences in the overall feeding environment. Prevailing temperature conditions have no influence on maximum size, but only dictate the time required to achieve that size (Figure 3.8). Temperature sensitivity is species-specific and, in DEB models, does not demonstrate a pattern in relation to the size of organisms. It is not clear whether patterns of temperature sensitivity exist among primary, secondary, and tertiary producers.

However, an analysis of DEB parameters for different types of species indicated a relationship between energy flow and cell complexity, specifically an increase in maintenance costs and food requirements with increasing cell complexity. For instance in the Wadden Sea, the maintenance costs of flatfish species are much higher than those of various bivalve species (van der Veer *et al.*, 2001, 2006). In terms of the effects of body size on energy flow, DEB parameters illustrate the trade-off between body size and energy reserves. Organisms (or species) with a small body volume (or body size) have low energy requirements and low energy reserves to survive periods of starvation, whereas organisms (or species) with a larger body volume (or body size) have higher energy requirements, but also have higher energy reserves. This is probably reflected in the increasing trends in body size with latitude. Ongoing efforts to utilize DEBs more extensively on fish species include a recent comparison of growth predictions obtained from DEBs and traditional "static" energy budgets within variable environments (van der Veer *et al.*, 2009) and a thorough comparison of DEB parameter estimates among various species (van der Veer *et al.*, In press).

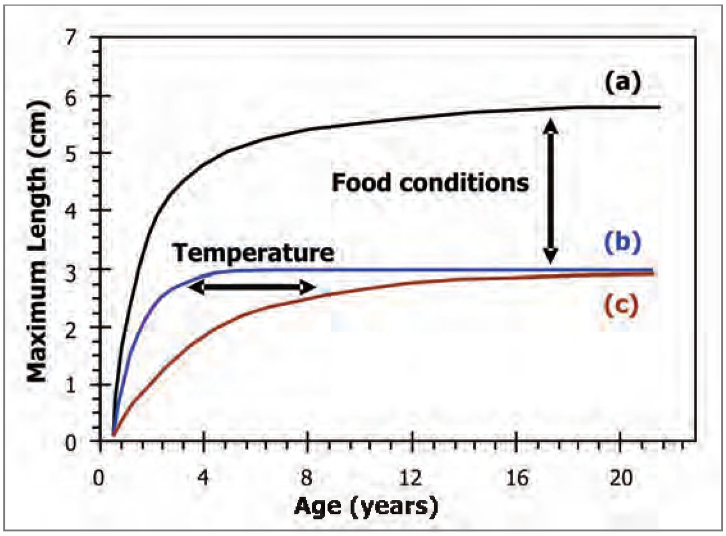


Figure 3.8. Growth curves resulting from different food and temperature conditions, according to the DEB theory: (a) high temperature and high food conditions; (b) low temperature and high food conditions; and (c) high temperature and low food conditions (from Kooijman, 2000).

3.7 Physiological responses to interacting factors

This section has focused on the effects of temperature because it is a key controlling factor of various physiological processes. However, climate change will affect a variety of environmental factors that will act synergistically to affect the physiology of individuals and dictate the response of populations and stocks of a species.

The main synergistic factors include salinity, oxygen saturation, and pH (acidification). Other factors may include levels of turbulence and light (turbidity). The physiological impacts of these factors are species specific. This is clear from studies examining the growth response of various marine fish to different levels of single factors, such as salinity (e.g. Boeuf and Payan, 2001) and hypoxia (Thetmeyer *et al.*, 1999; Pilchavant *et al.*, 2001).

Of these factors, ocean acidification will undoubtedly play a major role. Although the survival of sensitive (early) marine fish life stages to decreased pH has been examined (e.g. Parra and Yúfera, 2002), research on the growth response of fish to realistic levels of CO_2 (and its impact on pH) is still largely lacking (see review by Ishimatsu *et al.*, 2008). Moreover, recent results suggest that responses of fish to ocean acidification may be unexpected; for example, a recent study indicates sublethal impacts on olfaction and behaviour affecting migration–settlement success in a coral reef fish (e.g. Munday *et al.*, 2009).

In short, efforts to predict climate impacts on marine fish and shellfish using physiological modelling (or purely correlative approaches) will be hampered by a less than thorough understanding of the synergistic impacts of multiple interacting factors. In this respect, there is an urgent need for measurements of growth energetics and/or threshold tolerance levels of key life stages within experiments that utilize replicated, multifactorial treatment groups (e.g. temperature × oxygen × pH).

4 Spatially explicit, three-dimensional, physical–biological modelling

Corinna Schrum

4.1 Introduction

This section reviews the current state-of-the-art in three-dimensional, spatially explicit ecosystem modelling of lower trophic levels (phytoplankton and zooplankton) coupled to the physical processes (hydrodynamics). Various approaches used to build three-dimensional hydrodynamic (physical) models are reviewed and a critique is provided of three-dimensional, spatially explicit ecosystem or NPZD (nutrient–phytoplankton–zooplankton–detritus) models. Efforts to evaluate the performance of three-dimensional, physical, and lower trophic-level models are reviewed, including the ability of models to capture long-term environmental variability. Within coupled three-dimensional ecosystem models, current issues relating to the lack of life-cycle closure and the dynamic coupling of feedbacks between biology and physics and between trophic levels (including larval and later life stages of zooplanktivorous fish) are also highlighted.

4.2 Background

Climate-driven processes act as bottom–up controls on the dynamics of marine ecosystems, and marine systems are subject to variability in these processes at different spatial and temporal scales. On interannual and decadal time-scales, climate is a strong driver, controlling environmental conditions through both direct and indirect pathways. Direct pathways include, for example, changes in temperature, which influence rates of growth and mortality, and changes in light conditions, which influence photosynthesis. Indirect pathways include advective and turbulent nutrient and biomass fluxes. The interplay of these processes is complex and not sufficiently resolved by statistical approaches. Hence, the development of deterministic models that are able to resolve climatic impacts by integrating different processes and their combined impact is critical to both the projection of future ecosystem states and the management of ecosystem-based resources.

Although realistic models and their results are complex, they are always a simplified approximation of reality; hence, their projections are uncertain. Uncertainties arise because of the assumptions made, processes neglected, unknown or incomplete understanding of processes, unresolved subscale processes, and uncertainties in numerical schemes and boundary conditions. Therefore, the application of different models is recommended (e.g. an ensemble approach) in order to assess the possible ranges of uncertainties in projections. The validity of the models used needs to be investigated and discussed, and uncertainties arising from the schemes and parameterization used need to be assessed.

The field of physical and physical–biological modelling is very wide and covers a variety of different model approaches. Approaches range from 0-day simplified empirical or statistical models to very complex, highly resolved, detailed or small-scale process models to complex-process, three-dimensional, globally integrated, biogeochemical models. A basic introduction to the numerical approaches and concepts behind the state-of-the-art models used to resolve early life stages of fish was presented by North *et al.* (2009) and aimed at early career modellers and lay-readers. This manual includes an extensive discussion of particle-tracking models and parameterizations utilized within individual-based models (IBMs) of larval fish.

However, other topics, such as hydrodynamic models, NPZD models, and the links between IBMs and NPZD models, were covered only superficially. This section is intended to fill this gap, address the state-of-the-art, and emphasize the uncertainties that limit a model's predictive capacity with respect to the following topics:

- hydrodynamics;
- lower trophic-level dynamics;
- current long-term simulation on regional scales;
- higher trophic-level dynamics and closure of ecosystems;
- processes not currently addressed.

4.3 Physics

The essential requirement for spatially resolved modelling of marine ecosystems in a varying climate is a hydrodynamic core capable of simulating spatial and temporal variability in the abiotic environment. Previously established schools in hydrodynamic modelling differ in their choice of vertical coordinates (particularly geopotential vs. isopycnal vs. terrain-following) and finite-element vs. finite-difference methods. Although unstructured meshes and finite elements represent the next generation of ocean models (e.g. Pain *et al*., 2005), the most robust and mature hydrodynamic models are still based on structured-grid, finite-difference modelling. This last approach is also the most common in current ocean global-climate modelling, e.g. HAMSOM (HAMburg Shelf Ocean Model; Schrum and Backhaus, 1999); POLCOMS (Proudman Oceanographic Laboratory Community Model System; Holt and James, 2001); ROMS (Regional Ocean Modelling System; Shchepetkin and McWilliams, 2005). The long history of these developments, and the efforts spent in the validation and optimization of existing model systems, allows for robust, stable, and efficient simulations, which are critically important attributes for high-quality, long-term simulations. The choice of grid (B-grid vs. C-grid), and the inclusion of free-surface, vertical-mixing schemes and boundary-layer-resolving modelling, are additional differences among hydrodynamic models.

The different concepts and numerical methods used in hydrodynamic modelling have their advantages and disadvantages (see the discussion in Haidvogel and Beckmann, 1999). A great amount of literature exists on the shortcomings of the particular approaches for specific areas. Shortcomings are interrelated and include, for example, internal-pressure, gradient, and truncation errors in sigma or terrain-following coordinate models (e.g. Berntsen and Thiem, 2007; Allen *et al*., 2003), and the weak representation of bottom-boundary currents in geopotential or z-level models (e.g. Beckmann and Doescher, 1997; Doescher and Beckmann, 2000), or of intersecting isopycnical layers with the sea surface. Depending on the particular application and region, these errors may produce deviations in transports that are in the order of magnitude of typical mean ocean currents [$O(10^{-1}\ \mathrm{m\ s^{-1}})$]. Berntsen and Thiem (2007) demonstrated that even the same model (in this case, the ROMS model), when used with different numerical schemes (all of them implemented in the standard coding), can produce deviations in water transport that are in the order of the mean signal and can even lead to reversal of the original transport signal (Figure 4.1).

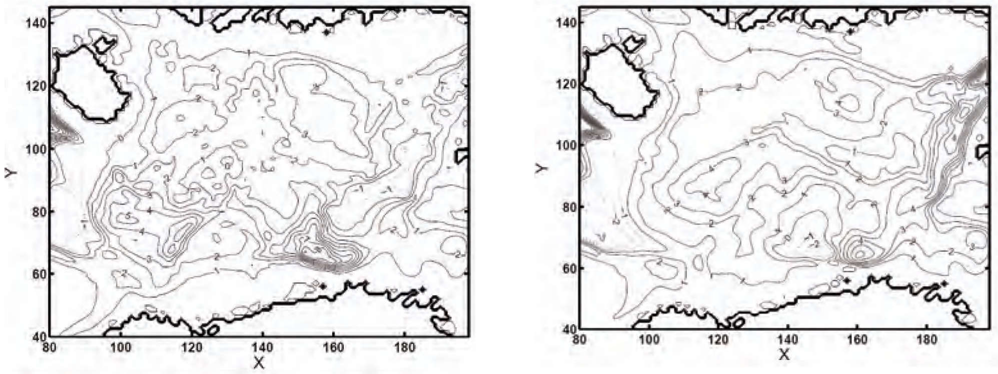


Figure 4.1. Modelled stream function in the Norwegian Sea using the ROMS model with implementation of two different numerical algorithms. (Figure from Berntsen and Thiem, 2007.)

Model intercomparisons, such as those performed for the North Sea in the frame of the EU project NOMADS2 (NOrth sea Model ADvection Study 2; Delhez *et al.*, 2004), have highlighted the problem and provided an impression of the range of results that can be achieved using different model approaches for hindcasting. The example in Figure 4.2 displays the modelled temperature differences between the surface layer and the rest of the water column. Here, differences of more than 5 °C in mean area temperature occur among the different models. Similarly, the different models demonstrate large deviations in volume transport across a section in the northern North Sea. Here, the range of deviations of the average transports is on the order of magnitude of 2, and even the direction of net flow (inflow or outflow) seems to deviate.

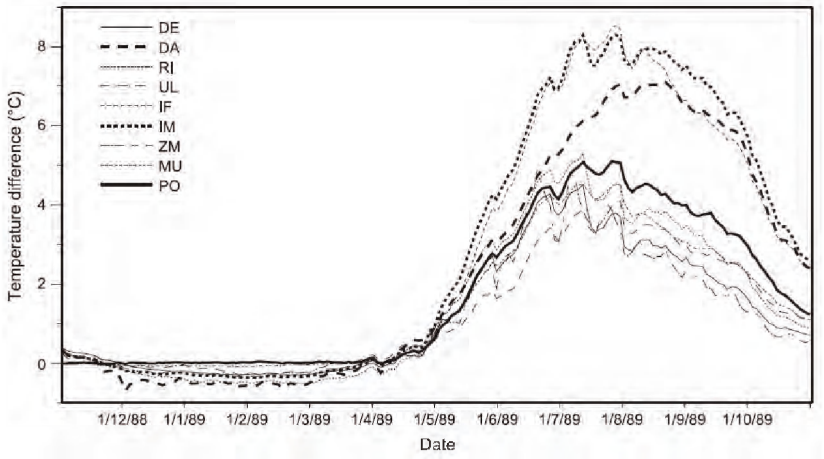


Figure 4.2. Evolution of temperature difference between the upper 20 m and the rest of the water column in nine different models. Comparison performed in the NOMADS2 project. (Figure from Delhez *et al.*, 2004.)

The problems and identified uncertainties are highly relevant when modelled time-series are used to study ecosystem dynamics and when temperature, salinity, or transports are used as input data for biological models. It is therefore essential that the physical models used in ecosystem research are validated in detail. These validations need to be comprehensive, addressing different time- and spatial-scales, and involving a large number of variables. Specific outcomes from these validation exercises are quantitative measures of model performance in the simulation of climatic-induced variability and estimation of model bias for the climatic mean result. Such detailed validations have currently been performed and published for only very few models. The most extensive uncertainty analysis on interannual time-scales has been performed for ECOSMO (ECOSystem MOdel; Janssen, 2002; Janssen *et al.*, 2001; Figure 4.3). Uncertainty analysis for model physics utilizing a two-year simulation has been performed for POLCOMS-3d ERSEM (European Regional Seas Ecosystem Model, Physics; Holt *et al.*, 2005; see Figure 4.4). Broader efforts to validate ecosystem model parameters are still rare, and most material has been published for the POLCOMS-3 d ERSEM (Lewis *et al.*, 2006; Allen *et al.*, 2007a; Figure 4.5), with validations limited to only a two-year simulation. Hence, even for this model, it is yet unclear how well it reproduces interannual variability.

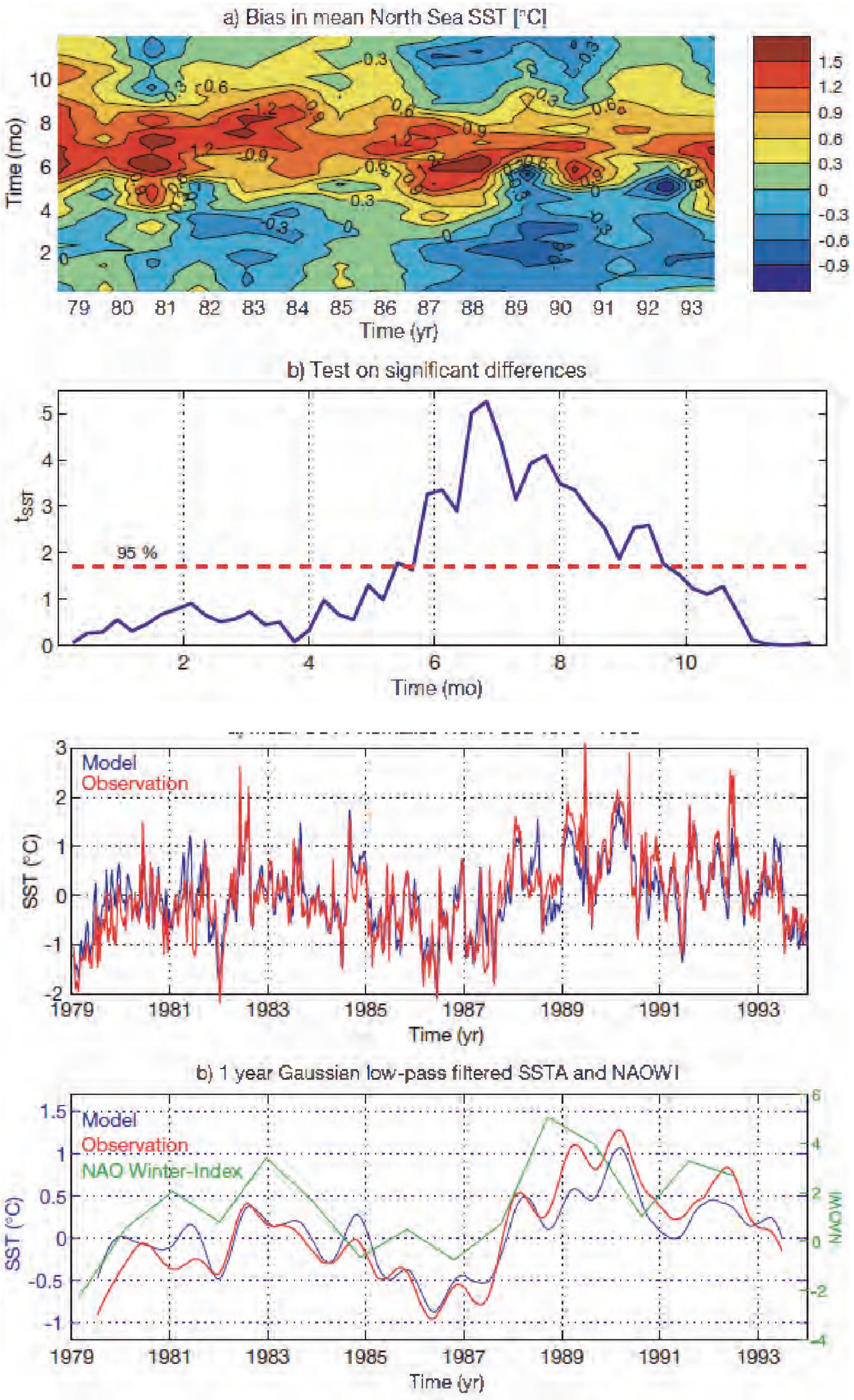


Figure 4.3. Temperature bias (left) and comparison of modelled and observed SST anomalies (right) for the ECOSMO model. (From Janssen *et al.*, 2001.)

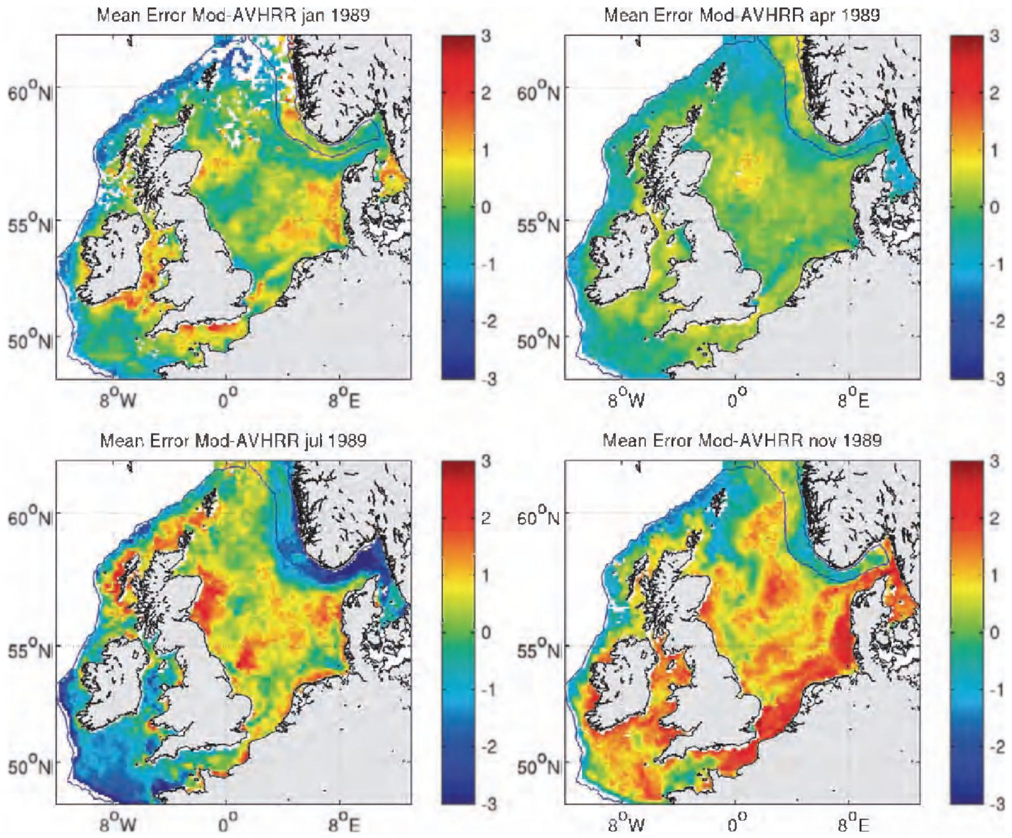


Figure 4.4. Monthly mean SST error (model AVHRR (Advanced Very High Resolution Radiometer)) in °C. (Figure from Holt *et al.*, 2005.)

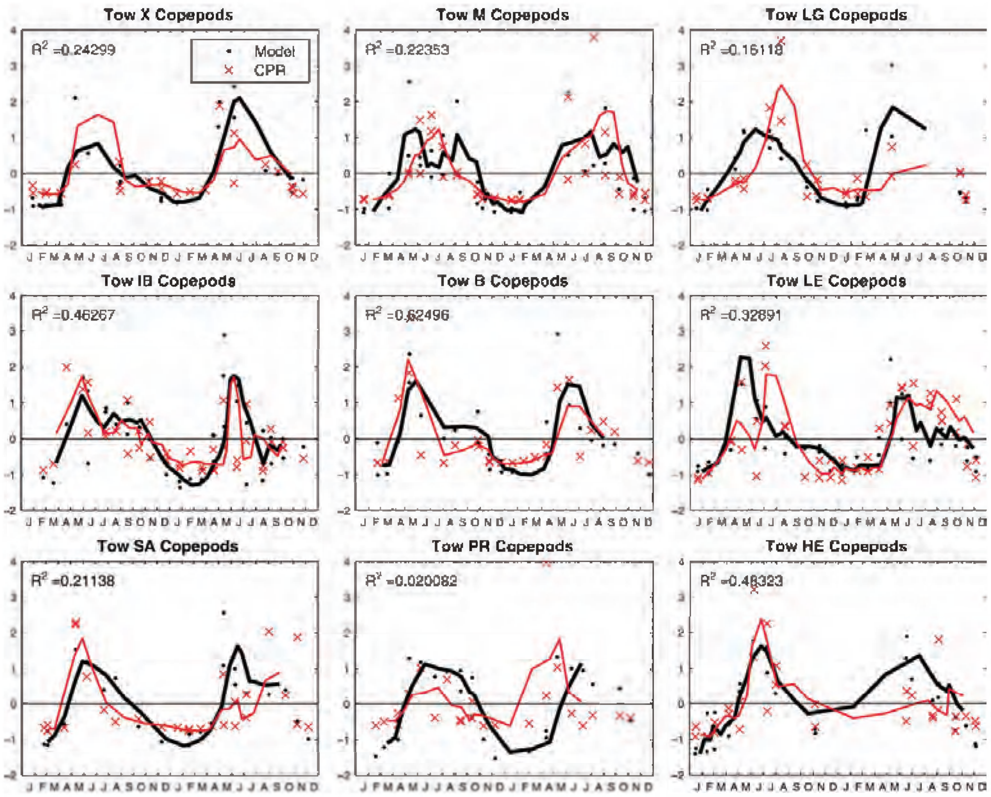


Figure 4.5. Standardized CPR copepods vs. omnivorous mesozooplankton model data for individual tow routes with three-day running mean (solid line). Black = model data; red = CPR data; dots = individual model tow points; crosses = individual CPR tow points. (Figure from Lewis *et al.*, 2006.)

Furthermore, the identified deviations and uncertainties from hydrodynamic modelling, which are highly relevant to coupled, physical–biological modelling using state-of-the-art NPZD models, has been highlighted by Skogen and Moll (2005).

4.4 NPZD concepts and modules

Different regional model systems for coastal ocean and shelf waters have evolved over the years, and a variety are currently implemented and coupled with Eulerian lower trophic-level ecosystem modules. Full referencing is impossible, so we will concentrate on model developments, particularly the modelling of long-term (and climatic) variability of three-dimensional hydrodynamics and their impact on ecosystem dynamics. Each of the following state-of-the-art models employs different solution strategies.

North Sea. Models include NORWECOM/POM (NORWegian ECOlogical Model/Princeton Ocean Model; Skogen *et al.*, 1995, 2004); ECOSMO (Schrum *et al.*, 2003, 2006a, 2006b); ROMS-NORWECOM (only offline coupled, see Svendsen *et al.*, 2007); ECOHAM v3 (ECOsystem model HAMburg, version 3; Pätsch and Kühn, 2008); and POLCOMS-3d ERSEM (Allen *et al.*, 2001).

Baltic Sea. The major model systems used are: ERGOM (Baltic Sea Ecosystem Model; Neumann, 2000); ECOSMO (see above); and the RCO-SCOBI (Rossby Centre Ocean – Swedish Coastal and Ocean BIogeochemical model; M. Meier, pers. comm.; physics only, e.g. Meier *et al.*, 2003). Recently, the Danish Meteorological Institute (DMI) has implemented a model system for the North and Baltic seas based on the operational model of the Bundesamt für Seeschiffahrt und Hydrographie, Germany (http://www.bsh.de). Long-term simulations are planned but have not yet been performed.

Barents Sea. Similar systems are applied: SINTEF (Stiftelsen for industriell og teknisk forskning; Slagstad and McClimans, 2005; Wassmann *et al.*, 2006); ECOSMO (physics only; Harms *et al.*, 2005; Schrum *et al.*, 2006a); and ROMS-NORWECOM (offline coupled, as described by Svendsen *et al.*, 2007).

Bay of Biscay and English Channel. The hydrodynamic MARS-3D model has been developed at Ifremer and used for long-term integrations (Huret *et al.*, 2007; Lazure and Dumas, 2008). MARS-3D is currently coupled to an ecosystem module to be used for long-term simulations (ECO-MARS-3D).

4.5 Long-term simulations

Only a few examples of multidecadal, coastal-ocean hindcasts have been published. These include: the 40-year (1960–1999) simulations of the Irish Sea with POLCOMS (Young and Holt, 2007); the 1958–2004 simulations of the North and Baltic seas conducted with HAMSOM (ECOSMO hydrodynamic core, see Schrum *et al.*, 2003); the recently performed hindcasts conducted with ROMS/POM-NORWECOM (Skogen *et al.*, 2007); and the RCO model simulations for the Baltic Sea (Meier *et al.*, 2003).

Coupled physical–biological simulations are rare and include the 25-year simulation with ECOSMO (available online at ftp://ftp.uib.no/pub/gfi/corinna/RECLAIM/) in the North and Baltic seas, and the offline simulation with ROMS (Svendsen *et al.*, 2007). A table summarizing the state-of-the-art for most coupled (physical–biological) and uncoupled (physics only) long-term runs performed in the coastal waters of the Northeast Atlantic and the North, Baltic, and Barents seas, including published and unpublished work, was published in the interim status report of the European

COastal-shelf sea OPerational observing and forecasting system (EU-IP ECOOP, 2007; Table 4.1).

Table 4.1. Compilation of currently available long-term, coupled, physical–biological and purely hydrodynamic model runs (undisturbed climate mode) in major key institutions in Europe (IMR = Institute of Marine Research, Bergen, Norway; UiB-GFI = University of Bergen, Geophysical Institute, Bergen, Norway; POL/PML = Proudman Oceanographic Laboratory/ Plymouth Marine Laboratory, UK; IOW = Institute for Baltic Sea Research, Warnemünde, Germany; SMHI = Swedish Meteorological Hydrological Institute, Norrköping, Sweden; Ifremer, France.) Table taken from ECOOP interim status report (EU-IP ECOOP, 2007) and modified to exclude unavailable runs and include the Bay of Biscay.

LONG-TERM SIMULATIONS, AUGUST 2007	BEGIN	END	RESPONSIBLE PERSON
IMR: Global ROMS (physics, 20 km res.)	1958	2005	P. Budgell
IMR: North Atlantic/Arctic NORWECOM/ROMS (prim. prod. 20 km res.)	1981	2006	M. Skogen
IMR: North Sea+ POM (physics, 10 km res.)	1985	2005	M. Skogen
IMR: North Sea+ NORWECOM/POM (prim. prod. 10 km. res.)	1985	2005	M. Skogen
IMR: North Sea, ROMS future climate (test)	2070	2100	B. Ådlandsvik
UiB-GFI: ECOSMO North Sea/Baltic (physics, 10 km)	1958	2004	C. Schrum
UiB-GFI: ECOSMO North Sea/Baltic (physics, 10 km)	1979	1993	C. Schrum
UiB-GFI: ECOSMO North Sea/Baltic (physics, prim. prod., sec. prod., 10 km)	1980	2004	C. Schrum
UiB-GFI: ECOSMO Barents Sea (physics, 7 km)	1958	1997	C. Schrum
POL: NE Atlantic (physics, 12 km)	1960	2005	R. Proctor/I. Allan
POL/PML: NE Atlantic (physics + ERSEM, 12 km)	1988	2005	R. Proctor/I. Allan
POL/PML: NW Shelf (physics + ERSEM, 7 km)	1988	2000	R. Proctor/I. Allan
IOW: ERGOM Baltic Sea (coupled physical–biological, 3–9 nautical miles)	1960	2000*	T. Neumann
SMHI: RCO-SCOBI, Baltic Sea (coupled physical–biological, 6 nautical miles)	1902	1998	Kari Eilola
SMHI: RCO-SCOBI, Baltic Sea (coupled physical–biological, 6 nautical miles); climate change scenarios	2071	2100	Kari Eilola
SMHI: RCO-SCOBI, Baltic Sea (coupled physical–biological, 6 nautical miles); nutrient reduction scenario	1902	1998	Kari Eilola
SMHI: RCO-SCOBI, Baltic Sea (coupled physical–biological, 6 nautical miles); nutrient reduction scenario	2071	2100	Kari Eilola
Ifremer: MARS-3D, Bay of Biscay, hydrodynamics only	1990	2007	Martin Huret

*** partly extensions to 2003.**

4.6 Closure, higher trophic variability, uncertainties, and limitations

The three-dimensional ecosystem modules currently being used to study marine ecosystems and related environments are still quite simple. Typically, they resolve the ecosystem under consideration into as many as three nutrient cycles and one or two functional groups of phyto- and zooplankton. Additionally, oxygen and one or more detritus class(es) are considered. Models of intermediate complexity, such as ERGOM (Baltic Sea Ecosystem Model; Neumann, 2000), SINMOD (SINtef ocean MODel; Slagstad and McClimans, 2005; Wassmann *et al.*, 2006), and ECOSMO (Schrum *et al.*, 2006a), are closed by prescribing zooplankton mortality, whereas models containing only one trophic level (phytoplankton) prescribe mortality caused by zooplankton grazing. Models operating in three dimensions that include a third trophic level (e.g. planktivorous fish) are very rare. One example is ERSEM, which has been applied within the North Sea and British coastal waters (POLCOMS-ERSEM; Allen *et al.*, 2001; Blackford *et al.*, 2004; Holt *et al.*, 2005; Allen *et al.*, 2007a, 2007b). A second example is NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) and NEMURO.FISH (NEMURO For Including Saury and Herring; see Kishi *et al.*, 2007a, 2007b).

More complex, higher trophic-level models simulating end-to-end ecosystem dynamics, such as the EcoSim ecological/optical model (Bissett *et al.*, 1999a, 1999b, 2004), have been linked only offline to the spatially integrated output of three-dimensional hydrodynamic models (Harvey *et al.*, 2003; Christensen and Walters, 2004), and little has been done to incorporate these within spatial-explicit approaches. Consensus on how to build a more complex system has yet to be reached. The most prominent issues concern the lack of dynamic closure on higher trophic levels, which currently poses an important limitation on the predictive potential of ecosystem models for use in studies of climate-impact and/or ecosystem-based fishery management approaches (Cury *et al.*, 2003).

A variety of models, with various levels of complexity and usefulness, are available for evaluating the ecosystem effects of fishing (see Robinson and Frid, 2003). These models have been used to make predictive estimations ultimately for management purposes, particularly in the last few years. This has been undertaken with non-dynamic models for testing scenarios and the response of the ecosystem to changes in effort and spatio-temporal area closures (e.g. Dinmore *et al.*, 2003; Zeller and Reinert, 2004; Hiddink *et al.*, 2006a). Dynamic ecosystem models had been identified as potentially powerful tools. However, their immediate applicability to considerations of ecosystem effects of fishing is limited by the lack of detailed representation of higher components of the foodweb (Robinson and Frid, 2003).

Recently, spatially explicit modelling approaches have been applied to resolve recruitment dynamics for different fish species by either (i) employing complex, three-dimensional species-specific IBMs (Hinrichsen *et al.*, 2002; Daewel *et al.*, 2008a), or (ii) utilizing three-dimensional model estimates of integrated primary production as a proxy for recruitment potential (Svendsen *et al.*, 2007). These spatially explicit approaches are generally tailored to particular processes, such as bottom–up control or food limitation. These models focus on early, passively drifting life stages and do not yet included juvenile and adults (life-cycle closure). Therefore, they are currently of limited applicability to the resolution of climate-driven changes in population dynamics. Scenarios based on these models cover only the bottom–up control of the early life stages (and not top–down/predation mortality). Moreover, uncertainties arise because of coupling issues: larvae IBMs require size spectra input, whereby NPZD models provide total biomass (Daewel *et al.*, 2008b).

The simplicity of model approximations, the lack of closure, and the diversity of concepts can be problematic when it comes to the assessment of climatic variability impacts, marine resource management, and predictions of potential scenarios. Impact studies carried out by Denman and Peña (2002) demonstrated that model estimates were significantly influenced by different ecosystem model concepts. Moreover, hydrodynamic model and coupling mode accounted for significant differences in the ecosystem assessments reported by Skogen and Moll (2005). In these assessments, extensive tuning was required before a simple ecosystem model could be used within another hydrodynamic framework; in addition, the best-fit simulations, employing two different ecosystem cores, exhibited significant deviations (twofold or greater) in local annual mean primary production (Figure 4.6) and clear differences in modelled interannual variability (Figure 4.7). The two ecosystem modules estimated different, even reversed, trends in total productivity, a fact that would significantly affect scenario predictions based on these concepts. The relevant conclusion from this study is that research is needed to identify valid model systems (i.e. to identify the key processes that need to be included for estimation of total productivity) for respective regions in order to ensure the scientific quality and value of scenario predictions.

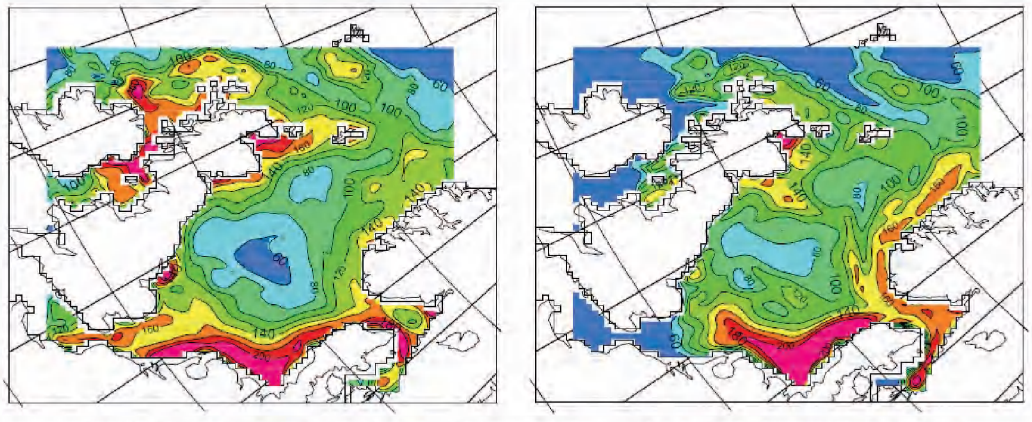


Figure 4.6. Mean annual production (g C m^{-2} year^{-1}) from the NORWECOM model (left panel) and the ECOHAM1 model (right panel; figures from Skogen and Moll, 2005).

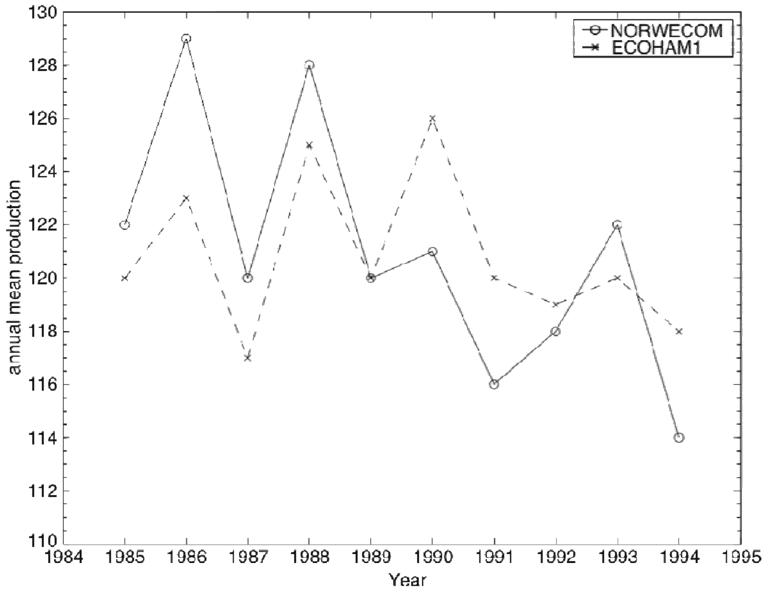


Figure 4.7. Mean annual production (g C m^{-2} year^{-1}) from the NORWECOM and ECOHAM1 models. (Figure from Skogen and Moll, 2005.)

4.7 Other processes not currently addressed in state-of-the-art models

The range of processes not yet addressed is much broader. Deterministic consideration of climatic-induced changes in the ecosystem, such as ocean acidification (Bellerby *et al.*, 2005) and changes in species composition (Beaugrand *et al.*, 2002), which will affect uptake, growth, and mortality rates, are currently not incorporated in state-of-the-art, spatially explicit, ecosystem models. Moreover, feedback mechanisms from biology to the physical system, which are currently not included for most of the models, are becoming increasingly important for the quality of modelled thermodynamics (Morel and Antoine, 1994; Ohlmann *et al.*, 2000a, 2000b) and atmospheric response (Shell *et al.*, 2003). Their importance has been demonstrated for global and climate models, but their effects have been generally ignored for regional and coastal models. However, Gentsch (2001) demonstrated that consideration of these mechanisms in a coastal-ocean model, by using monthly mean chlorophyll data, leads to changes in modelled sea surface temperatures (SSTs) of up to 2°C, which is far from negligible. This is expected to directly affect stratification intensity, nutrient fluxes, baroclinic transports, and temperature distribution in the water column; hence, its consideration is of crucial importance for the quality of oceanographic models.

There is also an urgent need to improve light modelling in order to allow reliable simulation of lower trophic-level dynamics (especially in the coastal zone). Therefore, it is imperative to consider as state variables not only the biogeochemical properties, but also the inherent optical properties (IOP), such as absorption and backscattering, and to compare results directly with estimates from remotely observed or *in situ*-measured quantities. Conversion of biogeochemical properties into optical parameters is also needed to realistically model the underwater light field, which is used as input to calculate model processes, such as photosynthesis and photochemistry. The optical consequences of seawater constituents, including dissolved materials, phytoplankton, and non-algal particles (NAP), need to be included in ecosystem models. The interaction of light with these materials needs to be computed in order to obtain realistic depth- and wavelength-resolved light fields. However, with very few exceptions (e.g. Bissett *et al.*, 1999b), most ecosystem models do not include the physics and bio-optics associated with the underwater light field. The development of ecosystem models that include optics was recently recommended by Rothstein *et al.* (2006), who reviewed the state-of-the-art of modelling harmful algal blooms. Climate change is expected to have consequences for the light regime in the atmosphere (cloud cover, aerosols) and in the coastal seas (turbidity from land discharge or resuspension of sediments in shallow areas). Such changes will affect, in turn, lower trophic-level productivity and, thereby, the entire ecosystems.

5 Disentangling climate from anthropogenic effects

Brian MacKenzie and Asbjørn Christensen

5.1 Introduction

Disentangling the effects of different drivers of variability in fish populations has been difficult for several reasons. For many of the populations and species of interest (e.g. those in estuarine, coastal, and shelf seas), some of the most important drivers (e.g. exploitation, eutrophication, habitat change) have intensified at approximately the same time during the past few decades or before the start of most time-series of analytically derived or survey-based estimates of abundance (Lotze and Worm, 2009). Hence, potential causes are often correlated over long time-scales and/or we are now investigating a new forcing (climate change) on populations in ecosystems whose structure and function have changed significantly from those present when the level of human impact was lower (Jackson *et al.*, 2001; Lotze *et al.*, 2006). In addition, there are often synergies between the different drivers (Brander, 2010; Perry *et al.*, 2010; Planque *et al.*, 2010). For example, exploitation may make populations more vulnerable to other perturbations (Anderson *et al.*, 2008), including climate change. New and alternative methods and approaches are therefore necessary if progress is to be made.

In this section, we identify some of the methods which have been developing in recent years and which are helping to resolve the relative impacts of the different drivers and how their interactions affect fish populations. It is recognized that the effects do interact; for example, cod populations in the Northeast Atlantic are more likely to be influenced by the NAO when biomass is low (e.g. as a result of exploitation) than when it is high (Brander and Mohn, 2004). Hence fishing could make populations more vulnerable to the effects of climate change and other drivers on population abundance and foodweb dynamics (Anderson *et al.*, 2008; Brander, 2010; Daskalov *et al.*, 2007; MacKenzie *et al.*, 2007; Perry *et al.*, 2010; Planque *et al.*, 2010).

5.2 Potential approaches

5.2.1 Historical marine ecology

This approach involves the recovery of data from periods when anthropogenic effects (fishing and eutrophication) were less marked than in recent decades and compares past biological responses with climate variability. The approach is being followed in several programmes (e.g. retrospective and palaeo-oceanographic tasks within GLOBEC; History of Marine Animal Populations project in its Census of Marine Life). Data can be either written (e.g. landings, effort, distributions, sizes of fish; Poulsen, 2010) or non-written (e.g. fish remains at palaeo-oceanographic and anthropological sites; Emeis *et al.*, 2010; Finney *et al.*, 2010). The recovery and interpretation of data is most effective when investigators from both natural (e.g. fisheries, oceanography) and social (e.g. history, economics) scientific disciplines are involved.

There are now several examples of how this approach yields valuable information about fish populations and biodiversity during periods when the impacts of fishing and eutrophication were much less than today. Time-scales and time periods range from multidecadal to millennial (e.g. the early 1900s to prehistory). Examples of time periods, species, and regions are summarized in the literature (Pitcher, 2001; Pinnegar and Engelhard, 2008; Poulsen, 2010; Emeis *et al.* 2010; Finney *et al.*, 2010). These examples demonstrate that some populations underwent major variations in abundance long before there were any major human influences (i.e. climate variability has affected population abundance and productivity in the past), and that the abundance and distribution of most populations of what are considered the most desirable species have been severely reduced. Cumulatively, these studies demonstrate the levels of variability in abundance and distribution that might be expected under the regime of historical levels of anthropogenic impacts. They also provide potential baselines for rebuilding populations and ecosystems, and for identifying future levels of sustainability and potential climate-related changes in fish communities (Jackson *et al.*, 2001; Enghoff *et al.*, 2007; Pinnegar and Engelhard, 2008).

Care must be exercised when applying these historical levels to future recovery scenarios, because climate change in particular may occur at rates faster than in the past, and some populations and species may not be evolutionarily adapted to these rates (ICES, 2005d). In addition, recoveries or maintenance of present-day populations could be delayed or reduced as a result of changes to their life histories and characteristics caused by the various impacts of fishing (e.g. loss of population structure, including age, size, or genetic components). These changes may be less conducive to sustainability under future climate scenarios, particularly if exploitation is maintained at high levels. For example, fishery-induced changes in life histories could influence the interactions of individual populations or species in foodwebs. Finally, the species composition of present-day or future communities and ecosystems may differ from that expected, based on past knowledge, because of recent species invasions or transfers (Daskalov *et al.*, 2007) and because future foodweb structure and functioning may be sensitive to initial (present-day) species composition. Hence, exploitation can and does interact with other drivers, including climate change, to affect population vulnerability to exploitation (Perry, *et al.*, 2010; Planque *et al.*, 2010).

5.2.2 Experimental approaches

Carefully designed experiments can identify the critical tolerance thresholds to specific abiotic variables of different life-history stages and the vulnerability of individuals to species interactions and fluctuations in habitat characteristics (including substratum complexity and abiotic conditions; Pörtner and Knust, 2007; Rijnsdorp *et al.*, 2009). These approaches can be used to interpret past fluctuations in abundance and distribution, to estimate how populations and species could respond to new combinations of abiotic and biotic conditions in future, and to identify potential tipping points for the maintenance of key structuring species (e.g. prey or predator species) in foodwebs. For example, detailed physiological measurements have revealed the vulnerability of a North Sea fish species (eelpout (*Zoarces viviparus*)) to the combined effects of temperature and acidification (Pörtner and Knust, 2007). In the Baltic Sea, knowledge of the tolerance of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) eggs to salinity, temperature, and oxygen concentration (Wieland *et al.*, 1994; Vallin *et al.*, 1999; Nissling, 2004) allows identification of critical habitat sizes and distinction of environmental effects from fishery effects on multiannual population dynamics (MacKenzie and Köster, 2004; Köster *et al.*, 2005).

Experiments conducted *in situ* avoid potential fish stress reactions that create bias in measurements. This approach involves direct manipulation of fishing effort via closed or reduced-effort areas, or via spatial comparison of the effects of long-term differences in fishing effort on populations, communities, and ecosystems in neighbouring areas. Responses can be monitored over time for the detection of changes in biotic parameters (e.g. abundance, biodiversity, size). As most areas of interest are exploited commercially, the establishment of planned marine protected areas (MPAs) offers valuable opportunities to capture datasets of ecosystem responses with strong contrasts. Unfortunately, past monitoring activities accompanying MPA establishment have not been sufficiently intensive or comparable (Halpern, 2003) to allow the clear separation of the interacting anthropogenic and ecosystem factors required for further isolating the climatic factor.

5.2.3 Comparative approaches across space

Local (regional-scale) variations in fish populations and foodweb structure over moderately long time-scales (multidecadal) can often be useful indicators of overall levels of population productivity and ecosystem sustainability, or tolerance of human impacts. Spatial comparisons allow identification of relative effects of fishing and climate variability, because spatial differences in levels of exploitation and environmental variability may be greater than those experienced by individual local populations. These methods can be meta-analytical and at individual species or entire community and ecosystem levels. Examples include:

i) pan-Atlantic comparisons of cod stock–recruitment relationship parameters related to population reproductive rate and carrying capacity (Myers and Mertz, 1997; Myers *et al.*, 2001; Mantzouni *et al.*, 2010);

ii) effects of primary productivity on fishery yield across ecosystems in the northeast Pacific (Ware and Thomson, 2005; Leggett and Frank, 2008);

iii) effects of climate variability on the productivity of small pelagic clupeids (Cury and Roy, 1989; Bakun, 1996).

Consequently, knowledge of spatial responses to driving factors can be useful to understand how temporal variations might affect local populations and their interactions with other species. For example, cod recruitment or recruitment/spawner biomass in the North Atlantic is correlated with temperature (Planque and Frédou, 1999; Drinkwater, 2005), but the direction of the relationship (positive–negative) depends on geography (positive in colder areas, negative in warmer areas). Sprat recruitment in the Baltic and Black seas varies with temperature in a geographically specific manner, similar to that for cod (MacKenzie and Köster, 2004). In nearly all of the cod and sprat examples, correlations within sites were relatively weak, but the cross-system comparisons were stronger.

The meta-analytic approach has recently been extended to the entire ecosystem level in order to evaluate the relative roles of top–down (i.e. fishing) and bottom–up controls on foodweb structure and function (Frank *et al.*, 2006; Leggett and Frank, 2008). By compiling abiotic and biotic datasets across several trophic levels in several Northwest Atlantic ecosystems, it is now possible to see that the relative importance of control mechanisms varies geographically in structured ways and, to some extent, with temperature and overall level of primary productivity.

5.2.4 Advances in process modelling and model interfacing

Process modelling plays a key role in quantifying climate-change impact, because climate-change predictions from statistical modelling are, of necessity, based on extrapolation rather than interpolation. There has been major progress in process modelling of both oceanic responses to climate variability/change and the productivity and structure of marine ecosystems themselves (deYoung *et al.*, 2004b).

However, some technical issues remain (Kattsov *et al.*, 2001; Arzel *et al.*, 2006) for operational, global-general-circulation models (GCMs), and many qualitative and quantitative differences remain between predictions of alternative GCMs (Sarmiento *et al.*, 2004). The inclusion of the upper trophic levels and their interaction with lower trophic levels also remains a challenge (Oguz and Gilbert, 2007), because this task crosses disciplines and coupled models are generally computer-intensive. Moreover, the interface between climate and ecosystem models is still comparatively primitive, and much could be gained from standardizing the interface protocol and improving certain technical aspects of the interface exchange (e.g. feedback mechanisms).

As a result of these limitations, the combined consequences of climate change/variability and human impacts (e.g. fishing, eutrophication, and invasive species) are suboptimally represented, and the full range of uncertainty to variation in future driver magnitude is not completely represented by current model outputs. New attempts to link the models more effectively will increase model realism and sensitivity to different drivers. Upper trophic entities are most often modelled in Lagrangian individual-based models (Grimm, 1999), because even complex mechanisms are easy to implement in this framework. However, Lagrangian approaches are less suitable when density effects and rare events are important. Here, Eulerian techniques must be used, but methodological developments are needed in this field (Thygesen *et al.*, 2007). Another salient question at the modelling frontier concerns the optimal complexity representation required to achieve the best predictive power of models. Evidence (Constanza and Sklar, 1985; Fulton *et al.*, 2003) strongly suggests that increasing model complexity does not generally improve the predictive skill of a model, and a set of design paradigms for guiding the choice of model complexity is important for future developments in the field.

5.2.5 Advances in statistical modelling approaches

In recent years, new modelling and statistical approaches have been developed which allow evaluation of the responses of fish populations and communities to fishing, climate, and other anthropogenic drivers. These approaches can be based on community-level data and typically focus on the nature of changes in size composition of entire fish communities over time (Jennings and Blanchard, 2004; Andersen and Beyer, 2006; Pope *et al.*, 2006; Jennings and Brander, 2010). Shape and slope of size spectra could be used to identify and quantify the effects of fishing and climate change on entire fish communities. Additionally, size-spectrum theory can be used to estimate the relative influence of climate change and fishing on maturity-reaction norms (Christensen and Andersen, submitted), which are considered to be a sensitive ecosystem probe. One of the main diagnostic features associated with the spectral analyses is the fishing-related reduction in abundance of large fish over time (Pauly *et al.*, 1998).

Other recently developed and applied statistical modelling approaches include the development of non-parametric and non-linear time-series analyses that can accommodate complex (e.g. threshold) responses of fish populations to changing intensities of density-independent and density-dependent control (Stenseth *et al.*, 2002; Ciannelli *et al.*, 2004, 2005), including species interactions within and among populations (Hjermann *et al.*, 2004a, 2007). These approaches are able to quantify past variations in more realistic ways than linear parametric approaches and are more likely to resolve relative impacts of various human drivers on fluctuations in fish populations. They could be used to identify the times at which regime shifts occurred and, thereby, major changes in fish productivity induced by, for example, climate variability.

5.2.6 Genetic approaches

Modern genetic methodologies are providing new insight into the sensitivity of fish populations to the impacts of fishing and climate variability (ICES, 2005d, 2006p). Fish populations undergo evolutionary changes in their life histories (e.g. age-at-maturity) when exposed to long periods of intensive fishing pressure (ICES, 2006p; Jørgensen *et al.*, 2007) and, in some cases, entire locally adapted populations can be eliminated by exploitation (Hiddink *et al.*, 2008a). Losses of natural genetic variation in life-history and physiological capacity caused by fishing or climate variability could increase the risk of population collapse. In addition, fish species consist of populations and individuals with different genotypes, which can confer advantages under changing climatic conditions. As environmental conditions change in time and space, the frequencies of particular genotypes may also change. For example, there are strong spatial gradients in the intraspecific genetic variability of several fish species (e.g. cod, herring, turbot) through the Danish straits into the Baltic Sea, which overlap the strong salinity gradient (Nielsen *et al.*, 2003, 2004; Bekkevold *et al.*, 2005). Climate-related changes in salinity will probably affect the spatial distributions of these subpopulations. Also, the pantophysin (PAN I) locus has been used in comparative studies of cod populations in the Northeast Atlantic. Variations in frequencies of different alleles are, to some extent, correlated with spatial variations in temperature and salinity (Case *et al.*, 2005). However, temporal variations during much of the 20th century seem relatively small for populations in the North and Baltic seas, and around the Faroe Islands, and were not correlated with changes in sea temperature (Nielsen *et al.*, 2007).

6 Marine European climate: past, present, and future

Kenneth F. Drinkwater

6.1 Introduction

It has long been known that physical forcing strongly affects marine ecological processes. As early as the 1870s, Spencer Fullerton Baird, an American fishery biologist, recognized the importance of the environment in generating fluctuations in fish stocks (Lehodey *et al*., 2006). The expected links between the environment and fish stocks have played a significant role in the strong emphasis on hydrographic data collection by ICES since its inception in 1902. At about the same time, a systematic search began for relationships between physical conditions and different aspects of fish stocks (Helland-Hansen and Nansen, 1909). A strong warming period in the North Atlantic during the 1920s and 1930s led to significant changes in the distribution and production of several commercially important fish species, as well as in other components of the marine ecosystem (Jensen, 1939; Cushing and Dickson, 1976; Cushing, 1982), resulting in the first-ever meeting on climate change (ICES, 1949).

By the mid-1900s, the mechanisms through which the physical environment affects primary production had been elegantly elaborated by Sverdrup (1953). New sampling methods began to reveal the extent of the ocean's variability in the 1960s and 1970s, and it became increasingly clear that physical variability and its influence on marine ecology occurred over a multitude of spatial and temporal scales. By the 1990s, the role of large-scale atmospheric forcing, such as the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO), in determining changes in the marine environment were being firmly established. Increasingly, attention is turning to the role of future climate change and its possible influence on marine ecosystems.

This section reviews the knowledge of past climate variability and future climate change in European waters. The objective is to provide background for this and many of the other sections in this report that deal with past and possible future impacts of physical forcing on the marine environment, especially commercially important fish species.

This section includes: the identification of climate and physical oceanographic variables that are most important in influencing ecological processes (Section 6.2); brief descriptions of the physical background, i.e. topography, hydrographic conditions, and mean circulation (Section 6.3); ocean climate variability during the past 100 years, with emphasis on the NAO and the Atlantic Multidecadal Oscillation (AMO; Section 6.4); projected climate scenarios under global climate change and their effects on physical oceanography (Section 6.5); and a summary of the results (Section 6.6).

Climate is the slowly varying aspects of the atmosphere–hydrosphere–land system that are characterized statistically in terms of long-term averages and variability of climate elements, such as temperature, precipitation, winds. The period over which the "average" is determined is typically 30 years, as recommended by the World Meteorological Organization. *Climate variability* is the temporal variation around this average state and is associated with time-scales ranging from months to millennia and beyond, that is, longer than those associated with synoptic weather events do. *Natural climate variability* refers to climate variations caused by factors such as changes in solar radiation, volcanic eruptions, or internal dynamics within the climate system (Hasselmann, 1976), and pertains to any influence that is not attributable to, or influenced by, activities related to humans. Human effects on climate, such as those caused by greenhouse gas emissions or land use, are termed *anthropogenic influences*.

Climate change, on the other hand, is any systematic change in the long-term statistics of climate elements from one state to another where the new state is sustained over several decades or longer. The new state might be the result of changes in the mean level, the characteristic variability, or both. Climate change arises from both natural and anthropogenic causes. The United Nations Framework Convention on Climate Change (UNFCCC) has restricted its definition of climate change to causes arising directly or indirectly from human activity only, whereas it regards climate variability as changes attributable to natural causes. In recent years, this definition of climate change has often been adopted by the media, in policy documents, and in some scientific literature and has also been used interchangeably with *global warming*. Examples of natural climate change include shifts between ice ages and the warmer interglacial periods. In historical times, it includes multicentenial changes in the northern hemisphere, ranging from warm periods, such as the "Medieval Warm Period" (AD 890–1170), to colder periods, such as the "Little Ice Age" (AD 1580–1850; Osborn and Briffa, 2006). In the following, however, we restrict our use of the term climate change to that caused by humans.

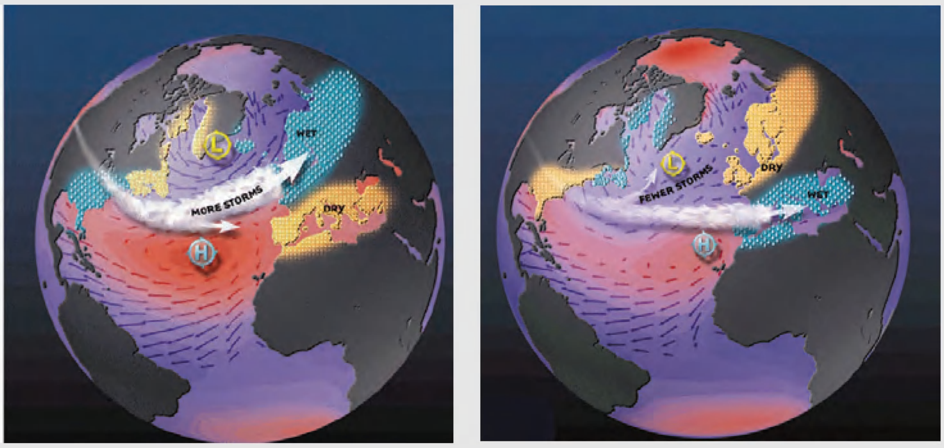
On multidecadal scales, the shift in the North Atlantic, from the generally warm period of the 1930s, to the 1960s, the colder period in the 1970s and 1980s, and the return to warm conditions in the 1990s, is known as the *Atlantic Multidecadal Oscillation* (AMO; Kerr, 2000). The AMO fits within the definition of climate change because it is multidecadal, but it perhaps fits better as an example of longer term climate variability. Other examples of climate variability include the strong decadal fluctuations associated with changes in atmospheric pressure systems, such as the *North Atlantic Oscillation* (NAO; see Sidebar 6.1).

6.2 Identification of important abiotic factors affecting marine ecological processes

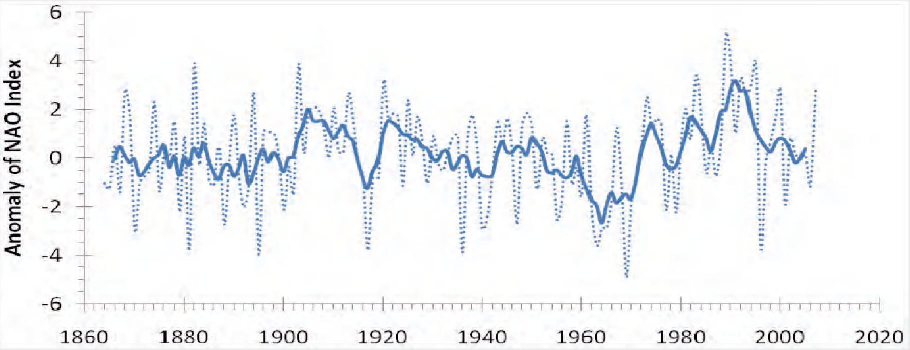
As one of the main aims of RECLAIM (RECovery of Logbooks and International Marine data) is to understand the role of physical forcing on marine ecology in European waters, it is important first to identify which of the abiotic variables are most important to biological processes. The important physical oceanographic variables for marine ecological studies include temperature, salinity, vertical density stratification, circulation patterns, upwelling, and sea ice. Temperature is important because of its effects on metabolism and on feeding and developmental rates. Salinity appears to have a less direct effect on organisms except at very low salinities (perhaps generally <10). However, salinity does have an important indirect effect because of its influence on stratification. Vertical density stratification affects mixing and, hence, nutrient fluxes to the surface layer. Also, stronger near-surface vertical stratification tends to result in more carbon being recycled in the upper layers of the water column and, hence, favours pelagic organisms, whereas weaker near-surface vertical stratification tends to result in more carbon reaching the benthos and demersal fish species. Circulation patterns influence water-mass boundaries, which in turn, influence species distributions. Currents also affect drift of particles, including phytoplankton, some zooplankton, and fish eggs and larvae. Upwelling influences nutrients and, hence, phytoplankton production, which in turn, affects higher trophic levels. Sea-ice formation and melting affects the salinity and stratification of the underlying waters. It also provides habitat for large marine mammals.

Sidebar 6.1. The North Atlantic Oscillation

The North Atlantic Oscillation (NAO), the dominant mode of atmospheric variability over the North Atlantic (Walker and Bliss, 1932; Hurrell, 1995; Hurrell *et al.*, 2003), involves north–south shifts in air masses between the subtropical and subpolar regions of the Atlantic. It is associated with changes in the large-scale, atmospheric-pressure patterns, particularly the Icelandic Low and the Azores High. The high- and low-pressure systems tend to weaken or strengthen at the same time, which gives rise to the oscillation. The NAO index is usually represented by the pressure difference between Iceland and the Azores (Rogers, 1985), Lisbon (Hurrell, 1995), or Gibraltar (Jones *et al.*, 1997), typically in winter. A positive NAO index is associated with a stronger north–south pressure gradient, stronger winds across the Atlantic, and warm conditions in northern Europe. The opposite occurs during negative NAO years.



Conditions under NAO negative conditions (left) and NAO positive conditions (right; courtesy of Martin Visbeck).



Time-series of anomalies of the DJFM NAO index (dashed line = annual values; solid line = five-year running means; based on data from http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

It is important to remember that many of these physical oceanographic variables are forced by the atmosphere. The important atmospheric variables include air temperature, precipitation, cloud cover, air pressure, and wind. The first two variables are important because of their effect on ocean temperature and salinity. Precipitation also determines river run-off and, together with air temperature, seasonal freshwater discharges into the ocean. Cloud cover affects the amount of solar radiation reaching the ocean surface and is therefore important in determining phytoplankton production. By changing light availability in the water column, it can also affect the feeding rates of some organisms. Changes in large-scale air-pressure patterns give rise to the NAO (Sidebar 6.1) and other climate indices. They also influence the winds, which in turn, determine the amount of vertical mixing in the water column and, hence, influence nutrient replenishment of the near-surface layers and feeding rates of small organisms through turbulence levels. Wind also drives ocean circulation patterns and upwelling. Air temperature, wind, and precipitation, through their effects on evaporation, determine the heat fluxes to or from the ocean to the atmosphere.

Is it possible to rank the importance of these atmospheric and oceanic variables in terms of their influences on the marine ecosystems for different regions, such as the open ocean, shelf areas, and coastal waters? Although the importance of the variables changes regionally, some general conclusions can be reached. Ocean temperature, because of its pervasive effect on organisms, will be important in all of the regions. Stratification is also of major importance in all regions because of its effect on the vertical structure of ecosystems. The major effects of wind on ecology are usually through mixing and circulation changes in the open ocean but, in the shelf and coastal regions, upwelling may become more important, depending on the wind direction and coastal orientation. Sea ice is only important in more northern regions, such as the Barents and the Baltic seas.

6.3 Physical background

In the first part of this section, the topographic features of the different regions are presented, because topography not only influences circulation and the ocean's response to atmospheric forcing, but also often affects biological processes (e.g. the strength of benthic–pelagic coupling, the ability of zooplankton to undergo diapauses). In the second part, hydrographic conditions and circulation patterns in the various regions are discussed, as it is important to know the mean conditions before discussing their temporal changes.

6.3.1 Topography

Throughout this paper, the term "Northeast Atlantic" refers to the region east of the European shelf. This consists of a deep abyssal plain that stretches westward to the Mid-Atlantic Ridge. Depths are typically 2000–4000 m. Occasional seamounts dot this landscape, with the volcanic archipelagos of the Azores, Madeira, and Canary islands to the south and Rockall Bank off Scotland to the north. The northern boundary is the Greenland–Scotland Ridge, which separates the Nordic seas from the rest of the North Atlantic. The Nordic seas include the Greenland, Norwegian, and Iceland seas. The first two seas reach depths of more than 3500 m, whereas the shallower Iceland Sea is mostly <2000 m. Northeast of the Norwegian Sea lies the Barents Sea. This is one of several shallow shelf seas that collectively form the continental shelf of the Arctic Ocean and is surrounded by the Norwegian Sea to the west, Novaya Zemlya to the east, Norway and Russia to the south, and the deep Arctic Ocean to the north. The Barents Sea has an area of 1.4 million km^2, with an average depth of 230 m and a maximum depth of approximately 500 m near the western entrance.

Farther south, between the UK and continental Europe, is the North Sea, a broad gradual slope from a depth of 100–150 m in the north to <50 m in the south. In the east, seawards of the Norwegian Shelf, lies the deeper (>200 m) Norwegian Trench. Including estuaries and fjords, the total surface area of the North Sea region is approximately 750 000 km^2. To the southeast is the Baltic Sea, a shallow, semi-enclosed region, with a total area of 415 000 km^2, that includes its narrow entrance, the Kattegat. The Baltic Sea has a complex topography consisting of several basins separated by ridges and shelf regions. To the southwest, the North Sea is connected to the Celtic and Irish seas by the English Channel. The shallow (<90 m) Irish Sea lies between Britain and Ireland and has an area of ca. 100 000 km^2. The Celtic Sea covers the area between southern Ireland, the English Channel, and the shelf break. Farther south is the Bay of Biscay, bordered to the east by France and to the south by Spain. It includes both a shallow shelf (<200 m) and a deep (maximum depth >4000 m) abyssal plain and has an area of ca. 223 000 km^2.

The Iberian coastal area includes the narrow continental shelf and adjacent slope off Portugal and north Spain. To the east, through the narrow (14 km) Strait of Gibraltar, lies the Mediterranean Sea. This is ca. 3680 km long, with an average width of 700 km, and is divided into the western and central Mediterranean, which are separated by the straits of Sicily and by the eastern Mediterranean. The western Mediterranean (mean depth ca. 1600 m) consists of two deep basins: the Algero–Provençal Basin and the Tyrrhenian Sea. The central Mediterranean includes the Adriatic and Ionian seas, and the eastern Mediterranean includes the Aegean Sea and the Levantine Basin. The Black Sea is an oval-shaped basin located north of Turkey, with an area of ca. 464 000 km^2 and a maximum depth of 2200 m. It is connected to the Aegean Sea through the shallow Bosphorus Strait, the Marmara Sea, and narrow Dardanelles.

6.3.2 Hydrography and general circulation

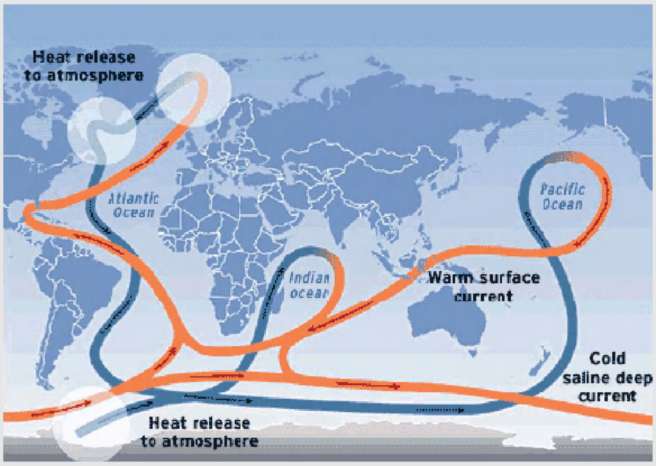
Before describing the general physical oceanographic conditions in the different European regions and seas, it is worth mentioning that the Northeast Atlantic is strongly influenced by large-scale, ocean-circulation patterns (Sidebar 6.2). This includes the transport of warm waters into the Northeast Atlantic, which contributes significantly to the relatively warm conditions in northern Europe compared with similar latitudes elsewhere in the northern hemisphere. Also important is the deep-water convection that occurs in the Greenland Sea, as well as in the Labrador Sea to the west (Sidebar 6.2).

Northeast Atlantic

To the east of the European Shelf lies the anticlockwise Subpolar Gyre, which extends across the entire northern North Atlantic (Figure 6.1) and carries relatively cold freshwater from the Labrador Sea into the Northeast Atlantic. South of the Subpolar Gyre lies the warmer, saltier, clockwise Subtropical Gyre. Its northern boundary is the Gulf Stream extension, known as the North Atlantic Current (NAC; Figure 6.1). As the NAC approaches Europe, it splits, with one branch flowing north into the Norwegian Sea and the other flowing south to join the Subtropical Gyre. The Subpolar Gyre varies in strength and is believed to have weakened or slowed down during the 1990s relative to earlier times (Häkkinen and Rhines, 2004). Coincident with the slow-down is a westward retraction of the eastern boundary, which allows more of the north-flowing, high-salinity branch of the NAC into the Norwegian Sea (Hátún *et al.*, 2005). This branch takes three main routes into the Norwegian Sea: through the Faroe–Shetland Channel, over the Scotland–Iceland Ridge, and through Denmark Strait eastwards across the Iceland Sea (Helland-Hansen and Nansen, 1909; Hansen and Østerhus, 2000).

Sidebar 6.2. The Thermohaline Circulation

Spatial differences in temperature and salinity generate density-driven circulation patterns that redistribute water masses between the equator and the poles. In the Atlantic, this drives the Thermohaline Circulation (THC), which carries warm water northwards via the Gulf Stream system and is part of the global "conveyor belt" circulation that links the world's oceans (Broecker, 1991). The other important component is the Meridional Overturning Circulation (MOC), because of sinking of winter-cooled water in the Greenland Sea. The Gulf Stream, together with the heat carried by atmospheric lows moving northeastwards across the Atlantic, ensure that Europe is much warmer than equivalent latitudes in North America (an average of 6 °C warmer at 44 °N and 15 °C warmer at 63 °N).



The thermohaline circulation (THC) is a global-ocean, circulation pattern that distributes water and heat both vertically, through the water column, and horizontally across the globe (www.ucsusa.org). Red = surface currents; blue = deep currents; white circles = areas of deep-water convection.

Nordic seas

Some of the warm, salty (7 °C, >35 psu) Atlantic Water that enters the Norwegian Sea flows into the North Sea, but most of it continues northeastwards through the Norwegian Sea (Figure 6.1), cooling and freshening en route (Blindheim, 1989; Blindheim *et al*., 2000). The cooling is a result of both air–sea interaction and mixing with the cooler waters in the Norwegian Sea, whereas the freshening is caused by mixing with Norwegian Sea water and by exchange and mixing with the Norwegian Coastal Current Waters that occupy the continental shelf off Norway.

The Atlantic Water in the Norwegian Sea extends from the surface to approximately 800 m depth. A branch of the Atlantic Water enters the Barents Sea (Figure 6.1), but most of the flow continues north along West Spitsbergen to form part of the West Spitsbergen Current (Blindheim, 2004). It again splits, some flowing into the Arctic Ocean and the remainder circulating southwards into the Greenland Sea (Figure 6.1), where it mixes with Polar Water emanating from Fram Strait (Helland-Hansen and Nansen, 1909; Blindheim, 2004; Blindheim and Østerhus, 2005). This admixture, known as Arctic Water, is separated from the Atlantic Water by the Arctic Front. This front tends to follow the Mohn Ridge between the Norwegian and Greenland seas and the Jan Mayen Ridge between the Norwegian and Iceland seas (Blindheim, 2004).

Sea ice, both formed locally and advected from the Arctic, covers much of the eastern Greenland Sea for most of the year (Vinje, 2001). Deep convection occurs in the Greenland Sea each winter as a result of surface cooling caused by overlying cold air masses and strong winds (Rhein, 1991, 1996; Dickson *et al.*, 1996). This cold, dense water forms the Greenland Sea Deep Water that flows through the Norwegian Sea and eventually out into the Atlantic through the bottom of the Faroe–Shetland Channel (Hansen and Østerhus, 2000). It joins the outflow of dense, cold, bottom waters from the Denmark Strait and flows around the Labrador Sea and south along the eastern margin of North America (see Sidebar 6.1).

Figure 6.1. A schematic of the surface circulation in the northern North Atlantic. (From AMAP, 1998.)

Barents Sea

The Atlantic Water that enters the Barents Sea continues to cool and freshen as it makes its way east and north before exiting the Barents Sea, principally between Novaya Zemlya and Franz Josef Land (Loeng, 1991; Schauer *et al.*, 2002). Cold, fresh Polar waters from the Arctic enter the Barents Sea, mainly between Svalbard, and exit south of Spitsbergen (Figure 6.1; Loeng, 1991). A narrow transition zone, called the Polar Front, separates the Atlantic and Polar water masses (Loeng, 1991; Harris *et al.*, 1998; Parsons *et al.*, 1996). Winter convection in the Barents Sea also provides cold intermediate water to the Arctic Ocean to a depth of 1200 m through sinking and subsequent northward advection through the Norwegian Sea (Schauer *et al.*, 1997). Sea ice typically covers the northern and eastern regions of the Barents Sea in winter (Loeng, 1979; Vinje and Kvambekk, 1991).

North Sea

Most of the Atlantic Water that flows from the Norwegian Sea into the northern North Sea enters via the Norwegian Trench, with a lesser amount coming in north of the Shetland Islands. These flows contribute to the general southward circulation that exists in the western North Sea and, together with the Norwegian Coastal Current, contribute to a mean anticlockwise circulation pattern (Figure 6.1; Helland-Hansen and Nansen, 1909; Winther and Johannessen, 2006). Large quantities of freshwater enter the southern North Sea through discharge from rivers, especially those in the Netherlands and Germany, as well as from the Baltic Sea outflow.

Baltic Sea

To the southeast of the North Sea lies the Baltic Sea. Large freshwater run-off into the Baltic creates low salinities (<10–20 psu in the surface layers) with strong horizontal salinity gradients (Kullenberg, 1981). The circulation is characterized by anticlockwise circulation around the basins and a general surface outflow (Figure 6.2). The latter eventually flows out through the Kattegat and Skagerrak and combines with the low-salinity waters in the southern North Sea to form the Norwegian Coastal Current (Helland-Hansen and Nansen, 1909; Sætre, 2007). The renewal of the water in the deep basins of the Baltic Sea occurs through a wind-driven exchange of water with the North Sea (Matthäus and Schinke, 1994; Lehmann *et al.*, 2004). This happens only intermittently, which often results in stagnant waters and anoxic near-bottom conditions in the Baltic Sea. Sea ice forms in the Baltic Sea during winter, on average covering 40% of its total area, and the length of the ice season extends for upwards of six months in the northern regions (Granskog *et al.*, 2006).

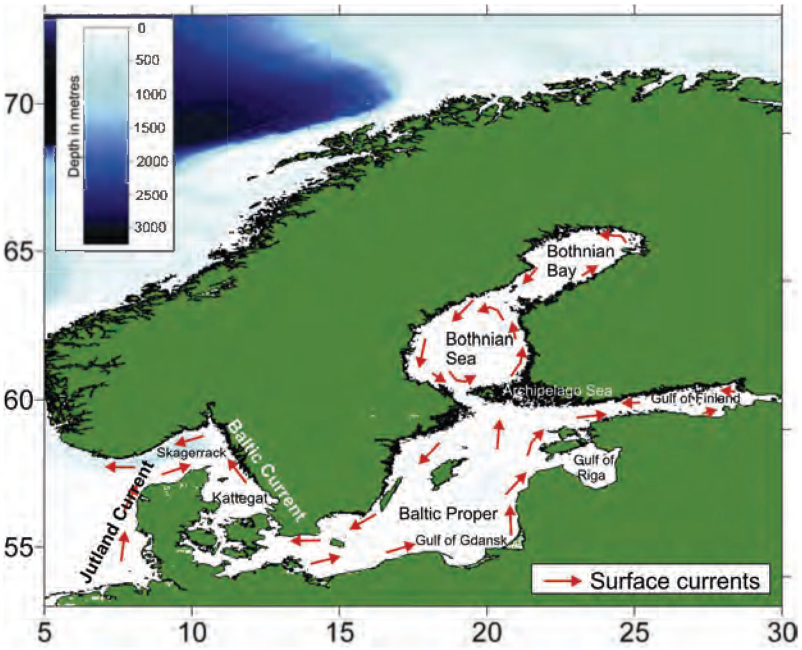


Figure 6.2. The surface circulation in the Baltic Sea. (From the Philippart *et al.*, 2007a.)

Irish and Celtic seas and the English Channel

Much of the Irish Sea is tidally mixed, except for a stratified patch west of the Isle of Man, and it is bounded to the north and south by tidal fronts. The remainder of the Irish Sea, as well as the Celtic Sea and Western English Channel, are strongly stratified, but with many pronounced surface fronts. The English Channel becomes less stratified from west to east, with the eastern basin being tidally mixed (Pingree and Griffiths, 1978).

Bay of Biscay

Water masses in the upper layers (100–600 m) of the Bay of Biscay are derived mostly from North Atlantic Central Water (NACW), with temperatures varying between 10.5° and 12°C and salinity between 35.45 and 35.75 psu (Boucher, 1985). From 600 to

1500 m, the water masses are of Mediterranean origin. The relatively weak residual currents over the shelf in the northern Bay of Biscay are directed northwestwards (Pingree and Le Cann, 1989), whereas farther south, there is a marked seasonal variability, with the flow being northwest during winter and southeast during the rest of the year (Le Cann, 1982). In the vicinity of the larger estuaries (e.g. the Loire and the Gironde), run-off results in low-salinity surface waters that turn and flow north.

Iberia

The Iberian coastal region has a weak circulation pattern, but with seasonal variability (Valdés and Lavín, 2002). Upwelling is predominant in the region, with the most intensive and geographically extensive upwelling occurring along the west Iberian coast. Several rivers enter along the Galician coast, producing low-salinity surface waters. One of the main oceanographic features is the Iberian Poleward Current (IPC), which carries warm, salty waters from the Mediterranean Sea (Figure 6.3). This current is part of a general flow north along the edge of the European shelf that extends from the Iberian Peninsula to the northern North Sea.

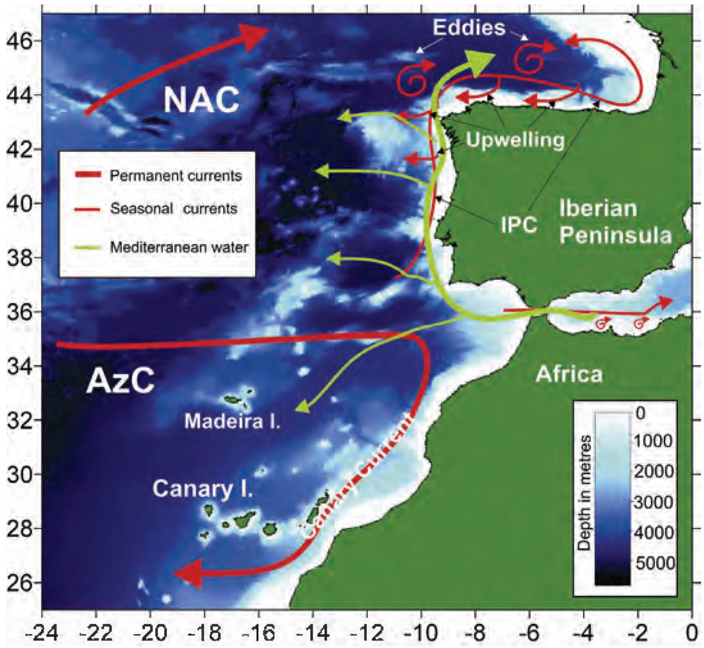


Figure 6.3. The surface circulation in Iberian waters. NAC = North Atlantic Current; IPC = Iberian Poleward Current; AzC = Azores Current. (From the Philippart *et al.*, 2007a.)

Mediterranean Sea

The Mediterranean Sea is an inverse estuary with relatively cold, lower-salinity surface water entering through the Strait of Gibraltar from the Atlantic Ocean (Robinson *et al.*, 2001). Although the circulation in the major basins tends to be anticlockwise, there is also a general east-flowing surface current throughout the Mediterranean Sea (Figure 6.4). As the waters move eastwards, they become warmer and saltier. The increasing salinity is caused by evaporation exceeding freshwater input (a combination of precipitation and river run-off). The density of the water also increases eastwards and eventually sinks, primarily in the vicinity of the Levantine Basin (Robinson *et al.*, 2001). This high-salinity water then tends to flow west at depth and eventually spills out through the Strait of Gibraltar below the surface inflow (Béthoux *et al.*, 2002). It flows down the continental slope until it reaches an equivalent density at ca. 1000 m. Part of the flow moves along the slope of the Iberian Peninsula (Ambar *et al.*, 1986; Coelho *et al.*, 2002). In addition, some of the water separates to form distinct eddies, called "Meddies", which move slowly through the eastern Atlantic and can be traced by their high salinities and temperatures.

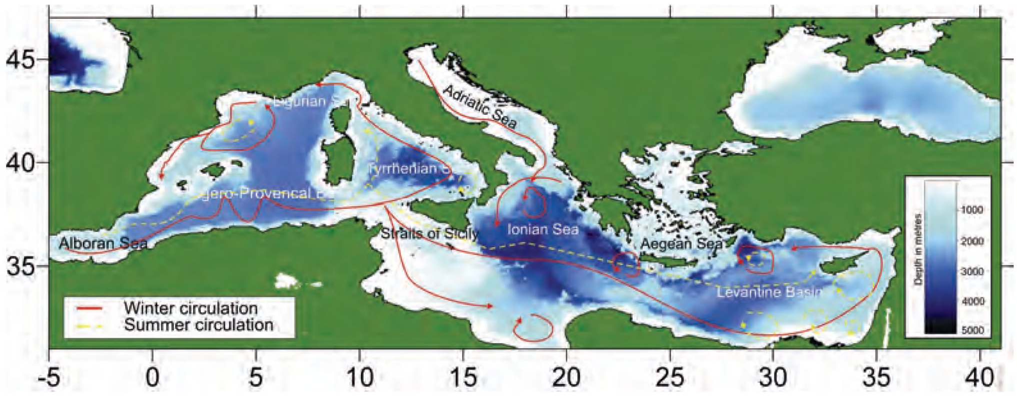


Figure 6.4. The surface circulation in the Mediterranean Sea. (From the Philippart *et al.*, 2007a.)

Black Sea

Large quantities of freshwater run-off enter the Black Sea, the primary river being the Danube. These contribute to an anticlockwise circulation, known as the Rim Current, in the near-coastal regions around the Black Sea. The circulation in the deep basin, on the other hand, is dominated by two anticlockwise gyres (Figure 6.5). The relatively high run-off also maintains a low-salinity surface layer throughout the Black Sea. Relatively warm, salty water from the Mediterranean intermittently enters through the Bosphorus Strait and, being of higher density than the surface waters in the Black Sea, sinks into the subsurface layers. This maintains strong stratification, resulting in little mixing between the two layers. Consequently, the subsurface waters are not reoxygenated and become anoxic.

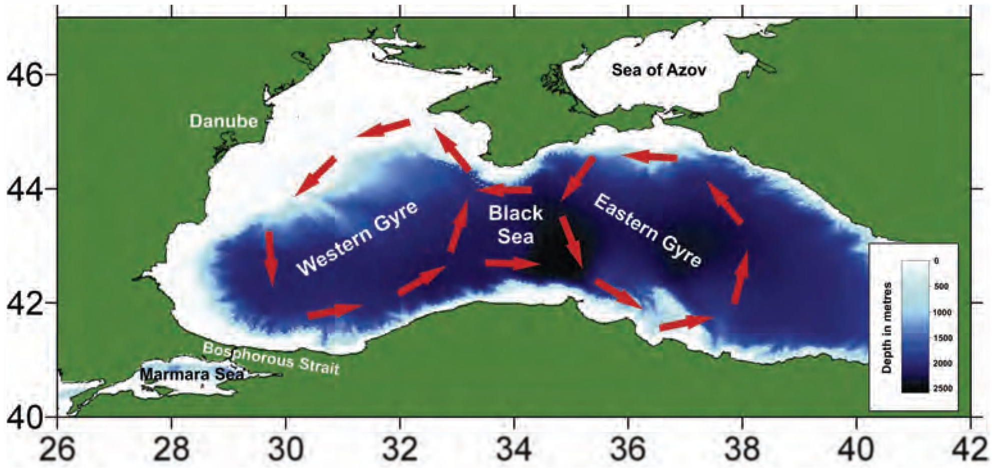


Figure 6.5. The surface circulation pattern in the Black Sea. (From the Philippart *et al.*, 2007a.)

6.4 Ocean variability

Like the atmosphere, the ocean undergoes variability at a multitude of temporal scales, ranging from daily to centennial and longer. Because our primary interest is in the longer term responses of the marine ecology to ocean variability, especially of fish, and because these occur mostly at interannual time-scales or greater, it is these scales that are the focus of this discussion. However, there are two important things to remember.

i) These longer time-scales are caused by persistence at the shorter time-scales, e.g. interannual variability in stratification or upwelling in an area may be caused by more frequent or more intensive windstorms passing overhead every few days, or higher temperatures may be caused by more northerly storm tracks bringing warm air from the south.

ii) The temporal and spatial scales tend to be linked, so that interannual changes may be consistent within a region, interdecadal changes between regions, and multidecadal changes at ocean-basin scales.

6.4.1 The North Atlantic Oscillation

At interannual to decadal time-scales, much of the ocean variability in European waters is linked to the NAO (see Sidebar 6.1; Hurrell, 1995). One of the first to examine the surface temperature response in the North Atlantic to the NAO index was Bjerknes (1962). In most European waters, a positive NAO index produces warm conditions (Visbeck *et al*., 2003). Although the NAO index captures variability in the north–south pressure gradient, it does not reflect changes in the centre of action of the pressure systems in the east–west direction. Such changes do occur; indeed, there has been a more easterly distribution of these centres since the late 1970s compared with earlier decades (Lu and Greatbatch, 2002; Jung *et al*., 2003). These can change the relationship between the NAO and local oceanographic responses.

Nordic and Barents seas

Although much of the temperature variability in the Barents Sea is associated with variations in the NAO index (Ottersen and Stenseth, 2001; Dippner and Ottersen, 2001; Ingvaldsen, 2005), the strength of the temperature–NAO correlations varies temporally, increasing after the early 1970s; this was attributed to an eastward shift in the Icelandic Low (Ottersen *et al*., 2003). In the Norwegian Sea, the Atlantic Current tends to be stronger and more closely confined to the Norwegian coast, whereas it is weaker and extends farther offshore during its negative phase (Blindheim *et al*., 2000; Skagseth *et al*., 2004). Blindheim *et al*. (2000) also suggested a positive correlation between the Atlantic inflow into the Barents Sea and the NAO index, a result supported by current-meter data (Ingvaldsen, 2005) and consistent with the temperature relationship.

Baltic Sea

The interannual variability of the Baltic Sea is also modulated by the NAO. Baltic sea-level elevations are positively correlated with the NAO index through its effect on winds (Andersson, 2002). There is temporal variability in the strength of the correlations and the highest values were obtained during the last couple of decades. At times, however, local winds that are not correlated with the NAO can also be important in determining sea-level elevations. Freshwater run-off and salinity in the Baltic are also correlated with the NAO index, with higher run-off and, subsequently, lower salinities tending to occur during NAO positive years. High NAO years are also associated with reduced ice cover in the Baltic Sea (Launiainen *et al*., 2001).

North Sea and Bay of Biscay

In the central North Sea, NAO positive conditions result in warmer sea surface temperatures (SST; Pingree, 2005). This is believed to result from increased inflow of

Atlantic Water into the North Sea, as well as increased heat input from the atmosphere. On the other hand, reduced circulation of the North Atlantic Current and increased flow north along the European Shelf edge occur during negative NAO phases (Pingree, 2002, 2005). During such years ("Navidad" years), warm water enters the Bay of Biscay and can propagate northwards along the shelf to the west of Ireland (Pingree and Le Cann, 1989; Pingree, 2002). In exceptional Navidad years, the poleward warming extends as far north as Norway (Garcia-Soto *et al.*, 2002).

Iberia and the Mediterranean Sea

From high-resolution, palaeoclimatic records for western Iberia, the NAO was found to determine the variability in precipitation–river input during cold periods (negative NAO) and marine upwelling during warmer periods (positive NAO), a scheme that is reversed in the Galician region (Lebreiro *et al.*, 2006). The NAO is also the main factor influencing winter rainfall patterns and temperature over the Mediterranean region (Krichak and Alpert, 2005).

Black Sea

The NAO predominantly regulates variations in the Black Sea (Oguz *et al.*, 2006). Relatively cold and dry winters occur during the positive phase of the NAO, and milder and wetter winters during its negative phase. The NAO teleconnection is further modulated by the East Atlantic–West Russia (EAWR) atmospheric pattern, comprising the low- and high-surface-pressure-anomaly centres over the North Atlantic and Eurasia (Oguz *et al.*, 2006). During the 1980s, the upper water column of the Black Sea cooled significantly in response to large increases in the NAO index, with a >1.5°C drop in the winter mean SST in the early part of the decade.

6.4.2 The Atlantic Multidecadal Oscillation

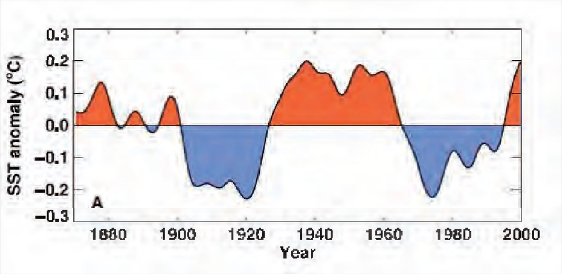
In addition to the variability mentioned above, there is evidence of multidecadal variability with a period of 60–80 years. This period is known as the Atlantic Multidecadal Oscillation or AMO (see Sidebar 6.3).

Northeast Atlantic, Nordic seas, and Barents Sea

During the 1920s and 1930s, there was an increase in the transfer of heat from low to high latitudes (Brooks, 1938; Ahlmann, 1949; Rogers, 1985). This was caused by the Icelandic Low pressure system being located farther east than usual, which resulted in southerly winds pumping warm air into northern Europe and over the Nordic seas (Overland *et al.*, 2004). After 1925, average air temperatures began to rise rapidly and continued to do so into the 1930s. They remained relatively high, although variable, into the 1950s and until cooling began in the 1960s. Sea temperatures also rose, not only in surface layers (Thomsen, 1937; Jensen, Ad. S., 1939; Smed, 1947, 1949; Tåning, 1953), but also in subsurface waters down to 500 m off West Greenland (Jensen, Ad. S., 1939; Dunbar, 1946) and in the deep waters of the Barents Sea (Drinkwater, 2006). The warming was accompanied by a reduction in sea ice, e.g. in the Iceland Sea (Lamb and Johnson, 1959; Schell, 1961), in the Barents Sea (Beverton and Lee, 1965), around Svalbard (Brooks, 1938), and in the Barents and Kara seas (Ahlmann, 1949). Modifications in the ocean circulation patterns, in addition to the air–sea fluxes, contributed to the warming of waters in the north. There is thought to have been increased flow of Atlantic Water to the west and north of Iceland that pushed the colder East Icelandic Current farther offshore, consistent with sea-ice distribution and the increased southwesterly winds off northern Iceland (Stefánsson, 1954). The branch of the North Atlantic Current west of Svalbard increased in strength (Brooks, 1938), along with the inflow of Atlantic Water to the Barents Sea (Bengtsson *et al.*, 2004).

Sidebar 6.3. The Atlantic Multidecadal Oscillation

The Atlantic Multidecadal Oscillation (AMO) index is defined by the SST pattern in the North Atlantic (Kerr, 2000; Sutton and Hodson, 2005) and is associated with the variability in the MOC (see Sidebar 6.1). Through much of the Northeast Atlantic, the Nordic and Barents seas, south to the Celtic Sea, and into the North Sea, the general pattern is one of relatively cold in the early part of the 20th century, warm from the 1920s to 1960s, cool through the 1970s to 1980s, and warm during the last decade of the 20th century and into this century. The highest temperature changes associated with the AMO occur in the northern regions.



The sea surface temperature variability associated with the AMO index obtained from www.worldclimatereport.com.

By the 1960s, temperatures had cooled in these regions, sea ice had expanded, and the flow of the NAC had decreased. During the past decade, there have again been high air and sea temperatures throughout much of the North Atlantic, with the largest increases occurring in northern regions (Johannessen *et al.*, 2004; ICES, 2006i). Convection in the Greenland Sea, caused by winter cooling, has decreased to the extent that deep waters are no longer being renewed. The southerly outflow through the Faroe–Shetland Channel decreased by 20% in the past 50 years (Hansen *et al.*, 2001), and there is evidence from satellites that the north flow of surface waters has decreased since the 1970s (Häkkinen and Rhines, 2004). In the deep, south-flowing waters of the Greenland Sea, there has been a 40-year trend towards decreasing salinity that has spread throughout much of the northern North Atlantic (Dickson *et al.*, 2002), causing a general freshening of the whole Atlantic (Dickson *et al.*, 2003; Curry *et al.*, 2003).

In the Barents Sea, temperatures, as measured at the western entrance and along the Kola Section off Russia, have been relatively high since the beginning of the 1990s, and 2001–2005 has been the warmest five-year period since 1900 (Lien *et al.*, 2006). This has been caused both by increased air temperatures caused by reduced heat lost to the atmosphere and by warmer Atlantic Water inflow to the Barents Sea. Although the volume flux of the inflow has declined in recent years, the Atlantic Water itself is much warmer (Lien *et al.*, 2006). Coinciding with the high temperatures, sea-ice coverage has declined, with a record low in winter 2005 (Sorteberg and Kvingedal, 2006). Warmer than normal temperatures have also been observed off West Spitsbergen as a result of the influx of the warm waters of the West Spitsbergen Current (Walczowski and Piechura, 2006). Waters in the Greenland Sea have also being warming since the 1990s, especially in deep waters (Figure 6.6).

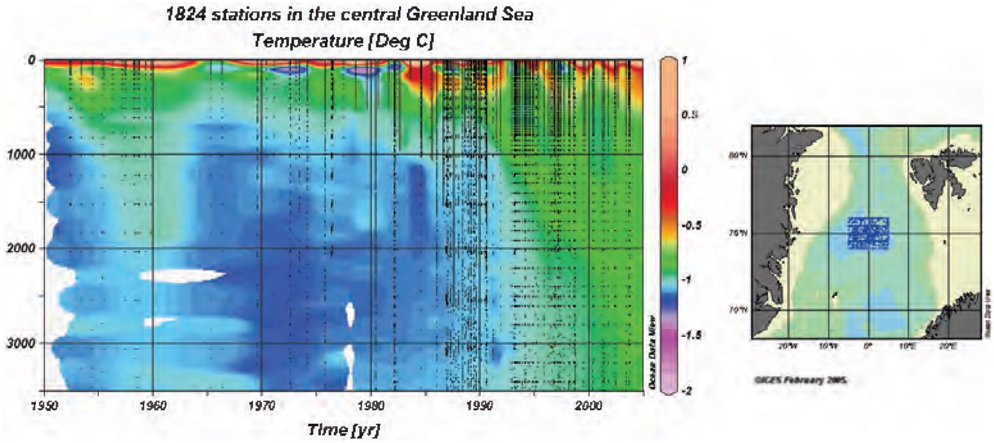


Figure 6.6. Time-series of temperature with depth (left panel) in the central Greenland Sea (area shown in right panel). The black dots in the left panel represent station data. (From www.ices.dk.)

In Iceland, sea temperatures and salinities have increased, both off the south coast, which is bathed in warm Atlantic Waters, and off the north coast, where there tend to be fluctuations between warm Atlantic Waters from the south and west and Arctic Waters from the north. Long-term monitoring of the two regions has demonstrated a gradual increase in salinity and temperature in the south since 1996 (Malmberg and Valdimarsson, 2003; ICES, 2006i) and a continuous warm period since the mid-1990s in the north (ICES, 2006i). In the south, there has been a temperature rise of ca. 1 °C and a salinity increase of 1 psu. In the north, the changes have been higher: 1.5 °C and 1.5 psu respectively. The latter is a result of the increased flux of warm Atlantic Water (Jónsson and Valdimarsson, 2005) and is related to a decrease in the southerly winds along west Iceland (Logemann and Harms, 2006). From model studies, Logemann and Harms (2006) found that, during the period 1997–2003, decreasing southerly winds caused a 30% increase in the volume and heat transport by the Atlantic Waters around west Iceland, leading to a warming of North Icelandic Shelf waters by 0.5 °C.

North Sea

In the North Sea, two climatic periods stand out within the past 50 years. During the most recent change, in the late 1980s, a pronounced modification occurred in large-scale, hydrometeorological forcing and ecosystem parameters, including a marked increase in oceanic inflow and SST (Beaugrand, 2004). This warm-temperate period has continued to the present day. The previous change occurred in the late 1970s and was characterized by low temperatures and salinities, a reduced inflow of Atlantic water, and cold Boreal conditions (Reid *et al.*, 2003).

Celtic Sea, Irish Sea, Bay of Biscay, and Iberia

Observations of SSTs in the Celtic Sea reveal that, following a warm period in the 1880s, temperatures cooled until the early 20th century, increased from around 1920, and remained warm until the 1960s (Southward *et al.*, 2005). A cooler period followed the extremely cold winter of 1962/1963 and continued well into the 1980s; since then, accelerated warming has been apparent. Similar changes have been seen in the Bay of Biscay (Planque *et al.*, 2003a; Blanchard and Vandermeirsch, 2005), the Irish Sea (Evans *et al.*, 2003), and the eastern English Channel (Woehrling *et al.*, 2005). The recent rapid warming in surface temperatures (0.055 °C year^{-1} over 30 years) has occurred in all of the oceanic areas of the Bay of Biscay, but the increase was not significant in coastal areas (Koutsikopoulos *et al.*, 1998; Llope *et al.*, 2006). In locations very near the north coast of Spain, the SST long-term trend appears to be negative (Borja *et al.*, 2002). A decreasing salinity trend in surface and subsurface waters towards the southern Bay of Biscay has been observed from the mid-1990s (González-Pola *et al.*, 2005). An average sea-level rise of 2.12–2.91 mm year^{-1} in the past 50 years was detected in the northwest Iberian Peninsula (Marcos *et al.*, 2005), with a 6.5 mm year^{-1} rise between 1991 and 2001. A decreasing trend in the upwelling index and the seasonality of upwelling off the north coast of Spain has also been detected (Llope *et al.*, 2006). Recent evidence points to large-scale warming of the Mediterranean basin (Béthoux *et al.*, 1990; Astraldi *et al.*, 1995; Walther *et al.*, 2002).

6.5 Projections of climate change

The latest IPCC (2007) report concludes that anthropogenically induced global warming is well underway and that temperatures are projected to continue to rise. These projections or scenarios are generated from coupled, atmosphere–ocean, global-circulation models (GCMs). These suggest that annual air temperatures will rise throughout Europe relative to recent conditions, with the lowest increase (1–2 °C) in the Mediterranean, Iberian, and North seas, the Northeast Atlantic, and southern Nordic Sea regions. Temperature increases will be higher (4–6 °C) in the more northern regions, such as the northern Nordic seas and the Barents Sea, and highest (up to 7 °C) in the Arctic (ACIA, 2005). Owing to its high capacity to store heat, the ocean will not warm quite as much as the land. Throughout Europe, the frequency of extreme high air and ocean temperatures will increase, and extreme low temperatures will decrease. There will be a decrease in the daily temperature range, with night-time lows increasing more than daytime highs.

Precipitation and run-off will increase in northern Europe and the Arctic, but decrease in warmer regions, such as the Mediterranean (IPCC, 2007). In the Arctic, annual precipitation is projected to increase by 20%, with a 30% increase during winter (ACIA, 2005). With the increase in temperature, more precipitation will fall as rain in northern and upland regions, resulting in an increase in run-off in winter and a decrease in spring. At higher altitudes, much of the precipitation will continue to fall as snow in winter, but the spring peak in run-off will occur slightly earlier. The intensity of winter rainfall events north of 45 °N is expected to increase, whereas, to the south, there will be an insignificant change or a decrease (Frei *et al.*, 2006). In central Europe, river run-off will change by ~10% by the 2050s, but this is smaller than the observed natural multidecadal variability (Hulme *et al.*, 1999). In Mediterranean regions, the range in river flows between winter and summer will probably increase considerably, whereas in maritime western Europe, the increase will be less.

As temperatures rise, sea-ice coverage will decrease, with most climate models suggesting an ice-free summer in the Arctic by 2100 (Teng *et al.*, 2006). In the Barents Sea, the winter ice edge is projected to retreat northwards at a rate of ca. 10 km year^{-1} and be ice-free by 2070 (Furevik *et al.*, 2002). A significant loss of ice cover in the western Nordic seas is expected, which, by 2070, will be restricted to the northwestern Greenland Sea and the Baltic. The projected melting ice and increased precipitation and river run-off in northern latitudes will lead to decreases in surface salinity in the order of 0.5–1 psu in the Arctic Ocean, the western regions of the Nordic seas, and in the Baltic by the 2070s (Furevik *et al.*, 2002). Atlantic waters in the Nordic seas will spread farther eastwards and northwards, there will be more continental run-off (partially compensated by high-salinity Atlantic water), and the surface mixed-layer depth will increase as a result of stronger winds.

During the 21st century, there might be a gradual weakening by ca. 20% in the MOC (Hadley Centre[1]). Modelling studies to date, however, suggest that cooling of northern Europe caused by the reduced MOC is unlikely to happen in the next 100 years, and that the current trend of warming is likely to continue, with increases of 2°C and more over this time frame.

With melting ice caps and higher ocean temperatures, sea level is expected to rise throughout the globe by 13–68 cm by the 2050s. Low-lying areas adjacent to regions with low tidal range, such as the coasts of the Mediterranean, Baltic, and Black seas, are more vulnerable than most of the Atlantic Ocean and North Sea coasts (Nicholls and Mimura, 1998). As a result of the strong tidal regime and the effects of storm surges, many of the coastal regions of the North Sea, especially in the south, are particularly susceptible to rising sea levels and an increase in the frequency and severity of storms.

Climate-change simulations for the Baltic suggest temperature increases during all seasons, with a mean annual warming of 3–5°C in the atmosphere and 2–4°C in SST by the end of the 21st century (Graham *et al.*, 2006). One consequence is a decrease in the extent of sea ice by 50–80% over the same period. Winters will probably be wetter and, in the southern parts of the region, summers will probably be drier. As a consequence, winter river flows are expected to increase by as much as 50%, with the opposite pattern in summer.

Regional climate-change scenarios around the North Sea predict an increase in air temperature of 2–3.5°C by the 2080s, with high summer temperatures becoming more frequent, and very cold winters becoming increasingly rare (e.g. Hulme *et al.*, 2002; van den Hurk *et al.*, 2006). Water temperatures will also increase, but not as rapidly as over land. In the Bay of Biscay and English Channel, the predicted rise in temperature is 1.5–5°C over the next 100 years. Temperature changes along the northwest Iberian and French Atlantic coasts should be evident in the first half of the 21st century (Alcock, 2003).

The changes in wind over European marine areas remains uncertain, although the average and extreme windspeeds over northern Europe (IPCC, 2007) are expected to increase. The total number of cyclones in the Mediterranean Sea is expected to decrease, but it is unclear whether the number of intensive cyclones will change (Pinto *et al.*, 2006).

6.6 Summary

This brief review of the marine climate of the Northeast Atlantic demonstrates, from examination of past variability, that atmospheric forcing plays a very important role in controlling ocean variability. A significant proportion of the low-frequency (time-scales up to a decade) variability in the various regions of the North Atlantic are related to large-scale atmospheric patterns, such as the NAO. The NAO is a dominant atmospheric mode in the North Atlantic, and the NAO index is a measure of the atmospheric pressure difference between the Icelandic Low and the Azores High. Changes in this index have been related to variability in air temperatures and winds, as well as to sea temperatures and ocean circulation patterns in the Northeast Atlantic. The AMO is the dominant mode of variability at time-scales of 60–80 years and is related to the basin-wide ocean sea temperature patterns in the North Atlantic.

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[1] http://www.met-office.gov.uk/corporate/scitech0304/MetOfficeScience0304.pdf

However, it should be noted that there is still debate among climatologists and oceanographers as to whether or not the AMO is a true recurring phenomenon and, thus, a natural occurring climate mode. Although the NAO and AMO may account for much of the observed variability in physical ocean variables in the Northeast Atlantic, local climate conditions may also play an important role, and their nature and relative importance compared with the large-scale modes varies from region to region.

An important climate feature in recent years has been the rise in water temperature in much of the Northeast Atlantic, owing to increased warming of air temperature and, more importantly, to changes in circulation patterns. These are carrying more of the concern to governments and the public at large. Much research is being expended to improve projections of future oceanographic conditions under climate change. It is clear that the Northeast Atlantic marine areas will continue to heat up in future. The challenge is to determine by how much, as well as to determine how other ocean variables might change. These are required in order to determine the impacts on the biological components of the marine ecosystem.

7 Primary and secondary production

Christian Möllmann

7.1 Introduction

Marine plankton is a particularly good indicator of climate change for the following reasons (Hays *et al*., 2005): (i) there are no exploitation effects to confound the effect of climate; (ii) planktonic species are short-lived and, hence, respond quickly to physical oceanic conditions; and (iii) non-linear responses of plankton communities may amplify subtle environmental changes (Taylor *et al*., 2002). The benefits are counterbalanced by the generally low availability of long-term time-series for marine phyto- and zooplankton (Hays *et al*., 2005).

Climate can affect marine plankton in a number of ways. Central to the climate–plankton link is the effect of local weather on the timing and magnitude of stratification (Hays *et al*., 2005). Along with this comes variability in light levels, surface temperature, and nutrient recycling from deep layers, influencing phytoplankton growth and, hence, bottom–up processes of ecosystem regulation (Richardson and Schoeman, 2004). In addition to the indirect effect via phytoplankton, climate-induced changes in the physical environment (e.g. temperature, salinity, and advection) may directly affect zooplankton via physiology (Ottersen *et al*., 2004). Climate eventually affects the abundance and biomass of phyto- and zooplankton as well as their spatial (distribution) and temporal occurrence (phenology), altogether affecting the amount of food available to fish in time and space. Here, we review time-trends in phyto- and zooplankton, mainly in the eastern North Atlantic region, and their relation to climate-induced changes in the physical environment.

7.2 Changes in phytoplankton standing stocks and species composition

Climate-related trends in primary production on the scale of the world ocean have been identified from satellite measurements of ocean colour and ocean ecosystem models. Satellite-based investigations suggest that warmer surface temperatures will result in lower oceanic biomass and productivity (Behrenfeld *et al*., 2006), because increased stratification of the water column reduces nutrient supply for photosynthesis. This link between phytoplankton production and climate is found primarily in the tropics and mid-latitudes, where thermal stratification limits vertical mixing. Ocean ecosystem simulations support these results by demonstrating decreases in primary production attributable to increased temperatures intensifying stratification (Boyd and Doney, 2002; Le Quéré *et al*., 2003; Sarmiento *et al*., 2004). These studies, however, also reveal increased primary production at higher latitudes, which is attributable to improved mixed-layer light conditions and extended growing seasons (Polovina *et al*., 1995).

For the North Atlantic, only a few time-series studies have been published that investigate long-term phytoplankton trends in relation to climate change. The major source of information is the colour index provided by the Continuous Plankton Recorder (CPR; Corten and Lindley, 2003). Investigations on the scale of the North Atlantic demonstrated an increase in phytoplankton during the period 1948–2000 (Reid *et al*., 1998a; Edwards *et al*., 2001; Barton *et al*., 2003; Leterme *et al*., 2005). This trend parallels the increase in temperature caused by the North Atlantic Oscillation (NAO; Reid *et al*., 1998b; Edwards *et al*., 2001). The time-series of the NAO index and phytoplankton colour are, however, uncorrelated after removing the time-trend (Barton *et al.*, 2003). Nevertheless, there are parallel trends between NAO-related climate effects and phytoplankton indices in the Northeast Atlantic Shelf (Barton *et al.* 2003). Phytoplankton is affected mainly by light, as well as by nutrient availability and temperature, which, in turn, are affected by advection of water masses and by water column stratification. For the period 1948–1970, it seems likely that relatively cool sea surface temperatures (SSTs) and atmospheric conditions, together with increased northerly winds, reduced stratification and, hence, lowered nutrient availability. This may have limited phytoplankton production, whereas the opposite conditions have increased phytoplankton production during 1970–2000 (Barton *et al.*, 2003). Although the first period was associated with predominantly negative values, the later period was characterized by mainly positive NAO-index values (Hurrell, 1995).

Recent studies confirm an increase in phytoplankton standing stocks since the late 1980s as part of the North Sea regime shift, but suggest that nutrient availability was not the driving force. Using the CPR phytoplankton colour index and satellite-derived chlorophyll *a* data, McQuatters-Gollop *et al.* (2007) demonstrated that improved light conditions caused increases in phytoplankton production. In the recently less turbid North Sea, phytoplankton became free from light limitation and can now use the decreasing nutrients in the area more effectively. Similarly, Llope *et al.* (2009) argue against the importance of nutrients for the increase in phytoplankton. By performing a spatially resolved analysis of the CPR phytoplankton colour index, they demonstrate that increased solar radiation as manifest through increased SST and windspeed were responsible for the shift.

Support for the increase in phytoplankton being caused by climate warming in the subpolar North Atlantic comes from satellite observations (Ueyama and Monger, 2005). Increases in phytoplankton were observed largely during spring, whereas increases occurred between autumn and winter in the subtropical region. These patterns of variability can be explained largely by the pattern of interannual variability wind mixing. Increased wind-induced mixing during the bloom period reduced bloom magnitude over the subpolar and northern subtropical regions while enhancing it over the southern subtropical region. The major mode of interannual variability in the timing of North Atlantic blooms indicates a possible link to the NAO (Ueyama and Monger, 2005). The trend in phytoplankton is partly supported by Behrenfeld *et al.* (2006), who describe worldwide temperature-related phytoplankton fluctuations derived from satellite observations. Temperature-related decreases were most pronounced in the tropics and mid-latitudes. In contrast, at higher latitudes, improved mixed-layer light conditions and extended growing seasons may actually increase productivity (Behrenfeld *et al.*, 2006).

Together with the increased biomass, increased proportions of dinoflagellates and decreased proportions of diatoms in the phytoplankton have been reported for most of the Northeast Atlantic regions (Edwards *et al.*, 2002). This shift in dominance was caused mainly by increased stratification and low nutrient availability in offshore areas favouring dinoflagellates (Leterme *et al.*, 2005). This climate-induced development is most pronounced in the northern North Sea and the adjacent southern North Atlantic (Leterme *et al.*, 2006).

Developments similar to those observed for the North Atlantic and the North Sea have been reported for the Baltic Sea. Increased chlorophyll *a* has been observed in the eastern Baltic, Bornholm and Gotland basins (Wasmund *et al.*, 1998; Wasmund and Uhlig, 2003). In contrast to the North Atlantic, in the Baltic this is discussed mainly in relation to eutrophication (Wasmund *et al.*, 1998). However, the dominance change from diatoms to dinoflagellates during the spring bloom is linked to climate-related processes. Warm winters, especially since the late 1980s, have resulted in a lack of deep mixing, favouring dinoflagellates over diatoms (Wasmund *et al.*, 1998).

7.3 Changes in zooplankton standing stocks and species composition

Although the availability of long-term zooplankton time-series to study the effect of climate on marine ecosystems is still limited (Perry *et al.*, 2004), there is generally more information available than for phytoplankton. A comprehensive description of North Atlantic zooplankton time-series is provided by ICES (ICES, 2006j). Temperature-related, long-term increases in standing stocks have been observed in the western Atlantic on Georges Bank since the 1990s. In the eastern Atlantic, significant increases have been reported for Selvogsbanki (south of Iceland) and the central Baltic Sea, whereas decreases have been reported for the Gulf of Finland (Baltic Sea) and at Helgoland (North Sea; ICES, 2006j). The decrease in the Gulf of Finland is discussed as an effect of decreasing salinities (Lumberg and Ojaveer, 1991) and changed climatic conditions (Hänninen *et al.*, 2000).

Again, the most comprehensive information for the North Atlantic region is provided by the CPR survey (Corten and Lindley, 2003). The most striking feature of the time-series since 1946 is a general, long-term decline in total copepod abundance southeast of Iceland and west of the British Isles, although some areas demonstrate no trend (e.g. northern North Sea). In the western North Atlantic, total copepod abundance has remained relatively unchanged since 1946. Highest copepod abundance is in the eastern North Atlantic and particularly in the southeastern North Sea (Edwards *et al.*, 2007; ICES, 2006j). The long-term changes in zooplankton populations are probably related to the increase in phytoplankton since the 1980s (Richardson and Schoeman, 2004). This large increase in phytoplankton colour since the late 1980s in most regions was related to the temperature increase (Edwards *et al.*, 2001) and corresponds well with temperature–zooplankton relationships reported by Beaugrand (2003).

Using a number of time-series from the North Atlantic, ICES (2006j) found time-series in higher latitudes to have a greater anomaly span (the difference between the minimum and maximum anomaly values) than those in lower latitudes. As water temperature generally decreases with increasing latitude and zooplankton production depends on water temperature, anomaly spans were investigated further as a function of mean water temperatures. Indeed, a good relationship between both variables was found, confirming that cooler waters had a higher anomaly span. Growth and production of zooplankton depend on food availability and water temperature. Hence, in regions with colder water, the gradient between winter and summer air and water temperatures may be larger than those in the warmer water regions. These larger differences would lead to stronger seasonal winds and mixing between surface and deeper, nutrient-rich waters, resulting in stronger phytoplankton blooms and ultimately stronger zooplankton responses (ICES, 2006j).

Long-term changes in species composition and diversity of the copepod community related to hydroclimatic changes have been reported for the Northeast Atlantic (Beaugrand, 2003). The main finding of these analyses is a positive relationship between copepod diversity and the NAO index. Furthermore, there is a change in dominance between the main copepods (*Calanus finmarchicus* and *C. helgolandicus*), which display opposite relationships to temperature: *C. finmarchicus* is favoured by cold temperatures, whereas *C. helgolandicus* is favoured by warm temperatures.

(Beaugrand, 2003). Another important factor determining the abundance of *C. finmarchicus* in the North Sea is advection from their overwintering areas west of the Shetland Isles, as well as a climate-driven process (Heath *et al.*, 1999).

As is true of the adjacent North Sea, the overall abundance of zooplankton in the Celtic Sea has declined in recent years (ICES, 2006j), with substantial drops in *Calanus* abundance now below the long-term mean. *Calanus finmarchicus* is known to overwinter in the Faroe–Shetland Channel, and the abundance of these is known to have been reduced in recent years. In recent years, major changes in zooplankton composition were reported. A main change was the decrease in *Pseudocalanus elongatus*, which was the most abundant species during the period 1988–2004, when it contributed nearly 12% of the total zooplankton abundance; it is now down to 2.3%, the lowest abundance observed over the whole time-series. Total zooplankton abundance demonstrated two decreasing trends from 1988 to 1995 and from 2001 to 2005. This is mainly the result of relatively low abundance of the spring species *Paracalanus*, *Pseudocalanus*, and *Acartia clausi*.

A dominance change in zooplankton, as observed in the North Sea, could also be demonstrated for the Baltic Sea (Möllmann *et al.*, 2000, 2003b). Climate-induced salinity and temperature changes caused a switch from *Pseudocalanus acuspes* to *Acartia spp.* and *Temora longicornis*. Salinity in the central Baltic is strongly dependent on inflow events of highly saline and oxygen-rich North Sea water. The frequency of these events has been reduced since the 1980s, resulting in decreased salinities and oxygen in the Baltic deep water. *P. acuspes* depends strongly on hydrographic conditions in the deep water (Renz and Hirche, 2006); consequently, the long-term trend in *P. acuspes* is correlated with the salinity level (Möllmann *et al.*, 2000, 2003b). In contrast, *T. longicornis* and *Acartia spp.* are situated higher in the water column and are, hence, more influenced by water temperature (Schulz *et al.*, 2007). Temperature has increased since the late 1980s, and this increase is correlated with the long-term trend of the two calanoids (Möllmann *et al.*, 2000, 2003b).

For the southern Bay of Biscay, zooplankton time-series are available from 1988 (La Coruña and Vigo), 1991 (Santander), 1993 (Cudillero), and 2001 (Gijón) onwards. Long-term changes in zooplankton abundance at Santander demonstrated a slightly decreasing trend, probably caused by the longer duration of the water column stratification. The latter could have limited the interchange of nutrients from deeper to surface waters and, consequently, the growth of zooplankton (Valdés and Moral, 1998).

Off the northwest Iberian Peninsula, i.e. in the coastal and neritic regions off Galicia (northwest Spain), the classical pattern of seasonal stratification of the water column in temperate regions is masked by upwelling events from May to September. These upwelling events provide zooplankton populations with favourable conditions for development in summer. Zooplankton standing stocks in La Coruña demonstrated an increasing trend since 1997 as a result of increased seasonal upwelling.

Finally, increases in jellyfish abundance have been reported from different parts of the world ocean (Richardson *et al.*, 2009). Data obtained from the CPR demonstrate in the central North Sea a positive relationship with the NAO and Atlantic inflow to the northern North Sea. Since 1970, jellyfish frequency has been also significantly negatively correlated with mean annual pH, independent of NAO trends. Jellyfish frequency increased in the mid-1980s, coincident with the reported regime shift in the North Sea and tracking trends in phytoplankton colour (Attrill *et al.*, 2007; Richardson and Gibbons, 2008). However, in general, a multitude of factors might have caused the jellyfish increase, such as overfishing, eutrophication, and translocations, necessitating further investigation (Richardson *et al.*, 2009).

Ocean acidification may negatively affect calcifying plankton, opening ecological space for non-calcifying species. Recently, a study of climate forcing of jellyfish reported the first analysis, suggesting that there were more jellyfish (generally considered a non-calcifying group) when conditions were more acidic (lower pH) from one area within the North Sea. We examined this suggestion for a number of areas in the North Sea and beyond in the Northeast Atlantic using coelenterate records from the CPR and pH data from ICES for the period 1946–2003. We could find no significant relationship between jellyfish abundance and acidic conditions in any of the regions investigated. We conclude that the role of pH in structuring zooplankton communities in the North Sea and further afield, at present, is tenuous.

7.4 Phenologic and biogeographic changes in phyto- and zooplankton

Marine trophodynamics depend strongly on the distributional overlap and relative timing of important events, such as the spring bloom. Recent studies provided evidence that increased temperatures can change the timing of the spring phytoplankton bloom, however with varying levels and directions of response (Edwards and Richardson, 2004). At Helgoland Roads, the mean diatom bloom was delayed and shifted to the end of the first quarter of the year in relation to warming (Wiltshire and Manly, 2004). Data from the CPR survey, however, demonstrated that, in general, diatom spring blooms in the North Sea are relatively fixed in time (Edwards and Richardson, 2004). CPR data, in general, indicate a positive correlation between increased temperatures and the peak in the seasonal cycle of dinoflagellates and diatoms. In zooplankton, copepods and other holozooplankton in summer demonstrated positive correlations to SST, whereas those having peaks in spring and autumn did not (Edwards and Richardson, 2004). Despite the observed variability in the phenological response to increased temperatures, mismatches in timing between successive trophic levels have been observed, with important ramifications for ecosystem functioning (Edwards and Richardson, 2004).

In addition to temporal mismatches in trophodynamics, temperature-induced changes in spatial distribution can also cause disruptions in species interactions. For the North Sea and the adjacent Atlantic Ocean, substantial changes in the biogeography of calanoid copepods have been demonstrated in relation to climatic warming (Beaugrand *et al.*, 2002). Warm-water species have extended their northward extension by more than 10° latitude, whereas the number of cold-water species decreased. These biogeographic changes are related to the northern hemisphere temperature and the NAO index.

A further example for a change in distribution of copepod communities related to climate-induced changes in hydrography and important for fish production has been observed in the central Baltic Sea. The dominant copepods in the area have different horizontal distribution patterns. Although *P. acuspes* concentrates in the centre of the deep Baltic basins, the other two copepods are mainly distributed at the fringes of the basins (Hansen *et al.*, 2006). The dominance change from *P. acuspes* to *T. longicornis* and *Acartia spp.* (Möllmann *et al.*, 2003b) has, hence, resulted in a redistribution of the zooplankton biomass. This redistribution of the copepod biomass has reduced the overlap with first-feeding larvae of cod (*Gadus morhua*), contributing to the low recruitment levels of the fish stock since the early 1990s (Hinrichsen *et al.*, 2002, 2005).

7.5 Summary

Figure 7.1 summarizes the effect that climate has on marine phyto- and zooplankton and how this may propagate to higher trophic levels, i.e. mainly fish. Generally, there can be two lines of effects: (i) effects on standing stocks (i.e. biomass and abundance) of phytoplankton, which exert bottom–up effects on zooplankton or direct effects on zooplankton standing stocks; and (ii) effects through changes in distribution and phenology potentially causing spatio-temporal mismatches between adjacent trophic levels. Both lines of effects may cause food limitations for upper trophic levels, i.e. mainly early life stages of as well as adult planktivore fish.

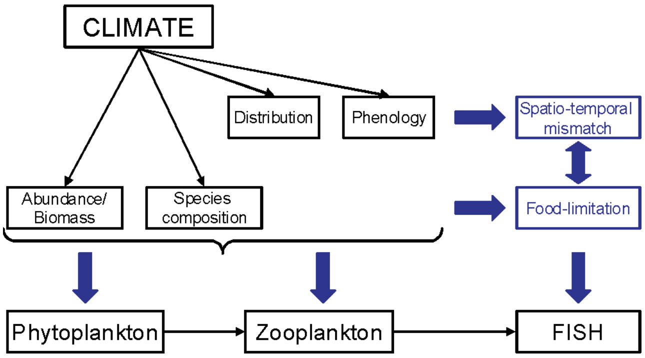

Figure 7.1. Schematic representation of the effect of climate on marine phyto- and zooplankton populations, and their effect on fish production.

8 Ecosystem structure and function

Mike R. Heath and Alejandro Gallego

8.1 Introduction

8.1.1 Objectives

This section presents an overview of the literature that considers how the marine ecosystem, and particularly the fishery ecosystem, may be subject to reorganization in response to pressures on the component species resulting from climate change (see Section 6) and exploitation by fishing. Reviews of the ecological response to climate change over a range of different ecosystems (e.g. Walther *et al.*, 2002; Section 10) have emphasized the complex and indirect nature of the effects of climate on ecosystem dynamics in the marine environment. These effects include: modifying primary and secondary production (see Section 7); offsetting the match between producers and consumers (e.g. Stenseth *et al.*, 2002); affecting migration patterns and spatial distribution of species; and influencing physical processes (e.g. upwelling), which, in turn, affect nutrients, production, and prey availability to higher trophic levels, etc. Furthermore, human exploitation may intensify these climate-change effects on marine systems (Walther *et al.*, 2002; Enghoff *et al.*, 2007; Section 5). In this context, because fishing is such a major component of the mortality of many fish species, we consider the impacts of climate change and fishing together.

8.1.2 Section outline

We start our literature review on how marine ecosystems respond to climate and fishery pressures by defining the concepts of "ecosystem structure" and ecosystem function" (Section 8.1.4), then examine the effect of climate and fishing on species richness (Section 8.2) and regime shifts (Section 8.3). We review a number of ecosystem control hypotheses (Section 8.4), namely top–down vs. bottom–up control, "oscillating control", and trophic cascades (Sections 8.4.1–8.4.3), and conclude with a section on management considerations (Section 8.5).

8.1.3 Overall relevance

As stated in the Foreword, climate change will affect fishery resources and challenge managers to develop sustainable exploitation strategies. Individual taxa at all trophic levels in the ecosystem, not only exploited species, may be influenced by climate change, if only as a consequence of thermal response (e.g. see Section 3). However, the system as a whole may have dynamics that cannot be simply deduced from knowledge of individual species responses, owing to the complex network of non-linear, predator–prey interactions involved in the foodweb (Scheffer and Carpenter, 2003). This section goes beyond the focus on individual taxa to examine the effect of climate and fisheries on ecosystem-level responses, namely ecosystem structure and ecosystem function. Focusing on ecosystem-level responses is particularly relevant, because some of the analyses of the effect of climate and fisheries (e.g. Eide, 2008) are based on the assumption that the current ecosystem structure is preserved, and this may not be a realistic scenario.

8.1.4 Definitions

Although a number of national and international policy drivers (Bergen Declaration[2], EU Habitats Directive[3], etc.) refer to the concepts of ecosystem structure and function, there is still considerable variability in the accepted meaning of these terms (MRAG and UNEP-WCMC, 2007).

The concept of **ecosystem structure** generally refers to both "the biotic and abiotic attributes of the ecosystem". The latter include elements such as the physical structure of the substratum (e.g. seabed type, grain size) and the physico-chemical structure of the water column (e.g. temperature, salinity, oxygen, current), whereas the former includes factors such as community structure, functional groups, species richness, biodiversity, and species attributes (longevity, size, reproductive strategy, range, distribution, habitat preference, etc.).

Ecosystem function is often related to the biotic (and sometime abiotic) processes that take place within the ecosystem. For example, the definition by Naeem *et al.* (2002), "the activities, processes or properties of ecosystems that are influenced by its biota" links ecosystem function to the concept of biodiversity, and is used by a number of authors who focus on the role of individual habitats and species (e.g. Bremner *et al.*, 2006; Hiscock *et al.*, 2006). Elements of ecosystem functioning identified by Hiscock *et al.* (2006) are: energy transfer, elemental cycling, productivity, food supply and export, and modification of physical processes.

Here, we review the effects of climate and fishing on ecosystem structure and function, including species richness, regime shifts, ecosystem controls, and trophic cascades.

8.2 Species richness

Species richness (i.e. the number of species present) is an important element of ecosystem structure and foodweb complexity. Latitudinal gradients in species richness are well documented across terrestrial, freshwater, and marine systems, with fewer species present at higher latitudes, although the causes remain unclear (Townsend *et al.*, 2003). Gradients in primary production, seasonality, specialization of predators, environmental harshness, and evolutionary age of the system have all been examined in the ecological literature, but none provides unambiguous explanations (Begon *et al.*, 2006). In the ocean basins, species richness of fish communities has been noted to decline with poleward distance from the tropics in both hemispheres (Cheung *et al.*, 2005), with co-varying effects as a result of depth (Macpherson and Duarte, 1994; Macpherson, 2003). In the North Atlantic, there appears to be a correlation between richness and temperature, such that for a given latitude, both richness and temperature are greater in the eastern Atlantic than in the western Atlantic (Frank *et al.*, 2007). Semi-enclosed seas, such as the Baltic and Mediterranean, tend to be outliers in the latitudinal pattern of richness. The former is colder and younger in a geological and evolutionary sense than the North Atlantic in general, and it exhibits lower species richness than expected for the latitude, whereas the Mediterranean is warm for its latitude and provides habitat for both temperate and subtropical species.

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[2] http://www.ospar.org/html_documents/ospar/html/bergen_declaration_final.pdf.

[3] http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=CELEX:31992L0043:EN:HTML or *Official Journal L 206, 22/07/1992 P. 0007–0050*

It has been predicted that climate change will lead to changes in local and regional species richness through species extinctions and latitudinal range shifts (see Section 10). Hiddink and ter Hofstede (2008) demonstrate that, in the North Sea, species richness of fish, a group of ecological and socio-economical importance, has increased over a 22-year period, and that this rise is related to higher water temperatures. The number of fish species displaying increased distribution ranges in the North Sea (mainly smaller species of southern origin) was eight times greater than those whose range decreased (primarily large and northern species). This increase in species richness can be explained by the fact that fish species richness, in general, decreases with latitude. This observation confirms that the interaction between large-scale biogeographic patterns and climate change may lead to increasing species richness at temperate latitudes.

Fishing can also lead to considerable changes in species richness. An analysis of decadal changes in Mediterranean foodwebs, in relation to exploitation, demonstrated that biomass of higher trophic levels increased under no-fishing scenarios, and the mean trophic level of the community and the fish/invertebrate biomass ratios were substantially lower in exploited foodwebs (Coll *et al.*, 2009a).

In addition to species richness, life-history strategies of different species can also be affected by climate as an ecosystem-scale response. There is evidence for foodweb-wide modifications in life-history strategies in response to environmental forcing, resulting from frequency and amplitude shifts in resource availability over varying temporal and spatial scales (Suryan *et al.*, 2009).

8.3 Climate effects on marine ecosystems, including regime shifts

A wide range of environmental effects (correlated with the NAO index) on species physiology, spatial distribution, competition, and predation have been identified, as well as complex, non-linear effects on population dynamics (Ottersen *et al.*, 2001; Stenseth *et al.*, 2002). However, disentangling climatic and anthropogenic effects (Section 5) on ecosystem function is sometimes problematic. For example, some of the indices proposed to measure changes in ecosystem function, such as the slope of the size spectrum (based on the principle that size determines an individual's trophic position in the ecosystem), are affected by human activities (fishing; Gislason and Rice, 1998) and environmentally mediated changes in species growth (Gislason, 2001). A comprehensive review of the response of North Atlantic marine ecosystems to climate variability has been compiled by Drinkwater *et al.* (2003).

However, the results of such correlative approaches have been controversial, and correlations between physical and biotic time-series often lack robustness over time (e.g. Reid *et al.*, 1998a; Skud, 1982; Solow, 2002), unless the underlying processes can be identified (e.g. Agostini *et al.*, 2008). Collie *et al.* (2004), Scheffer *et al.* (2001), and Scheffer and van Nes (2004) have categorized ecological responses to physical forcing as (i) nearly linear; (ii) non-linear, but single valued; and (iii) multiple stable states, which might be termed "regime states". Of particular concern is the possibility of alternative stable states, because the implication is that shifts between states caused by physical forcing are not automatically reversed by relaxation of the forcing. In the context of foodweb control, the scenario would also apply to trophic cascades induced in top–down controlled systems by, for example, the removal of a key predator (see section 8.4.3). Thus, the cause of regime shifts is not exclusively physical forcing, and fishery-induced regime shifts have also been described in the literature (e.g. Savenkoff *et al.*, 2007). Although Steele (2004) states that, so far, there is little evidence that changes in ocean climate such as *El Niño*, the Pacific Decadal

Oscillation, or the North Atlantic Oscillation can induce alternative stable states in marine ecosystems, such hypotheses are relatively common and extend beyond the recent past into more distant historical records, such as those analysed by Gutierrez *et al.* (2009).

Recently however, a wealth of studies demonstrated the existence of alternative stable states in various terrestrial and aquatic ecosystems (Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003; Kimmel *et al.*, 2009). The term "regime shift", describing the transition between different states, was first used for marine ecosystems to describe dominance changes between fish populations (e.g. the fluctuations between anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*)) in several regions of the world ocean (Lluch-Belda *et al.*, 1989). Nowadays, regime shifts are defined mainly on the basis of changes in the ecosystem as a whole (Collie *et al.*, 2004). They are usually occasional to frequent and abrupt changes in ecosystem structure and function, occurring at multiple trophic levels and on large geographic scales (Bakun, 2006; Collie *et al.*, 2004; Cury and Shannon, 2004; deYoung *et al.*, 2004a; Lees *et al.*, 2006).

Marine ecosystem regime shifts have been explained mainly as a result of multiple causes, namely climatic regime shifts, overexploitation, or a combination of both (Scheffer and Carpenter, 2003; Lees *et al.*, 2006). They have been described for various marine ecosystems, with the most prominent examples coming from the North Pacific (Hare and Mantua, 2000), the Scotian Shelf off Canada (Choi *et al.*, 2005), the US Northwest Atlantic continental shelf (Link, 2002), the North Sea (Beaugrand, 2004; Weijerman *et al.*, 2005), the Black Sea (Daskalov, 2002; Daskalov *et al.*, 2007), and the Baltic Sea (Möllmann *et al.*, 2008, 2009).

8.4 Ecosystem control hypotheses and trophic cascades

8.4.1 Bottom–up vs. top–down control

Production of higher trophic levels in the ecosystem has traditionally been considered a function of primary production and the efficiency of transfer between trophic levels (Aebischer *et al.*, 1990; Schwartzlose *et al.*, 1999; Chavez *et al.*, 2003). Indeed, impoverished regions that are starved of nutrients and the trace elements required for phytoplankton growth can support only small fishery yields. In contrast, regions where oceanographic processes or major river inputs deliver large quantities of nutrients to the surface waters typically support substantial fisheries.

Comparing across ecosystems in the Northwest Atlantic, Frank *et al.* (2006) found a positive correlation between long-term average primary production and fishery yield. However, within individual ecosystems, the relationship over time between primary and higher trophic-level production was clearly positive in some and clearly negative in others. Positive relationships between prey and predator time-series are indicative of resource-driven or bottom–up control of the foodweb components, whereas inverse relationships indicate predation-driven or top–down control. The latter has long been recognized in some lake systems and in nearshore or intertidal marine communities, where species richness is low and the system is dominated by a small number of predators (Chapin *et al.*, 1997).

Recently, it has become clear that both bottom–up and top–down control may also pertain in open-shelf ecosystems, and that fluctuations between these states are important signals of pressure caused by fishing and/or climate changes. Frank *et al.* (2006, 2007) concluded that the species-poor, low-primary-production systems, which predominate at high latitudes and low temperatures, are fundamentally top–down controlled, whereas low-latitude, species-rich, high-primary-production systems are fundamentally bottom–up controlled. Deeper eastern ocean boundary systems are more strongly influenced by bottom–up forcing, whereas shallower western ocean boundary systems, mainly continental shelves, are generally more strongly influenced by top–down forcing, although synchronous events are also observed to have taken place around the world's oceans (Megrey *et al.*, 2009).

In the North Sea, Heath (2005) demonstrated that the pelagic foodweb had underlying bottom–up control during the 1970s, 1980s, and 1990s, with significant positive correlations between zooplankton and planktivorous fish production, and between planktivorous and pelagic piscivorous fish production during the period 1973–2000. Similarly, Frederiksen *et al.* (2006) demonstrated that, off the Scottish east coast in the northwestern North Sea, the foodweb connecting zooplankton through planktivorous fish (sandeels) to breeding success of seabirds was also bottom–up controlled. Frank *et al.* (2007) found that, given the species richness in the North Sea, these correlations were consistent with the emergent pattern of bottom–up vs. top–down control for shelf ecosystems around the North Atlantic. However, Heath (2005) also noted that, for the benthic foodweb, there was a highly significant negative correlation between the consumption of macrobenthos by demersal fish and the production of macrobenthos carnivores, which was symptomatic of top–down control. Thus, within the same geographic domain, different branches of the foodweb displayed fundamentally different control mechanisms.

Similarly, several authors have identified simultaneous bottom–up and top–down control in the pelagic ecosystems of major upwelling regions (e.g. Benguella, Peru). In this case, small planktivorous fish play a key role in the system, but the guild is often dominated by only a single species (sardine or anchovy). Higher trophic levels are subject to bottom–up control by the abundance of planktivorous fish prey, whereas zooplankton is subject to top–down control, also by planktivorous fish acting as predators. Fishing can also become an important predatory impact, taking over consumption of small pelagics from declined natural predators (Watermeyer *et al.*, 2008). Such systems have been termed as being under "wasp-waist" control (Rice, 1995; Bakun, 2006; Hunt and McKinnell, 2006).

A key factor that may dictate whether a system is prone to top–down or bottom–up control may be species redundancy, or the fungibility of species (i.e. the degree to which species are interchangeable with others of the same functional type within a given ecosystem). In the relatively species-rich North Sea, Heath (2005) noted that sprat, herring, sandeels, and Norway pout appeared to be functionally interchangeable within the planktivorous fish guild. As a consequence, the production of the guild as a whole was clearly bottom–up driven by zooplankton production, although the constituent species had undergone boom-and-bust phases in response to the fishing and climatic factors, which bore little or no relation to underlying plankton production. For example, as herring production declined through the 1970s, sprat production expanded to fill the foodweb niche vacated by herring, but reversed in the 1980s as herring stocks recovered.

In contrast to the North Sea, the planktivorous fish guild at high latitudes in the North Atlantic (e.g. Barents Sea) is dominated by capelin and herring, with few other fungible species present, and capelin dynamics demonstrate more evidence of top–down control by piscivory than of bottom–up control by zooplankton (Hjermann *et al.*, 2004b). In the context of the latitudinal gradient in species richness and trophic control, noted by Frank *et al.* (2006, 2007), the scope for species fungibility is presumably reduced in species-poor systems, making them more prone to top–down control. Thus, in the species-poor Baltic Sea, cod and sprat abundance demonstrate a strong inverse correlation, indicating top–down control of sprat by cod, with cod dynamics being affected by a combination of fishing and climatic factors (Alheit *et al.*, 2005; Köster *et al.*, 2003a, 2003b; Möllmann *et al.*, 2008). Similarly, Worm *et al.* (2006) noted that the proportion of fisheries in a collapsed or extinct state (indicating top–down control by fishing) declines monotonically with species richness.

8.4.2 Oscillating control

Fishing, and climatic factors that affect the productivity of individual species, also have the capacity to shift a system between bottom–up and top–down control. For example, Hunt *et al.* (2002) demonstrated a pattern of reversibly alternating control in the Bering Sea pelagic ecosystem between bottom–up in cold regimes and top–down control in warm regimes (Figure 8.1). Similarly, Litzow and Ciannelli (2007) describe changes in the trophic control of the ecosystem along the shelf south of the Alaska Peninsula (North Pacific). The system was initially bottom–up controlled in the early 1970s (as indicated by positive correlations between prey (mainly shrimp and capelin) and predators (mainly Pacific cod)), shifted to top–down control during the late 1970s, coincident with a rise in temperature, then reverted to bottom–up control. The oscillation between control processes coincided with a change in state of the system: from a situation in which shrimp and capelin abundance (measured by catch per unit of effort (cpue) in surveys and commercial landings) was high and Pacific cod were scarce to one in which cod abundance was ~50-fold greater and shrimp and capelin had declined by a factor of ~100. The mechanism of the state change was hypothesized to be warming-mediated shifts in the survival of Pacific cod larvae, related to the timing of zooplankton production, and to temperature-dependent migration patterns of cod.

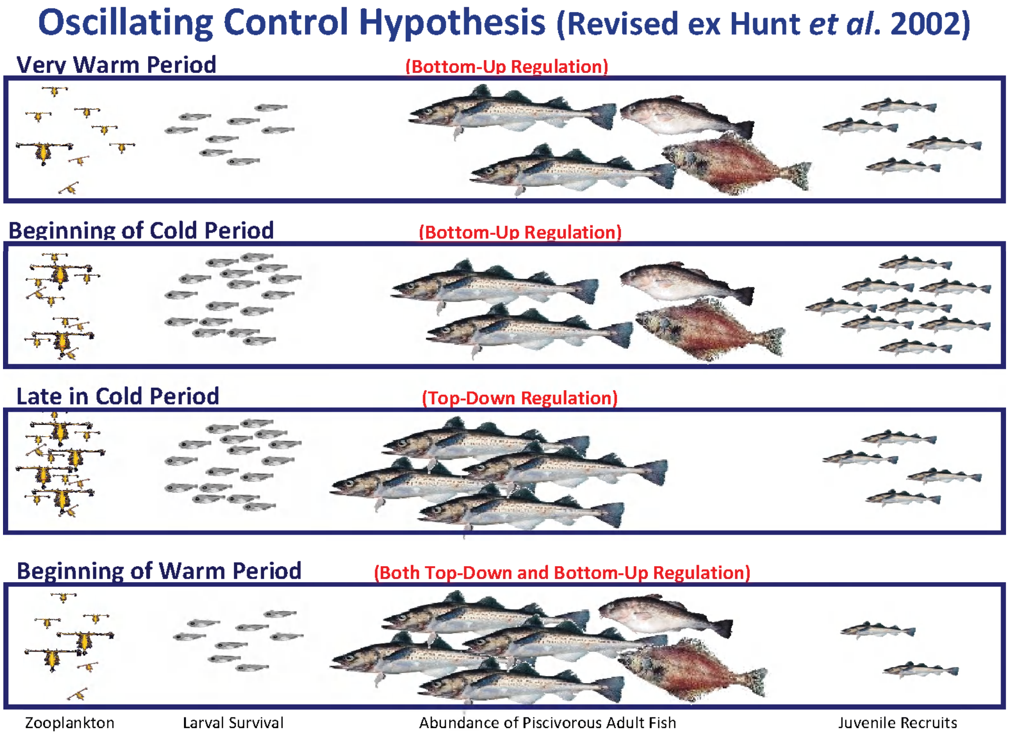


Figure 8.1. Schematic illustration of oscillating control, modified from Hunt *et al.*, (2002; G. Hunt, University of California, Irvine, California, pers. comm.). The number of recruits affects not only pollock population dynamics but also the availability of age-1 pollock to predators, such as marine birds and pinnipeds. Prolonged, very warm periods are very bad for recruitment because there are few/no large *Calanus marshallae* in the system and no shelf euphausiids (*Thysanoessa raschii*). The result is that, in warm periods, age-0 pollock do well in spring but have little in the way of lipid-rich food in summer, resulting in poor body condition and poor overwinter survival. Additionally, cannibalism increases as the larger fish switch from eating large crustacean zooplankton to small fish. In cold periods, there appear to be fewer age-0 in spring/summer because copepod production is limited by water temperature and larval–juvenile pollock survival is limited by food availability, but survivors are in much better condition and the ensuing over-winter survival can result in a strong year class. Higher abundance of age-0 pollock in summers of warm years is consistent with the original Oscillating Control hypothesis of Hunt *et al.* (2002), but their failure to recruit, despite a declining adult biomass, is not (Hunt *et al.* 2008). The alternating top–down and bottom–up control of pollock populations is likely to be modulated by the effect of 0-group overwintering starvation and the switching of predators from large crustacean zooplankton to age-0 pollock in warm years when these alternative prey is scarce (Hunt *et al.*, in press).

8.4.3 Trophic cascades

Top–down controlled systems are sensitive to overfishing and depletion of predator species (Christensen *et al.*, 2003), which can lead to large-scale reorganization of the trophic structure caused by the release of lower trophic levels from grazing pressure, termed a "trophic cascade". Such changes represent significant departures from the natural state which have other, often unforeseen, consequences and which may or may not be reversible in decadal time-scales, even by intervention to eliminate fishing mortality. Examples are the increase in shrimp production and fisheries in high-latitude ecosystems, where cod has been depleted by fishing (Worm and Myers, 2003; Frank *et al.*, 2005). In the Black Sea, overfishing of marine predators provoked cascading changes, resulting in increases in abundance of planktivorous fish and jellyfish, a corresponding decrease in zooplankton and increase in phytoplankton (Daskalov, 2002), and a decrease in the mean trophic level in the ecosystem (Daskalov, 2000). In the Baltic Sea, a combination of climate change and overfishing caused the collapse of the cod stock, leading to a trophic cascade involving zoo- and phytoplankton (Casini *et al*., 2008a). For example, in the Baltic Sea, dominance within the zooplankton changed as a result of reduced salinity and increased temperature.

The change in hydrography also affected the reproductive success of the major fish species, resulting in a change in dominance from a piscivorous fish (cod) to a planktivorous species (sprat), with overfishing amplifying the climate-induced changes at both trophic levels (Möllmann *et al*., 2008). Pinnegar *et al*. (2000) reviewed 39 documented trophic cascades (eight of which include humans as a trophic level) from 21 locations around the world; all but two of the cascades are from shallow systems underlain by hard substrata (kelp forests, rocky subtidal, coral reefs, and rocky intertidal).

Species loss or invasion through environmental events may also precipitate trophic cascades in top–down-prone systems. For example, unusually warm conditions during summer 1999 caused mass mortality of invertebrate species in the northwestern Mediterranean (Cerrano *et al*., 2000; Perez *et al*., 2000), allowing other species, pre-adapted to the new conditions, to replace them and potentially precipitating foodweb restructuring. In the Black Sea, there was a population explosion in the mid-1980s of the introduced gelatinous species *Mnemeopsis leidyi* (Grishin *et al*., 1994), which became a major competitor with indigenous pelagic fish stocks for zooplankton production (Grishin *et al*., 1994; Shiganova, 1998). This compounded the effects of overfishing (Daskalov, 2003), leading to a trophic cascade manifested as extreme phytoplankton blooms (Yunev *et al*., 2002).

8.5 Management considerations

Recent evidence demonstrated that climate change and fishing often together affect ecosystem structure and function. Ultimately, they can trigger a shift of an ecosystem to another permanent state (Scheffer *et al*., 2001; Scheffer and Carpenter, 2003). However, a prerequisite for this occurrence is a loss of resilience, which makes the system more fragile to perturbations (Folke *et al*., 2002; Folke, 2006). Discontinuous regime shifts demonstrating hysteresis in their response may have heavy costs for society (Scheffer *et al*., 2001). Restoring an ecosystem to a more desirable state after it has turned to another stable state usually requires drastic and expensive interventions (Scheffer and Carpenter, 2003; Suding *et al*., 2004). Therefore, the goal of management must be to sustain the stability of domains rather than trying to control fluctuations (Scheffer *et al*., 2001; Folke, 2006), although understanding the mechanisms of ecosystem-state changes is critical to making inferences about both the causes and appropriate management responses (Frisk *et al*., 2008).

From a management point of view, the consequences of forcing ecosystems between alternative stable states, or along strongly non-linear trajectories with strong hysteresis, are clear (Beamish *et al*., 2004). Such changes, usually precipitated by fishing in combination with climate change, occur mostly in top–down controlled ecosystems, which are most likely to be found at high latitudes. Identifying such systems, based on species richness, primary production characteristics, and temperature, seems to be an important step towards devising more holistic schemes for ecosystem harvesting. Another development indicated by such considerations is a move toward fishery management targets based on functional groups, in addition to those based on target species, with the aim of conserving ecosystem stability as well as individual species (Hughes *et al*., 2005).

9 Ecosystem productivity in the Mediterranean and Black seas

Georgi M. Daskalov

9.1 Introduction

This section reviews recent research into relationships between climate and ecosystem productivity in the Mediterranean and Black seas. Both seas are deep, enclosed basins, and global and regional climate affects them mainly through atmospheric teleconnections. The major teleconnection pattern in the area is the North Atlantic Oscillation (NAO; Wallace and Gutzler, 1981). The NAO is characterized by a dipolar pattern of the atmospheric pressure field, and its effects on the regional climates of the Mediterranean and Black seas often have an opposite sign (e.g. Demirov and Pinardi, 2002; Oguz *et al.*, 2006). Another difference is water balance, which is positive in the Black Sea but negative in the Mediterranean. Therefore, the influence of freshwater run-off (also influenced by the NAO) is very important in the Black Sea. Both seas have been populated, exploited, and explored by humans since antiquity, but major anthropogenic changes, such as fish stock collapses, cultural eutrophication, and invasions by alien species, have occurred in the second half of the 20th century.

9.2 Mediterranean Sea

A review of climate-related changes in the Mediterranean was published recently by Philippart *et al.* (2007a). The Mediterranean Basin is ca. 3680 km long, with an average width of 700 km, and is divided into the western and eastern Mediterranean basins, which are separated by the Straits of Sicily and the central Mediterranean, which includes the Adriatic and Ionian seas. The western Mediterranean (ca. 1600 m mean depth) consists of two deep basins, the Algero–Provençal Basin and the Tyrrhenian Sea. The eastern Mediterranean includes the Aegean Sea and the Levantine Basin.

The principal characteristics of the Mediterranean Sea include:

i) limited freshwater input (the Mediterranean as a whole has a freshwater deficit of 0.9 m year^{-1}, because evaporation exceeds precipitation and run-off);

ii) major water exchanges through the Straits of Gibraltar, with surface inflow of Atlantic waters (top 300 m) and deep outflow of high-salinity Mediterranean waters;

iii) small-amplitude tides (microtidal regime);

iv) high oxygen concentrations;

v) high deep-sea temperatures (>12.8 °C); and

vi) oligotrophic conditions, with low nutrient concentrations, that typically decrease eastwards.

Consequently, the western and eastern Mediterranean basins are characterized by different primary productivity, namely ca. 350–450 mg C m^{-2} d^{-1} in the western Mediterranean and ca. 150 mg C m^{-2} d^{-1} in the eastern Mediterranean (Turley *et al.* 2000). The much lower productivity in the eastern Mediterranean, together with the strong summer stratification of the water column and the tight control of the microbial loop, results in exceptionally low exports of primary organic matter to the seabed (Turley *et al.*, 2000). The Mediterranean Sea, being a warm sea located in temperate latitudes, hosts both temperate and subtropical species, and is therefore biologically diverse; it has also been diversified by its complex geological history and by the introduction of Indo-Pacific species via the Suez Canal after its construction in 1869.

9.2.1 Influence of climate change on the physical environment

Rixen *et al.* (2005) analysed trends in temperature and heat content in the Mediterranean since 1950. Temperature has increased at the surface and near the bottom in the western Mediterranean since the 1990s. Sea surface temperature (SST) in the eastern Mediterranean initially decreased around 1990 and then started to increase (Rixen *et al.*, 2005). A similar trend in SST was observed in the Black Sea (Daskalov, 2003; Oguz *et al.*, 2006). Bottom temperature in the eastern Mediterranean demonstrated a steady increase. The NAO was found to be positively correlated with temperature (negatively to wind) in the western Mediterranean and negatively to temperature (positively to wind) in the eastern Mediterranean, with intermediate effects in the central areas, including the Adriatic Sea (Demirov and Pinardi, 2002). This difference translated into opposite changes in circulation and deep-water composition in the western and eastern Mediterranean basins, respectively (Demirov and Pinardi, 2002; Rixen *et al.*, 2005). Rixen *et al.* (2005) have concluded that changes in the Mediterranean are strongly influenced by North Atlantic climate.

9.2.2 Influence of climate change on the biological populations and fisheries

In the past, most studies exploring the links between plankton and climate have focused on local environmental conditions, and significant links between plankton abundance and distribution vs. temperature and local wind strength and direction have been found (e.g. Menard *et al.*, 1994; Licandro and Ibanez, 2000).

More recently, the influence of Atlantic climate (as indexed by the NAO) has been explored. Large transport of water in the Corsica Channel was found to correlate to low NAO (Astraldi *et al.*, 1999). Increased circulation through the Corsica Channel is beneficial to the development of diatom blooms in Villefranche Bay (Gómez and Gorsky, 2003).

Molinero *et al.* (2005), who explored the influence of several indices of Atlantic, regional, and local (northwestern Mediterranean and Ligurian Sea, respectively) climate on zooplankton, found correlations between Atlantic climate (represented by the NAO, Gulf Stream index, and other climatic patterns) and zooplankton. They hypothesized a causal chain, linking Atlantic climate to water temperature in the northwestern Mediterranean, which was responsible for outbreaks of jellyfish during the 1980s. The high abundance of jellyfish was related to a marked drop in copepod abundance, explained by jellyfish predation.

In the western Mediterranean, climate influences the boundaries of biogeographic regions, with some warm-water species recently extending their ranges and colonizing regions where they were previously absent. The northward migration of species with an affinity for warmer waters has been demonstrated in several regions (Bianchi and Morri, 1994; Morri and Bianchi, 2001; see Section 10.3.7). The Ligurian Sea, one of the coldest areas in the Mediterranean, has a smaller number of subtropical species and a higher abundance of species characteristic of cold–temperate waters.

A large mass-mortality event was observed in 1999 (Cerrano *et al.*, 2000; Perez *et al.*, 2000), when a positive thermal anomaly during summer combined with an increase in the warm, mixed layer to a depth of 40 m (Romano *et al.*, 2000). This resulted in an extensive mortality of 28 invertebrate species (Perez *et al.*, 2000). The area affected by this climate anomaly extended from the French to the Italian coast and, to a lesser extent, affected the island of Corsica. Among benthic organisms, the most severely affected were sponges and gorgonians, such as *Paramuricea clavata, Eunicella singularis, Lophogorgia ceratophyta,* and *Eunicella cavolini* (Cerrano *et al.*, 2000; Perez *et al.*, 2000; Romano *et al.*, 2000). It is evident that temperature anomalies, even of short duration, can dramatically change Mediterranean faunal diversity.

Climate variability in the Mediterranean also favours disease outbreaks, because most pathogens are temperature sensitive. Studies performed on the coral *Oculina patagonica* identified the coral-bleaching bacterium *Vibrio shiloi* as an agent involved in the mass mortalities of Mediterranean coral (Kushmaro *et al.*, 1998). Mass mortalities of the gorgonian *Paramuricea clavata,* scleractinian corals, zoanthids, and sponges observed in 1999 in the Ligurian Sea were caused by a temperature shift in conjunction with the growth of opportunistic pathogens (including some fungi and protozoans; Cerrano *et al.*, 2000).

The list of exotic animals and plants that have invaded the Mediterranean, and particularly the eastern Mediterranean, continues to grow. The rise in seawater temperature may be partly responsible for changes in the range of some species, creating maritime corridors linking this region to other seas. The invasion of non-indigenous species has resulted in the dislocation of other species and, possibly, cascade effects on foodwebs (CIESM, 2002). Bianchi (1997) has suggested that Mediterranean marine biodiversity is undergoing rapid alteration. Because of the increased occurrence of warm-water biota, it has been said that the Mediterranean is experiencing a period of "tropicalization".

Despite an overall tendency towards sea surface warming, the eastern Mediterranean has experienced a short-term temperature decrease. This major climatic event, defined as the "eastern Mediterranean transient", with a decline in temperature of ca. 0.4°C, has resulted in a drastic decrease in faunal abundance and a significant change in faunal diversity (Danovaro *et al.*, 2001). Between 1992 and 1994, a temperature shift of 0.3°C resulted in a ca. 50% reduction of nematode diversity (and possibly the diversity of other groups). The extent of the impact was directly related to the extent of the temperature shift. After 1994, when temperatures gradually recovered to pre-transient values, biodiversity began to revert to a more "normal" situation.

Long-term change in the environment has been related to fish productivity in the Mediterranean. Bas *et al.* (1985) reported an intermittent tendency for the replacement of sardine (*Sardina pilchardus*) by anchovy (*Engraulis encrasicolus*), and vice versa. This has been seen not only off the coast around Castellón de la Plana (southeast Spain), but also off north Morocco. Around Castellón, there was a sharp decline in sardine in 1965, followed by a sharp increase in anchovy. These changes seem to have been less the result of fishing pressure and more a consequence of environmental factors. Variations in the composition of the phytoplankton, on which the larvae feed, seem to affect larval mortality and subsequent recruitment (Larrañeta, 1981).

Dominant species, such as sardine and anchovy, occupy alternate seasonal spawning niches (winter and summer, respectively; Sabatés *et al.*, 2007) that allow a more efficient use of the resources. Fish eggs and larvae were associated with hydrographic structures and processes, such as density fronts, estuaries, winter mixing, and stratification, which contributed to higher productivity and more efficient feeding (Sabatés *et al.*, 2007).

Suitable reproductive conditions are characterized by nutrient enrichment, concentration of larval food distribution, and local retention of eggs and larvae (i.e. the components of the so-called "ocean triad" of favourable fish reproductive habitats; Bakun, 1996). Such conditions, which have been associated with resident anchovy populations, have been found at the scale of the five Mediterranean sub-basins: the Aegean Sea, the Gulf of Lion and the nearby Catalan coast, the Alboran Sea, the Straits of Sicily/Tunisian coast, and the Adriatic Sea (Agostini and Bakun, 2002).

Transfer-function models were used by Lloret *et al.* (2001) to study the influence of Rhône and Muga river run-off and wind mixing on the productivity of demersal fish and invertebrate species in the Gulf of Lion (northwestern Mediterranean). This study demonstrated that enhanced hydroclimatic conditions resulted in higher catches and catch per unit of effort of 13 fish and invertebrate stocks. The authors suggested strong links between recruitment and local (river discharges, wind conditions) and global (NAO) environmental conditions.

In a related study by Lloret *et al.* (2004), time-series analyses were used to study the influence of river run-off and wind mixing on the productivity of anchovy and sardine in continental shelf waters surrounding the Ebre (Ebro) River. Landings of anchovy declined, whereas those of sardine increased. Ebre run-off demonstrated a progressive decline from 1960 until the late 1980s, and the wind-mixing index was highest during 1994–1996. The results of the analyses demonstrated a significant correlation between monthly landings of anchovy and freshwater input of the Ebre River during the spawning season (April–August). In contrast, monthly landings of sardine were significantly positively correlated with the wind-mixing index during the spawning season (November–March). The results provide evidence for the influence of riverine inputs and wind mixing on the productivity of small pelagic fish in the northwestern Mediterranean.

Sardine abundance in the northwestern Mediterranean was found to be negatively correlated with SST, and the recent warming trend may have contributed to the decrease in sardine and increase in the distribution area of the round sardinella (*Sardinella aurita*; Palomera *et al.*, 2007).

Recent efforts to understand the influence of climate on fish stocks and fisheries in the western Mediterranean were made under the EC Joint Research Centre's IDEA (IDentification Electronique des Animaux) project, and some results were published in a special issue of the *Journal of Marine Systems* (Massutí *et al.*, 2008a). Special attention was given to exploited demersal species, such as hake (*Merluccius merluccus*) and red shrimp (*Aristeus antennatus*; Abella *et al.*, 2008; Massutí *et al.*, 2008b; Maynou, 2008). Massutí *et al.* (2008b) explored the relationships between climate, abundance, and the fishery for hake and red shrimp off the Balearic Islands (western Mediterranean). Regional and global climate has been described by the mesoscale IDEA index and the large-scale NAO and Mediterranean Oscillation (MO).

Surface waters off the Balearic Islands are formed by low-salinity Atlantic water or higher-salinity Mediterranean waters and have high seasonal variations in temperature, ranging from 13 °C during winter to 26 °C during summer. In summer, a strong temperature gradient is established at depths between 50 and 100 m. Below this depth, there are higher-salinity Mediterranean waters, identified as Western Mediterranean Intermediate Water (WIW) and characterized by a temperature of ca. 12.5 °C, between 100 and 300 m, and Levantine Intermediate Water (LIW) with a temperature and salinity of ca. 13.3°C and 38.5 psu, respectively, between 200 and 700 m.

The interannual variability of the habitats around the Balearic Islands is related to the amount of WIW present in spring. These waters are formed by deep convection in the northern Mediterranean during winter. After relatively mild winters, northern waters from the Gulf of Lion flow south along the continental slope (Northern Current), reach the Balearic Islands channels, and divide into two branches. The main branch proceeds southwards, crossing the Ibiza Channel, whereas the minor branch recirculates cyclonically and returns to the northeast, forming the Balearic Current, which flows along the northern slope of the Islands. After cold winters, larger quantities of WIW are formed at intermediate layers. Reaching the channels in spring, this partly blocks the Northern Current when it reaches the Ibiza Channel, thus reinforcing the Balearic Current, but without any significant transport of Mediterranean waters through the Ibiza Channel into the Algerian Basin (Monserrat *et al.*, 2008; Massutí *et al.*, 2008b).

In order to obtain a reliable index for WIW presence and regional circulation, air–sea heat fluxes at the Gulf of Lion during winter, obtained from the meteorological NCEP/NCAR reanalysis, have been analysed and compared with other meteorological data, such as surface air temperature (Monserrat *et al.*, 2008). The standardized air temperature anomalies at 1000 hPa in the Gulf of Lion during winter (December–March) have been demonstrated to be the best indicator of the absence/presence of WIW in the Balearic Islands channels in late spring. Values above 1.0 for the standardized temperature anomaly indicate the absence of WIW in the Ibiza Channel. The high correlation obtained with available *in situ* oceanographic data allows the use of this index (so-called IDEA index; Monserrat *et al.*, 2008; Massutí *et al.*, 2008b) as an indicator of the presence of WIW and to conduct further analyses of regional climate and fisheries scenarios.

Massutí *et al.* (2008b) have applied modified stock–recruitment and generalized additive models in order to explore oceanographic scenarios of macro- and mesoscale climate regimes in relation to population dynamics of hake and red shrimp. They found that hake recruitment seems to be enhanced during low NAO and IDEA periods. During these periods, colder-than-normal winters generate large quantities of cold WIW in the Gulf of Lion, which flows south and reaches the Balearic Islands channels in spring, increasing productivity in the area. This oceanographic scenario could also favour the distribution of hake on the fishing grounds where the trawl fleet targets this species, increasing its accessibility to the fishery. The abundance of red shrimp also seems to be enhanced by the high MO index periods, which could reflect increased presence of the saline and warm LIW in the area.

Maynou (2008) investigated fluctuations of red shrimp landings in the Catalan Sea in relation to the NAO index. He found similar long-term oscillations, with dominant periods of 7–8 and 12–13 years, and significant correlations between the mean annual NAO index and annual catches in each port, with some time-lags (1–3 years). He proposed that NAO-induced environmental variability may enhance the food supply of red shrimp and, hence, strengthen the reproductive potential of particular year classes, resulting in increased catches 1–3 years later.

9.3 Adriatic Sea

The Adriatic Sea extends northwestwards from 40°N to 45°45'N and has a maximum length of ca. 770 km. It has a mean width of ca. 160 km, although the Strait of Otranto in the south, through which it connects with the Ionian Sea, is only 85–100 km wide. Its total surface area is ca. 160 000 km^2. The depths of the coastal waters are closely related to the geomorphology of the coastline: where coasts are high and mountainous, depths are considerable. The site of maximum depth in the Adriatic Sea, situated south of the central area, is ca. 1300 m. The Po River, which is situated in the northern part of the Adriatic Sea, is the main source of freshwater inflow. The seasonal peaks of phytoplankton production in the northern Adriatic tend to coincide with maximum Po River flow rates (Revelante and Gilmartin, 1976).

In the Adriatic Sea, winds can cause water-column mixing, advection, and deepening of the strong spring–summer stratification in the outflow region of the Po River (Russo and Artegiani, 1996). Dominant winds are the Bora and the Sirocco. The Bora is a cold, dry wind, blowing from the Balkans and funnelling along the valleys of the Dinaric Alps. In the specific areas where it reaches the Adriatic Sea, it is very strong and causes intensive heat loss from the sea surface (Santojanni *et al.*, 2006a). Its direction varies locally (from north–northeast to northeast), and its duration typically spans a few (2–3) days; it is more frequent in winter. The Sirocco is a moderate, warm, wet wind that blows from the southeast along the major axis of the basin. It is more frequent in spring and autumn, and its duration is generally similar to that of the Bora.

With respect to water masses, two different thermohaline layers can be recognized in the central Adriatic: the surface layer (down to 20 m) and the intermediate layer (from 20 to 100 m, Grbec *et al.*, 2002). The surface layer is under a strong atmospheric influence, whereas in the intermediate layer, thermohaline fluctuations can be explained by the horizontal advection of saltier, warmer, and more nutrient-rich Mediterranean water. The water in this layer comes mostly from the Mediterranean and originates from LIW. High abundance of pelagic fish has been found in the intermediate layer (Kacic, 1980).

During the past 30 years in the Adriatic Sea, thermophilic species of ichthyofauna have increased (Dulčić and Grbec, 2000). Fish and zooplankton species that were previously rare are becoming more abundant, and other new species are being recorded (Dulčić and Grbec, 2000). These observations are related to increasing temperatures and salinity variations in the Adriatic Sea, which intensified after 1988 (Russo *et al.*, 2002). Other climate changes (increases in storm frequency and rainfall, and changes in windspeed and direction) have also had an impact on water properties (e.g. salinity, mixing, altered turbidity), which, in turn, have affected the whole Adriatic Sea ecosystem (Russo *et al.*, 2002). A number of phenomena, such as blooms of jellyfish (*Pelagia noctiluca*) and thaliaceans (Boero, 1996), harmful algal blooms (by several species of dinoflagellates), and red tides, were triggered by these meteorological and oceanographic changes (Boero, 2001). Increased surface temperatures, altered circulation, and precipitation changes causing increased stratification have been invoked to explain the increased frequency of bottom-water hypoxia or anoxia (lack or absence of oxygen) in coastal areas of the northern Adriatic. These phenomena, often associated with mass mortalities of fish and benthic fauna, alter foodwebs and may have important cascade effects on biodiversity.

The Adriatic Sea, furthermore, has undergone dramatic changes related to low temperatures. In winter 2001, it experienced a period of abnormally low surface temperatures (from 9°C to freezing) that led to mass mortalities of round sardinella (Guidetti *et al.*, 2002), with consequent alteration of the foodwebs. The Adriatic Basin is also the site of deep-water composition, as a result of the Bora winds and their association with decreased temperatures, although recent studies have reported a lack of open-sea convection related to higher temperatures and mild winter conditions. This phenomenon alters deep water and strongly reduces spring phytoplankton blooms and export production to the deep layers.

Cultural eutrophication is a strong anthropogenic driver in the Adriatic Sea. Studies of multiple time-series of plankton (from bacteria to zooplankton: Solic *et al.*, 1997) have revealed increasing long-term trends in both coastal and open-sea areas. Changes in seasonal abundance of phytoplankton are related to surplus nutrients. During the 1960s, the phytoplankton maxima occurred in spring and autumn, but more recently, they have also occurred in summer. The taxonomic composition of the phytoplankton has changed, so that the proportion of diatoms has decreased and that of dinoflagellates and coccolithophores has increased. In the zooplankton, copepods and appendicularians have decreased and cladocerans and thaliaceans have increased. Coherent decadal oscillations have also been registered in most of the time-series (Solic *et al.*, 1997), indicating strong dependence of biological productivity on natural factors, the most important of which are water exchange with the wider Mediterranean and water temperature.

Historical records indicate that sardine in the eastern part of the Adriatic Sea have undergone large fluctuations. Zupanovic (1968) linked periods of high sardine abundance (which alternated with periods of extreme scarcity) to strong inflow from the central Mediterranean (years of "ingression": Buljan, 1974) and severe winters, which produced intensive mixing of the water column. Regner and Gacic (1974) connected the fluctuations of sardine catches with solar activity. Sinovic and Alegria (1997) found that the highest index of sardine abundance coincided with years of high primary productivity and low temperature during the hatching period.

Grbec *et al.* (2002) have analysed indicators of regional climate and pelagic fish landings in the Adriatic. They formulated a new regional climate index called the MO (Grbec *et al.*, 2003), which accounts for the pressure difference between the eastern Atlantic and the Mediterranean and can be related to salinity and transport of LIW into the Adriatic (Grbec *et al.*, 2002, 2003). Grbec *et al.* (2002) found significant negative correlations between sprat and anchovy landings and the NAO, and positive correlations between sardine landings, salinity of intermediate water masses, and the MO. These results are consistent with later investigations by Santojanni *et al.* (2006a, 2006b; see below). In the Adriatic, sprat and anchovy prefer lower-salinity water, and their recruitment success can be associated with river inflow in the northwestern Adriatic (Agostini and Bakun, 2002). Sardine, on the other hand, can be associated with higher-salinity water and Mediterranean inflow, which explains the correlations found by Grbec *et al.* (2002) and Santojanni *et al.* (2006b).

Santojanni *et al.* (2006a, 2006b) have explored the relationships between sardine and anchovy recruitment and environmental factors. Santojanni *et al.* (2006a) analysed anchovy recruitment time-series associated with five environmental factors: surface air temperature, surface atmospheric pressure, quadrant specific windstresses, Po River run-off, and the NAO. They found correlations of anchovy recruitment with SSE, ESE windstress, and Po River run-off. Low levels of these environmental factors were observed just before the 1987 collapse of the anchovy, together with a high frequency of occurrence of northeasterly winds and an extreme positive value of the NAO index for the previous autumn. The relationships of sardine recruitment to Po

River inflow and NAO were analysed by Santojanni *et al.* (2006b), who found only weak correlations of sardine recruitment with both explanatory variables.

Coll *et al.* (2009b) analysed trends in several ecosystem components in the northern and central Adriatic Sea via dynamic foodweb modelling and their links to environmental changes. They used several environmental indices, such as SST, salinity, NAO, and MO, which they compared with the model outputs. The primary productivity estimated by the model has demonstrated a significant decreasing trend and was found to be positively correlated with the MO and negatively correlated with the average annual SST (demonstrating an increasing trend). The positive correlation with the MO is consistent with results obtained in the northwestern Mediterranean (Massutí *et al.*, 2008b). The results are also consistent with previous studies, suggesting that water warming and changing inflow of highly saline Mediterranean water into the Adriatic Sea may greatly affect fish communities (Dulčić *et al.*, 1999; Grbec *et al.*, 2002, 2003).

9.4 Black Sea

The Black Sea is a deep, mostly land-locked basin in eastern Europe. It is linked to the Mediterranean by the narrow straits of the Bosphorus and Dardanelles, and to the Sea of Azov by the Kerch Strait. The Black Sea is characterized by a positive water balance that results in a net outflow into the Mediterranean. With a drainage basin fivefold more extensive than the sea area (Ludwig *et al.*, 2009), it functions as a virtually isolated ecosystem and is sensitive to distant anthropogenic activities. Climate affects the Black Sea via atmospheric transfer and river inflow. The latter has been demonstrated to be a significant factor in the overall water balance and basin-scale circulation (Oguz *et al.*, 1995), together with nutrient loading from human activities on surrounding land. The Danube River provides ca. 70% of the freshwater inflow. Estimates revealed that 33% of phosphorus emissions were derived from agriculture and 56% from urban settlements; only 8% were considered to be of natural origin (Kroiss *et al.*, 2005). The physical environment of the Black Sea has a major influence across the foodweb at different time-scales (Daskalov, 2003) and has been demonstrated to be influenced by the Atlantic climate through cross-European atmospheric teleconnections (Polonsky *et al.*, 1997; Oguz *et al.*, 2006; Llope *et al.*, in press).

Usually, two concurrent types of trophic control are distinguished: control of prey by the consumer (top–down) and control of the consumer by the abundance and availability of prey (bottom–up). Top–down or bottom–up controls may dominate in a particular system. Fisheries exert a top–down influence, but can indirectly affect productivity and growth of non-target organisms and induce compensatory bottom–up effects. Bottom–up environmental influences affect productivity of the system and fish recruitment, but their effect on biomass may be dampened by predation. Once predation pressure is relaxed, productivity may increase (e.g. from eutrophication; Daskalov, 2002).

9.4.1 Bottom–up influences: hydroclimate and cultural eutrophication

Several studies have addressed physical processes and their links to biological productivity in the Black Sea. Physical variables (sea surface temperature, atmospheric pressure, salinity, sea level, etc.) were explored by Simonov and Altman (1991). Ovchinnikov and Osadchiy (1991) identified low-frequency patterns in long-term, winter air temperature data. Polonsky *et al.* (1997) found significant interdecadal variability in temperature, density, and run-off data in the northwestern

Black Sea. The importance of hydroclimate for biological productivity and fish stocks in the Black Sea was reviewed by Vinogradov (1991), Simonov *et al.* (1992), Sorokin (2002), and Daskalov (1999, 2003).

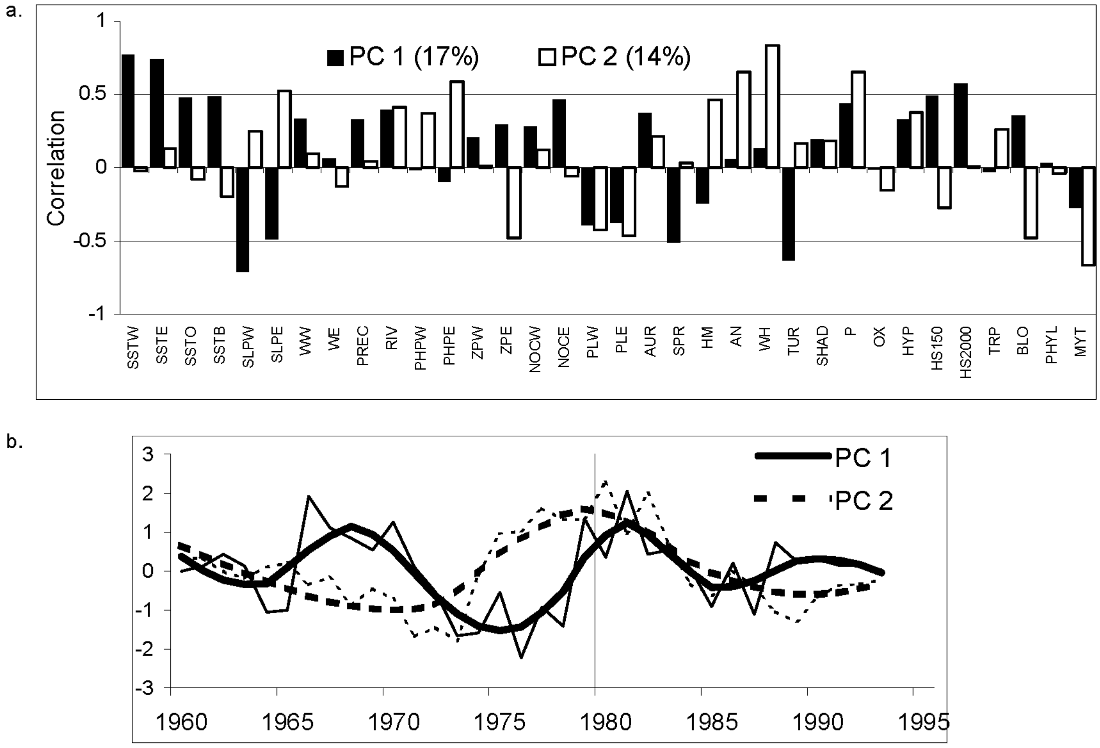


Figure 9.1. Evidence of long-term changes in hydroclimatic, biological, and anthropogenic indices from PCA: (a) correlation of the original variables to the first two principal components (PC1 and PC2, accounting for 17% and 14% of the total variance, respectively); (b) PC scores (light lines) and Loess smooth (bold lines) against time: PC1 and PC2 display ~10- and ~20-year cycles, respectively. Variables from different parts of the Black Sea are indexed as follows: SST = sea surface temperature; SLP = sea level atmospheric pressure; W = windspeed; PREC = precipitation; RIV = river run-off; PHP = phytoplankton; ZP = zooplankton; NOC = *Noctiluca scintillans*; PL = *Pleurobrachia pileus*; AUR = *Aurelia aurita*; SPR = sprat; HM = horse mackerel; AN = anchovy; WH = whiting; TUR = turbot; SHAD = shad; P = inorganic phosphorus; OX = oxygen; HYP = hypoxia; HS = hydrogen sulphide; TRP = transparency; BLO = phytoplankton blooms; PHYL = *Phylophora sp.*; MYT = black mussel. The letters W, E, O, and B at the end of the indices denote West, East, Odessa, and Batumi, respectively. (Modified from Daskalov, 2003.)

Decadal fluctuations are common in multiple physical and biological time-series (Figure 9.1). Major patterns of variability are apparent on seasonal, interannual (~1–5 years), decadal (~10–12 years), and interdecadal (~20–30 years) scales (Daskalov, 2003). Correlation between spatially isolated variables, such as Danube run-off (related to the catchment area in central and eastern Europe) and temperature at the coastal station in Batumi (eastern Black Sea) may indicate that global climatic factors influence physical characteristics and circulation in the Black Sea. As the Black Sea is a virtually closed basin, such global influences are mainly attributable to atmospheric transfer or river inflow. The latter has been demonstrated to be a significant factor for the overall water balance and basin-scale circulation (Simonov and Altman, 1991; Oguz *et al.*, 1995). The main possible sources of low-frequency variability for the Black Sea are the atmospheric teleconnections with the Atlantic (Polonsky *et al.*, 1997; Özsoy, 1999).

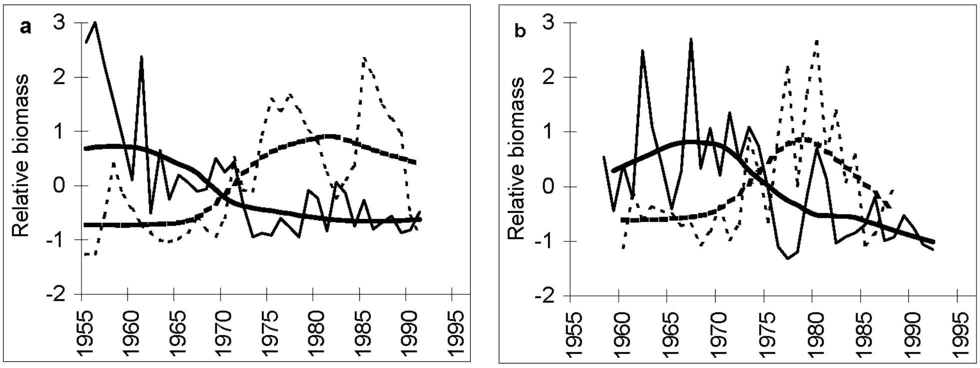


Figure 9.2. Inverse trends across consecutive trophic levels indicating trophic cascade: (a) pelagic predator fish catch (bonito, mackerel, bluefish (solid lines)) vs. planktivorous fish biomass (sprat, horse mackerel (dashed lines)); (b) zooplankton biomass (solid lines) vs. phytoplankton biomass (dashed lines). Light curves give original data (zero mean unit variance values); bold curves give non-linear trends smoothed by Loess. (Modified from Daskalov, 2002.)

Long-term trends in fish stock time-series may be related to variation in hydroclimate (Daskalov, 2003). A general increase in biological production was observed during the 1970s and 1980s (Figure 9.1). A long-term decline in temperature after 1965 may be responsible for increased upper-layer instability and convection (most important in winter; Simonov and Altman, 1991; Daskalov, 2003). This process intensifies divergence (upwelling) and mixing in the central zone and over the shelf (Ovchinnikov and Popov, 1987), leading to nutrient-enrichment of the upper layer. An increase in run-off, which peaked around 1980, may also have favoured increased productivity. By the end of the 1980s, the favourable conditions appear to have ended; run-off and windforcing decreased and temperature increased.

It is difficult to explain the massive phytoplankton blooms and the rise in small pelagic fish abundance during the 1980s solely by the influence of natural factors. Over the last few decades, the role of anthropogenic factors increased (Zaitsev, 1993; Bologa *et al.*, 1995), but these factors were strongly modulated by physical variability (Vinogradov and Simonov, 1989; Daskalov, 2003). After 1970, there was an increase in phosphorus discharge, correlated with increased hydrogen sulphide content, and inversely correlated with hypoxia coverage (Juravleva and Grubrina, 1993; Zaitsev and Mamaev, 1997; Daskalov, 2003). Phosphorus, hypoxia, and hydrogen sulphide indices demonstrated ~10-year variations similar to the run-off (Daskalov, 2003). Several studies have demonstrated that plankton blooms, hypoxia, and hydrogen sulphide production were controlled by river run-off, temperature, and wind, and that their adverse effects increased or decreased in relation to physical forcing (Fashchuk, 1995; Daskalov, 2003).

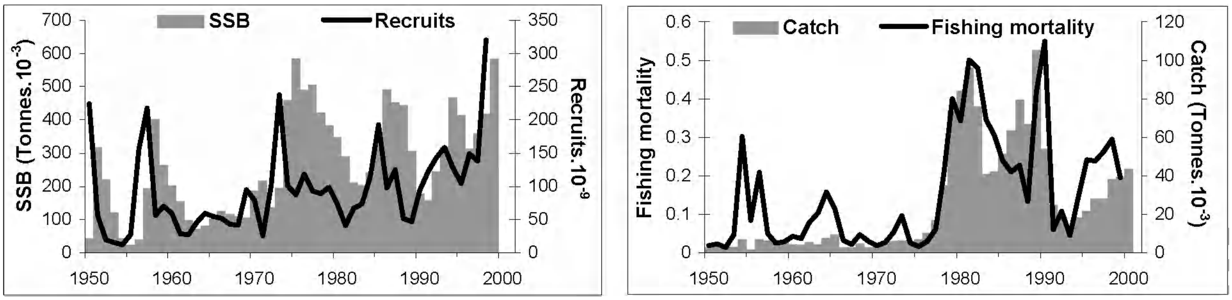
9.4.2 Top–down influences: overexploitation of marine predators and effects of predation

In the Black Sea, the classic scenario of "fishing down the foodweb" (Pauly *et al.*, 1998) has been taking place. However, in this system, unlike many other marine systems (Cury *et al.*, 2003), the removal of the top-predators produced a cascade effect on the whole pelagic foodweb, down to phytoplankton and nutrients (Daskalov, 2002; Figure 9.2).

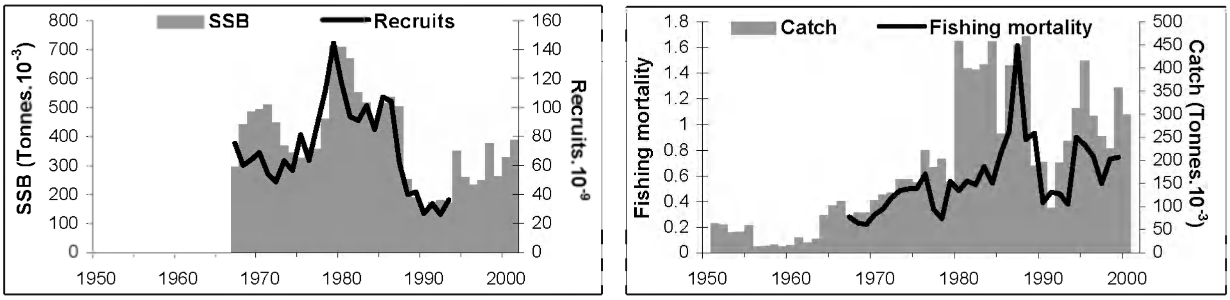
Major changes in ecosystem structure, biomass, and fisheries took place between the 1960s and 1980s. During the 1960s, piscivorous fish and zooplankton were more abundant and, as a result, phytoplankton and zooplanktivorous fish were heavily grazed (Figure 9.2). Fisheries targeted valuable piscivorous fish and cetaceans. The situation changed in the 1980s, when the strongest predatory effects were exerted by zooplanktivorous fish and gelatinous plankton, whereas fish catches were dominated by zooplanktivorous fish. Overfishing of marine predators provoked cascading changes, resulting in an increase in zooplanktivorous fish and jellyfish, and a corresponding decrease in zooplankton and increase in phytoplankton (Daskalov, 2002; Daskalov *et al.*, 2007; Figure 9.2). These structural changes led to a decrease in the mean trophic level in the ecosystem (Daskalov, 2000).

However, top–down effects on the ecosystem were not isolated from other influences of natural or anthropogenic origin. Eutrophication of both natural (cold weather, high river inflow) and anthropogenic origin peaked in the mid-1980s (Daskalov, 2003). Pelagic and demersal fish stocks responded differentially to anthropogenic impacts (Caddy, 2000), resulting in an increase in small pelagic stocks and a decrease in some demersal stocks, e.g. turbot (*Psetta maeotica*), during the 1980s (although others, such as whiting, increased during the 1980s; Prodanov *et al.*, 1997; Daskalov, 2003). The decrease in the commercially important turbot and shad (*Alosa kessleri pontica*) seems to be attributable mainly to overfishing (Prodanov *et al.*, 1997). However, both anadromous shad and demersal turbot recruitment series were correlated with river run-off and were marked by a similar decadal pattern (Daskalov, 2003). The decline in turbot was also related to eutrophication and bottom hypoxia (Daskalov, 2003).

a. Sprat



b. Anchovy



c. Horse mackerel

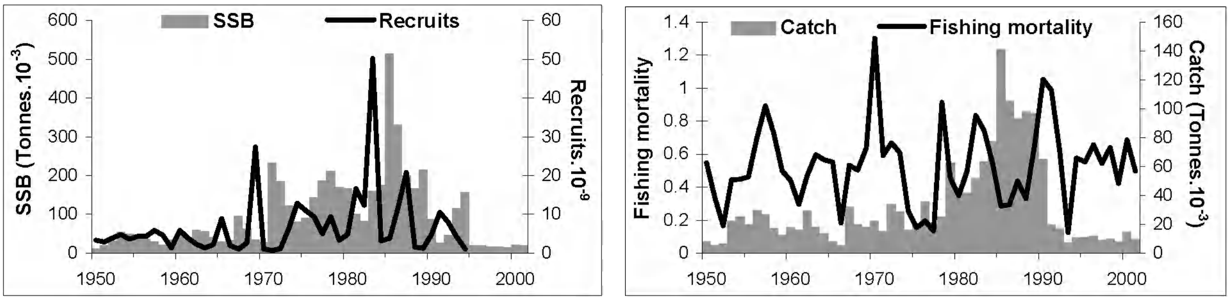


Figure 9.3. Time-series of recruitment, spawning–stock biomass (SSB), catch, and fishing mortality of: (a) sprat, (b) anchovy, and (c) horse mackerel.

9.4.3 Middle trophic levels: recruitment variability and fish stock collapses

In terms of biomass and landings, small zooplanktivorous fish are clearly dominant in the Black Sea (Prodanov *et al.*, 1997). As selective zooplankton feeders, they also have a very important role in structuring the pelagic foodweb (Daskalov, 2002). In the middle of the foodweb, the trophic interactions between zooplankton and zooplanktivorous populations are crucial to ecosystem functioning. Other important actors in this arena are the pelagic recruits of many fish and invertebrate species and zooplanktivorous zooplankton (chaetognaths, jellyfish, ctenophores).

By the late 1980s to early 1990s, almost all exploited Black Sea stocks synchronously collapsed (Prodanov *et al.*, 1997). Recruitment failures and heavy overfishing seem to be the main causes of the collapses (Prodanov *et al.*, 1997; Daskalov, 1999). Other major events accompanying the collapses were the maximum strength of coastal phytoplankton blooms (Daskalov, 2003) and the invasion and mass development of the exotic ctenophore *Mnemiopsis leidyi* (Grishin *et al.*, 1994). The situation clearly resembled a system-wide regime shift, in which many factors interplay to drive the pelagic ecosystem to a new state, characterized by depleted fish stocks, frequent blooms of phytoplankton and gelatinous zooplankton, and a generally deteriorated coastal environment (turbidity, hypoxia; Daskalov *et al.*, 2007).

Time-trajectories of abundance, catch, and fishing mortality (Figure 9.3) can be used to explore the mechanisms of stock collapse and recovery. Decadal fluctuations in fish abundance were observed and are probably related to changes in climate (Daskalov, 1999, 2003). The increase in biomass and catch of small pelagic fish during the 1970s and 1980s (Figure 9.3) promoted the expansion of powerful trawl and purse-seine fishing fleets and a steady increase in fishing effort (Anon., 1997; Gucu, 1997). Maxima of catch and fishing mortality were recorded in the late 1980s (Figure 9.3), parallel with the decrease in exploited biomass following recruitment failures in the previous years. Sharp reductions in biomass and catch in the early 1990s were described as stock collapses. Fishing effort and fishing mortality also dropped subsequently because of decreasing profitability of fishing. During the collapse phase, the size–age structure of the catch shifted towards a predominance of small, immature individuals (Gucu,1997; Prodanov *et al.*, 1997), and precocious maturation of young-of-the-year fish was observed (Mikhailov and Prodanov, 2002).

Although some scientists view the decline in sprat as a collapse, others interpret the decline in catches as the result of decreased fishing effort (because of the economic crisis) and misreporting. However, all of the survey indices consistently demonstrate a drop in biomass and recruitment (Prodanov *et al.*, 1997). In the mid-1990s, stocks of sprat and anchovy started to recover (Figure 9.3a and b). Abundance of sprat reached levels recorded in the 1980s, but catches were not so high because of the stagnated economies of Bulgaria, Romania, and Ukraine. Anchovy also recovered, but because fishing effort and catch remained relatively high (Zengin, 2003), the exploited biomass could not attain the high levels of the 1980s. Anchovy compete for food with *M. leidyi* (Grishin *et al.*, 1994), and this competition probably further affected anchovy population growth. Despite the partial recovery of anchovy and sprat stocks, levels of many other valuable stocks (e.g. turbot, bonito, bluefish, shad, and horse mackerel) have remained low (FAO, 2001), limiting the economic prospects of the fisheries (Zengin, 2003). The capacity for quick recovery of small pelagic fish in the Black Sea may be interpreted in the context of reduced predatory pressure and trophic-cascade theory (Daskalov, 2002).

Stock collapses in the Black Sea are a good example of how interactions between physical, biological, and anthropogenic factors may result in feedbacks that amplify the original signals and drive the system to an undesirable state. Thus, in most cases, overfishing can be associated with a natural decreasing trend in abundance (Figure 9.3; also Figure 3 in Pauly *et al.*, 2002). Environmental degradation (e.g. eutrophication and bottom hypoxia) can worsen the conditions for recruit survival, thus leading to stock collapse, as for Black Sea turbot (Prodanov *et al.*, 1997; Daskalov, 2003).

The population explosion of *M. leidyi* and its consequences for fish stocks illustrates the interaction between natural and anthropogenic factors creating several feedbacks at the ecosystem level. In the 1980s, the system was dominated by small pelagic fish and by the native jellyfish (*Aurelia aurita*). After 1985, *A. aurita* was replaced by *M. leidyi* in terms of biomass dominance (Grishin *et al.*, 1994). The explosions of *M. leidyi* in 1989 and 1990 corresponded to a decrease in abundance of most fish stocks (Figure 9.3). The exact causes of the timing of the *M. leidyi* onset are unclear, but decreased zooplankton consumption resulting from low abundance of overexploited fish stocks may be one of them (Grishin *et al.*, 1994; Prodanov *et al.*, 1997; Daskalov, 2003; Bilio and Niermann, 2004).

The rapid development of *M. leidyi* in subsequent years led to a large decrease in the zooplankton and strong competition for food between fish and native gelatinous plankton (Grishin *et al.*, 1994; Shiganova, 1998). Fish stocks were the most affected by the depletion of zooplankton. However, although fish larvae represent only a small part of the diet of *M. leidyi* (Tsikhon-Lukanina *et al.*, 1992), their consumption is unlikely to lead to fish recruitment failure. The fishery collapse may not be the only negative consequence of the *M. leidyi* invasion; the massive phytoplankton blooms in the late 1980s to early 1990s (Yunev *et al.*, 2002) can also be associated with a decrease in zooplankton grazing and a trophic cascade similar to the one that took place in the 1970s to 1980s (Daskalov, 2002). It was hypothesized that the newly introduced *Beroe ovata* (Konsulov and Kamburska, 1998) contributed to the regulation of *M. leidyi* and further recovery of fish stocks (Kideys, 2002). However, sprat and anchovy stocks started to recover after the decrease in fishing pressure, when *M. leidyi* was still abundant (Gucu, 2002; Daskalov, 2003; Bilio and Niermann, 2004). Therefore, the main factor leading to the fish stock collapse is now recognized to be overfishing, whereas the explosion of *M. leidyi* was an associated factor that depleted the zooplankton food resources available to fish larvae.

9.4.4 Effect of climate teleconnections and regime shifts in the Black Sea

Oguz *et al.* (2006) confirmed previously found relationships between climate and productivity in the Black Sea, and related Black Sea properties to large-scale climatic variability associated with the NAO. The NAO teleconnection to the Black Sea is opposite to that in the eastern North Atlantic and the western Mediterranean (Demirov and Pinardi, 2002). Relatively cold, dry winters occur during the positive phase of the NAO, whereas milder, wetter winters occur during the negative phase. The ten-year fluctuations observed in the NAO index can partially explain the Black Sea climate signal.

Regime shifts in connection with environmental and trophic drivers (fisheries, predation) were modelled using coupled statistical models (threshold generalized additive model (TGAM); Llope *et al.*, in press). The models were run in both hindcast and predictive modes, and successfully simulated the ecosystem dynamic, estimating the tipping points (thresholds) between alternative regimes. The models resolved for interactions between the global (NAO) and regional (eutrophication) drivers and the bottom–up (productivity) and (trophic cascade) effects. The global climate (indexed by NAO) has significantly influenced primary productivity in the Black Sea only when eutrophication (indexed by phosphorus loading from the Danube River) was at a high level. This may have been the result of increased river inflow (related to negative NAO) bringing more nutrients into the sea. The results also suggest that, if the structure of the original four trophic levels is restored (by the recovery of the top predators), eutrophication could be more efficiently handled by a more resilient system.

10 Changes in the distribution of fish

John K. Pinnegar, Georg H. Engelhard, and Georgi M. Daskalov

10.1 Introduction

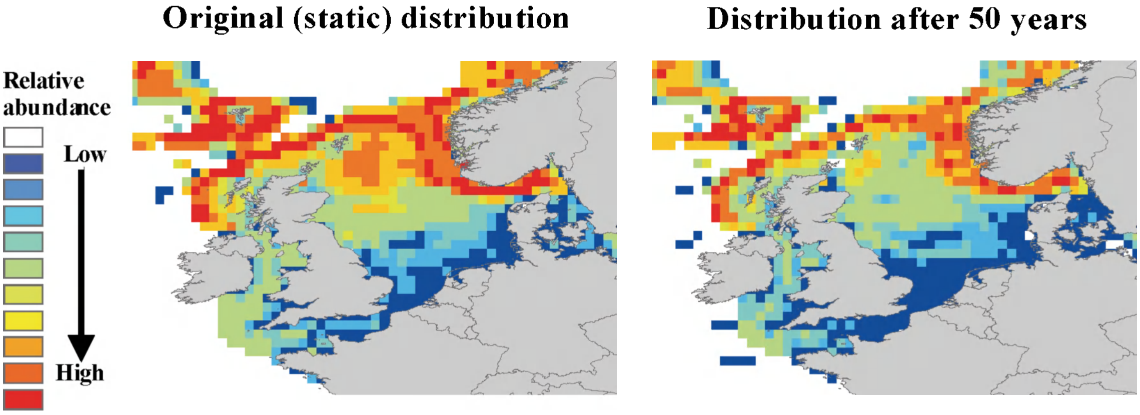
Temperature, together with food availability and suitable spawning grounds, is one of the primary factors in determining the large-scale distribution patterns of fish. Because most fish species or stocks tend to prefer a specific temperature range (Coutant, 1977; Scott, 1982), an expansion or contraction of the distribution range often coincides with long-term changes in temperature. These changes are most evident near the northern or southern boundaries of the species' range; theoretically, warming results in a distributional shift northwards, while cooling draws both warm- and cold-water species southwards (Rose, 2005). Statistical approaches, such as correlation analysis, have yielded important information on the pattern of change. For instance, the recent warming trend in the Northeast Atlantic has coincided with an apparent northward shift in the distribution of fish species from southern latitudes (Quéro *et al.*, 1998; Perry *et al.*, 2005; Beare *et al.*, 2004).

However, an important complication in assessing the impact of climate change on fish populations is the disentanglement of its effect from that of other drivers, such as fishing. In the North Sea, fishing mortality rates have been higher in the south than in the north (Heath *et al.*, 2003, 2008). Therefore, apparent changes in distribution (as indicated by Perry *et al.*, 2005) could be a consequence of local patterns of fishing pressure and different rates of depletion in spatially segregated substocks (Hutchinson *et al.*, 2001; Wright *et al.*, 2006). Daan *et al.* (2005) also raised the issue of more rapidly declining populations in the southern North Sea than in the northern North Sea. The effect of fishing may thus have interacted with the effect of climate and enhanced the apparent northward shift of fish species reported by Perry *et al.* (2005) and more recently by Rindorf and Lewy (2006).

Heath (2007a) looked at patterns in international fishery landings data for the entire Northeast Atlantic region, covering 341 taxonomic categories. Densities of landings of each species category (t km^{-2}) for all nations were summed for the decadal periods 1973–1979, 1980–1989, and 1990–1999, and expressed as a proportion of the total Northeast Atlantic landings. Changes in the mean latitude of landings of each species category indicated both northward and southward shifts between decades. More species shifted southwards than northwards between the 1970s and 1980s, and vice versa between the 1980s and 1990s. On face value, this seems to parallel the interdecadal changes in sea and air temperatures, both of which demonstrate cooling between the 1970s and 1980s and warming between the 1980s and 1990s.

Beyond the continued slow shift in fish distributions to more northern and deeper waters, information on the future prospects for fish communities as a result of climate change are somewhat limited and often highly speculative. Modelling strategies for predicting the potential impacts of climate change on the natural distribution of species have often focused on the characterization of a species' "bioclimate envelope" (Pearson and Dawson, 2003). In other words, by looking at the current range of temperatures tolerated by a species, it is possible to predict future distribution if we know how the physical environment in an area is likely to change in future. This approach is being applied to fish communities by a number of research groups across Europe (especially under the EU RECLAIM project). In addition, a worldwide analysis was recently carried out (Cheung *et al.*, 2009) using this technique, based on

1066 commercial fish and invertebrate species. This study suggests that climate change may lead to numerous local extinction events by the year 2050, especially in subpolar regions, the tropics, and semi-enclosed seas (e.g. the Mediterranean). It also suggests that pelagic species, such as herring (*Clupea harengus*) and anchovy (*Engraulis encrasicholus*), will move polewards by up to 600 km, and demersal species, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), by an average of 223 km (Figure 10.1).


Original (static) distribution

Distribution after 50 years

Figure 10.1. Output of the "bioclimate envelope" model for cod (*Gadus morhua*) in 2001 (original distribution) and 2050 (future distribution). Note: this is only one of the 1066 species considered in the global analysis carried out by Cheung *et al.* (2009).

10.2 Fishery implications

Distribution shifts may have knock-on impacts on commercial fishery catches because changes in migration or spawning behaviour affect the catchability of individuals with fishing gear. Populations may move away from (or towards) an area where fishing fleets operate and/or an area where spatial restrictions on fishing are in place (ICES, 2007h). Also, species distributions may shift across the boundaries between areas where quotas belong to different nations. For example, this situation could arise as a result of TAC allocations between Norway and the EU, or between Iceland and the EU, if species such as mackerel (*Scomber scombrus*) or herring move away from the EU sector. The EU fisheries may then no longer be able to catch their full quota within indigenous waters, leading to potentially difficult political negotiations between nations regarding future access to key fish stocks and national allocation keys. International law provides that coastal states have sovereign rights to manage fisheries in waters under their jurisdiction. It is estimated that >90% of the global fish catch is taken within waters under the jurisdiction of particular coastal states.

Biogeographic changes may also affect the distance that must be travelled by fishing boats to reach the target resources, with impacts on fuel costs and time at sea. An increase or decrease in the number and severity of storms could also affect the ability of fishing boats to access resources, particularly if a days-at-sea management regime is in place. In addition, local fleets may need to adapt to the appearance of new species, whether or not they are commercially valuable. In some cases, climate change may offer new opportunities; for example, UK and French vessels have recently adapted to target squid in the Channel. However, other species may pose a threat to fisheries by damaging fishing gears or acting as a vector for dangerous diseases, which subsequently have an impact on native stocks.

Non-stationarity of natural ecosystems has been a confounding factor influencing the apparent success or failure of closure areas in the North Atlantic, including the southern North Sea "Plaice box" (see van Keeken *et al.*, 2007). In the North Sea, juvenile plaice (*Pleuronectes platessa*) are typically concentrated in shallow inshore waters and move gradually offshore as they become larger. Surveys in the Wadden Sea, however, have demonstrated that 1-group plaice are almost absent from the area where they once were very abundant. This is probably linked to changes in the productivity of the region, but also to the changing temperature of the southern North Sea, which has warmed considerably in recent years. The "Plaice box" is now much less effective as a management measure than it was 10 or 15 years ago.

The boundaries (and expectations) of marine protected areas (MPAs) may need to be adaptive in future. For example, fishery closures in the Bornholm Basin of the Baltic Sea do not account for year-to-year environmental variability and particularly the periodic inflow of water from the North Sea, which greatly influences the spawning location and year-class strength of species like cod. In some years, the Bornholm closure area is successful in protecting much of the cod stock, but in other years, most of the spawning population is found outside the boundaries of the protected area; accordingly, the MPA offers no protection at all (for a review of Baltic closure areas, see ICES, 1999, 2004b).

Cheung *et al.* (2010) attempted to predict changes in global catch potential of exploited marine fish and invertebrates from 2005 to 2055 under various climate-change scenarios (based on their earlier paper using the "bioclimate-envelope approach", Section 10.1). The study suggests that climate change may lead to large-scale redistribution of global catch potential, with an average 30–70% increase in high-latitude regions, but a drop of up to 40% in the tropics. Maximum catch potential declines considerably at the southern margins of semi-enclosed seas (such as the Mediterranean and Baltic), but increases at the poleward tips of continental shelf margins. The European Economic Zones (EEZs) with the highest increase in catch potential by 2055 include Norway, Greenland, the US (Alaska), and Russia (Asia). In contrast, EEZs with the biggest loss in maximum catch potential include Indonesia, the US (excluding Alaska and Hawaii), Chile, and China.

10.3 Distribution of fish

10.3.1 Barents Sea

The waters in the Barents Sea have undergone marked temperature changes over the past 200 years, being relatively cold in the late 19th and early 20th centuries, warm from the 1920s to the 1950s, cool through the 1960s to the 1980s, and warm during the past decade or more (Drinkwater, 2006).

During the warm period of the 1920s to 1950s, the distribution of fish species, such as cod, haddock, and herring, expanded northwards and eastwards (Drinkwater, 2006). A similar geographic expansion of Atlantic-associated benthic invertebrate species occurred, whereas Arctic species declined (Berge *et al.*, 2005). During recent warming, large numbers of blue whiting (*Micromesistius poutassou*) have extended their distribution northwards as far as the western entrance of the Barents Sea, and blue mussels (*Mytilus edulis*) have appeared in Svalbard after a 1000-year absence (Berge *et al.*, 2005). Similarly, Gjøsæter (1998) has demonstrated that, in warm years, the overwintering areas of capelin (*Mallotus villosus*) in the Barents Sea extend farther east and north than in cold years (based on information in Ozhigin and Luka, 1985). Capelin larvae also seem to be distributed in different areas in warm and cold years.

In some years, the western limit is at 14–16°E (e.g. 1986/1987 and 1994/1995), whereas in other years, the western limit is much farther east, at ca. 30°E on the Varanger Peninsula in eastern Finmark (e.g. 1981–1985). The northward extension is normally at around 73–74°N. However, in years when the distribution is eastwards, the northern limit is also displaced far to the south, at 71–72°N.

Under projected warming in the Barents Sea, Atlantic species of fish and benthos are expected to extend farther eastwards and northwards, more species will spawn farther north, as observed for cod (Drinkwater, 2005), and new spawning sites are likely to be established. Herring and blue whiting will spread farther eastwards, and salmon (*Salmo salar*) abundance is likely to increase in Russian waters, as previously observed (Lajus *et al.*, 2005), and to extend to northern Spitsbergen. A study by Fossheim *et al.* (2006) considered the changing distributions of fish species in the southwestern and central part of the Barents Sea. Cluster and correspondence analyses suggested that the fish community consists of four distinct assemblages: northern, southern, deep, and central. Temperature explained 26.2% of the variation in the species data, and depth 14.5% of the variation.

10.3.2 Nordic seas

The Nordic seas, which include the Greenland, Norwegian, and Iceland seas, are a transition zone for warm, saline Atlantic Water on its way to the Arctic, and for cold, less saline, deep waters flowing from the Arctic to the Atlantic Ocean. The Greenland–Scotland Ridge forms a barrier between the deep waters of the Nordic seas and the North Atlantic.

Large ecosystem changes have been observed in this ecoregion in the recent past. For example, the abundance of Norwegian spring-spawning herring increased during the warming in the 1920s, decreased during the cooling period in the 1960s, but has risen again since the temperature increases in the 1990s (Toresen and Østvedt, 2000). During the warm period of the 1920s–1950s, herring migrated from spawning locations on the west coast of Norway and around the Faroes to feeding grounds off northeast Iceland (Vilhjálmsson, 1997). As the Arctic Front shifted southeastwards during the colder 1960s, the herring feeding grounds moved farther east to southwest of Spitsbergen. When colder climatic conditions and very high fishing mortality caused the herring population to decline to drastically low levels, the remaining individuals no longer migrated into the Norwegian and Greenland seas, but stayed near the Norwegian coast to both feed and spawn (Vilhjálmsson, 1997). In the 1990s, as temperatures warmed and the population increased, the population again began migrating back towards Iceland to feed (ACIA, 2005).

Capelin, the major prey of adult cod off Iceland, have moved farther northwest during the recent warming period, requiring the capelin fishing fleet to travel farther to obtain their catches. This distributional shift is somewhat similar to the response observed during the early 20th century when the capelin population shifted northwards. Increased abundance and spatial distribution of blue whiting has been observed in Icelandic waters, especially in the northern and eastern areas. Increased spatial distribution of Icelandic summer-spawning herring has also been observed, making acoustic measurement and fishing more difficult, and possibly affecting the natural mortality of this species (Björnsson and Pálsson, 2004). Changes in distribution have been noted for a number of other fish species, e.g. haddock, whiting (*Merlangius Merlangus*), and monkfish (*Lophius piscatorius*). Generally, the abundance of species that are on the northern boundary in Icelandic waters has increased, whereas cold-water species have retreated (Björnsson and Pálsson, 2004).

Much has been written about climate change and the distribution of cod in the Nordic seas region (e.g. Sundby and Nakken, 2008). Arcto-Norwegian cod tend to produce strong year classes in warm years and poor year classes in cold years. Along the Norwegian coast, cod spawning grounds tend to be displaced northwards during warm periods (1910–1940s, and 1980 to present), but spawning occurs farther south during cold periods (e.g. 1950s–1970s). A time-series for 1900–1976 on cod roe indices along the coast demonstrates that the southernmost spawning areas are more important during cold periods, and the northernmost ones in warm periods. After 1976, qualitative observations show that there have been poor spawning fisheries in the southernmost spawning areas, but from 2003 onwards, spawning has been observed along the coast of East Finnmark (in the far north), where it had not occurred during the previous 40 years (e.g. Sundby and Nakken, 2008).

Similarly, cod distribution has varied significantly around Iceland during warm and cool periods (Drinkwater, 2008). Prior to warming in the 1920s, Icelandic cod spawned almost exclusively off the south coast. However, as the waters warmed, cod spawning spread northwards until there were major spawning locations around the whole of Iceland (Sæmundsson, 1934). Interestingly, the condition of the cod south of the island declined, whereas those off the north coast were in good condition. This was attributed to a distributional change in capelin, the main prey for cod. Capelin spawning shifted to the north coast of Iceland, resulting in a scarcity of capelin along the south coast and, hence, a lack of food for the cod that remained there (Sæmundsson, 1934).

Much has been written about the effects of the early 20th-century warming on West Greenland cod. There are two subpopulations of cod off West Greenland: a local inshore cod, which is found mostly in the fjords, and a component that occupies the offshore banks. The abundance of inshore cod is generally low, but relatively stable, whereas the offshore cod has exhibited extremely large variability. The offshore cod spread northwards from the late 1910s to the early 1930s, from near the southern tip of Greenland to Upernavik, a distance of over 1200 km (Jensen, 1939). Most of the cod in West Greenland offshore waters are believed to originate in Iceland. Their rather sudden appearance in the 1920s is thought to be the result of a combination of increased transport of larvae from Iceland, because of the increased flow of the Irminger Current, and high survival of larvae once they reached West Greenland waters, owing to favourable environmental conditions (Jensen, 1949; Dickson and Brander, 1993).

Cod landings increased rapidly in 1924/1925, and the fishery yielded relatively moderate landings through the 1930s. The catch declined during the war years (late 1930s to mid-1940s). It then rose rapidly through the 1950s to a peak in the early 1960s before declining because of intensive fishing pressure and deteriorating climate conditions, as indicated by the drop in ocean temperatures. Off Greenland, during the latter half of the 1990s and into the present century, cod recruitment per spawning–stock biomass has increased compared with the low values typically observed since the 1970s (Wieland *et al.*, 2006). Since 2004, there has been inferred spawning off East Greenland, and in spring 2007, large cod were observed spawning there (ICES, 2007g) for the first time in many years. This is considered a good sign for future fisheries in West Greenland, because it is expected that many of the larvae and juveniles would probably be transported by the Irminger Current to West Greenland (from Drinkwater, 2008).

10.3.3 North Sea

Northward range extensions and changes in the geographic distribution of plankton and fish populations have been observed in the North Sea, and these have been related to regional climate warming (Brander *et al.*, 2003; Perry *et al.*, 2005). Warmer-water species of plankton, for example, have extended their range northwards by 1000 km in only 40 years, and colder species have retreated from the North Sea altogether (Beaugrand *et al.*, 2003). A study of 36 species of demersal (bottom-living) fish with varied biogeographic origins indicated that centres of distribution of species generally shifted by distances ranging from 48 to 403 km during 1977–2001 (Perry *et al.*, 2005). The mean latitude of species such as Atlantic cod and anglerfish or monkfish shifted northwards in relation to warming, whereas mean latitude did not change for some species; rather, a shift to deeper, cooler depths with warming was evident in these, e.g. plaice, cuckoo ray (*Leucoraja naevus*; Perry *et al.*, 2005). Hedger *et al.* (2004) also analysed the survey distributions of cod and haddock in the North Sea. These authors demonstrated that cod were found in deeper water during 1990–1999 compared with 1980–1989, but their distribution with respect to temperature was largely unchanged.

A study by Dulvy *et al.* (2008) has explored the year-by-year distributional response of the North Sea demersal fish assemblage to climate change over the 25 years from 1980 to 2004. The centre of gravity of latitude and depth of 28 species of bottom-dwelling (demersal) fish was estimated from species data collected by the autumn English groundfish survey. Individual species' responses were aggregated into 19 assemblages, reflecting physiology (thermal preference and range), ecology (body size and abundance–occupancy patterns), biogeographic origin (Boreal–Lusitanian and presence of range boundaries), and human impact (target, bycatch, and non-target). The whole North Sea demersal fish assemblage deepened by ~3.6 m per decade in response to climate change, and the deepening was coherent for most assemblages. The latitudinal response to warming seas was more heterogeneous and was a composite of at least two patterns: (i) a northward shift in the average latitude of abundant, widespread, thermal specialists (grey gurnard (*Eutrigla gurnardus*) and poor cod (*Trisopterus minutus*)); and (ii) a southward shift of relatively small southern species with limited occupancy and a northern range boundary in the North Sea (scaldfish (*Arnoglossus laterna*), solenette (*Buglossidium luteum*), bib (*Trisopterus luscus*), sole (*Solea solea*), and lesser spotted dogfish (*Scyliorhinus canicula*)).

The southward shift of warm-tolerant Lusitanian species is consistent with climate change acting through (i) the warming and increasing availability of shallow habitats in the southern North Sea, and (ii) NAO-linked inflows of warm water into the northeastern North Sea. The northern North Sea tends to be colder than the southern North Sea in summer, but the situation is reversed in winter. Some southern North Sea species were previously excluded from large areas of shallow inshore habitat in winter because these waters cool to <1°C. For example, sole tend to overwinter in deeper, warmer waters, before returning to the shallows in spring, in order to avoid the lethally cold winter temperatures (Henderson and Seaby, 2005). However, there is now anecdotal evidence that sole are arriving inshore earlier, owing to the rapidly warming seas in winter. During severe winters in the North Sea in the 1960s, mass mortality events were reported for Lusitanian species, such as sole and conger eel (*Conger conger*), but only rarely for Boreal species, such as cod, plaice, and dab (*Limanda limanda*; Woodhead, 1964a).

Brander *et al.* (2003) suggested that sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) have moved northwards in recent years and extended their ranges to include west Norway. Small numbers had occasionally and sporadically been caught in ICES Area IVa (the northern North Sea) since 1925 (Beare *et al.*, 2004), and anchovy were recorded as spawning in the Zuiderzee until it was dammed in 1932 (also in the German Bight during the 1950s and 1960s; Boddeke and Vingerhoed, 1996). However, numbers seem to have increased dramatically since 2000 and are now widely distributed (over almost 80% of the International Bottom Trawl Survey area), except in the most northern and western regions (Figure 10.2).

In 1996, a paper was published describing long-term variation in the abundance of southern species in the southern North Sea (Corten and van de Kamp, 1996) in relation to hydrography. Two periods of increase in the prevalence of southern species were described in the mid-1970s and 1990s. Both periods coincided with positive temperature anomalies, which, in turn, correlated with southerly winds over the Netherlands, indicating increased flow of Atlantic Water through the Straits of Dover. The authors concluded that the increases were not part of a systematic long-term trend, but instead were the result of increased transport of southern fish species into the North Sea and favourable winter temperatures.

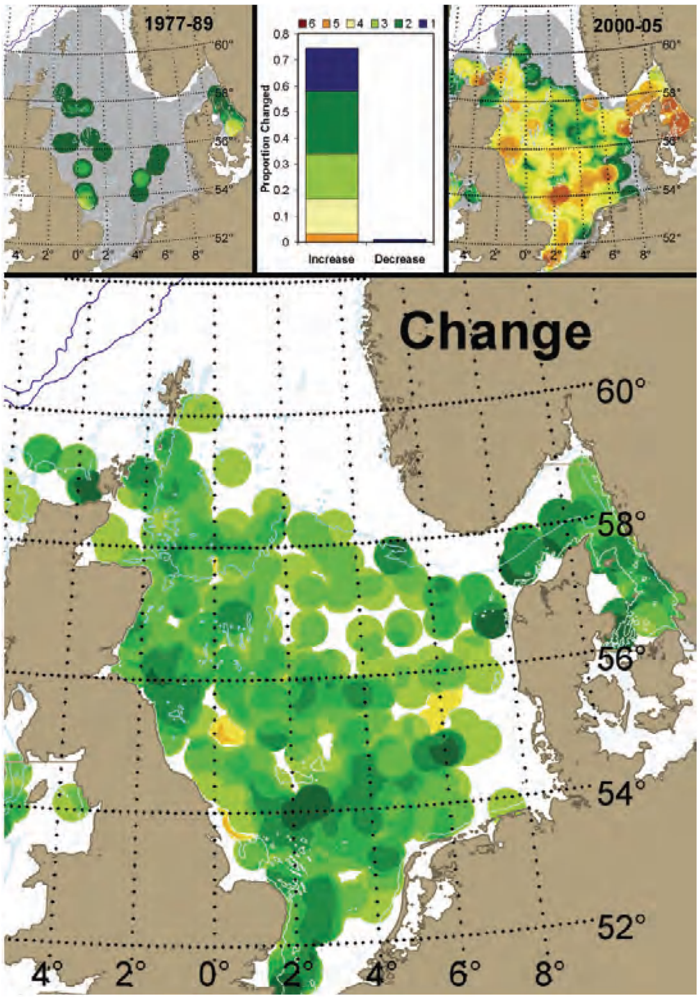


Figure 10.2. **Changes in distribution of anchovy (*Engraulis encrasicolus*) between 1977–1989 and 2000–2005 in the North Sea, Quarter 1: International Bottom Trawl Survey (from Tasker, 2008). Upper left panel: distribution in the initial period (1977–1989). Upper right panel: distribution in 2000–2005. Lower panel: the change in distribution between the two periods. Blue–green colours indicate an increase in density, with dark colours indicating the largest change; yellow–red colours indicate a decrease in density between the two periods, with red indicating the largest changes. The graph (upper centre panel) shows the proportion of the total survey area where an increase and decrease occurred, broken down by degree of increase or decrease (categories 1–6).**

Beare *et al.* (2004) revisited this issue and concluded that profound long-term changes are occurring. Most species classified as having southern biogeographic affinities exhibited almost exponential increases in abundance since the mid-1990s (which might be thought to support the case of Corten and van de Kamp, 1996). However, these increases were common to what is a very diverse range of fish species, encompassing a variety of taxa and habitat preferences. The lesser weeverfish (*Echiichthys vipera*), for example, is always confined to shallow, southern parts of the North Sea, whereas the bluemouth (*Helicolenus dactylopterus*) is a deep-water, shelf-edge species, yet both have demonstrated similar increases since 1990. Poor cod, John dory (*Zeus faber*), horse mackerel (*Trachurus trachurus*), mackerel, tub gurnard (*Trigla lucerna*), and red gurnard (*Aspitrigla cuculus*) have all increased in abundance over the past decade, but there were also peaks in the mid- to late 1950s, and mid-1970s, in addition to those observed more recently.

The invasion of the northern North Sea by bluemouth has been noted by Dutch scientists (Heessen *et al.*, 1996). The main invasion took place in 1991, with the sudden appearance of many small (6–8 cm) bluemouth in the northern North Sea, which then spread all around the shelf area until 1997. Abundance then began to diminish, and observations became limited almost exclusively to only two statistical rectangles north of Dogger Bank (Mamie *et al.*, 2007), and no bluemouth were recorded in Quarter 1 of 2004. Examination of the length–frequency data for bluemouth suggests that there have been two main recruitments (Mamie *et al.*, 2007): the first in 1991 and the second in 1998. Heessen *et al.* (1996) suggested that a large pulse of oceanic water entered the North Sea in 1990 (Heath *et al.*, 1991), and this might have transported bluemouth eggs and larvae into the area, where they then developed gradually. The study by Beare *et al.* (2004) adds further weight to this theory, because the influx of small bluemouth individuals noted in 1998 was probably related to eggs and larvae transported by another large Atlantic input that occurred during November and December 1997 (Edwards *et al.*, 1999).

There have been other, similar invasions of warm-water species, including the current influx of snake pipefish (*Entelurus aequoreus*; Lindley *et al.*, 2006; Harris *et al.*, 2007; Kloppmann and Ulleweit, 2007; van Damme and Couperus, 2008). It has been suggested that this influx might pose a threat to certain marine predators, notably seabirds (Harris *et al.*, 2007), but snake pipefish have also been reported as occurring in the stomach contents of commercially important fish species (Stafford *et al.*, 2006), possibly associated with a lack of "usual" prey types, such as sandeel (*Ammodytes marinus*). Kirby *et al.* (2006) speculated that the increased abundance of larval and juvenile *E. aequoreus* in Continuous Plankton Recorder (CPR) samples as far west as the Mid-Atlantic Ridge may coincide with the rise in winter, spring, and summer sea temperatures (January–September), when the eggs, which are brooded by the male, are developing and the larvae are growing in the plankton. Van Damme and Couperus (2008) put forward the alternative hypothesis that the sudden appearance of this species is a result of changes in zooplankton availability, which, in turn, have been caused by changes in the hydroclimatic environment.

Other species that have recently appeared in the North Sea for the first time (or have re-occurred after a very long absence) include the violet stingray (*Pteroplatytrygon violacea*), butterfish (*Stromateus fiatola*), thresher shark (*Alopias vulpinus*), and broad-billed swordfish (*Xiphias gladius*). The short-snouted seahorse (*Hippocampus hippocampus*) seems to be expanding its range northwards from its stronghold in the English Channel (Pinnegar *et al.*, 2008).

Throughout the geographic range of cod, many stocks occupy areas with mean annual seabed temperatures between 1 and 11°C, although the full thermal range extends from −1 to 19°C (Sundby, 2000). In the face of global warming, cod populations are predicted to retreat from southern areas, such as the North Sea, and expand into cooler, typically northern areas on yearly (Blanchard *et al.*, 2005) or decadal time-scales (Drinkwater, 2005). Cod are known to be capable of moving great distances (approx. 1000 km; Robichaud and Rose, 2004) and, hence, could theoretically relocate to anywhere in the North Sea. However, a study by Neat and Righton (2007), based on observations of the temperatures experienced by 129 individual cod (using data-storage tags), suggested that, by summer, most of the individuals in the south experienced temperatures considered superoptimal for growth. Cooler waters were within reach of the cod, and a small number of individuals migrated to areas that allowed them to experience lower temperatures, indicating that cod had the capacity to find cooler water. Most did not, however, suggesting that the changing thermal regime of the North Sea is not yet causing adult cod to move deliberately to cooler waters. Rindorf and Lewy (2006) have argued that a series of winters characterized by high temperatures, together with strong southerly winds (during the egg and larval phases), has led to an apparent northward shift in the distribution of juvenile cod. A concomitant northward shift by mature fish around the time of spawning was linked directly to a tendency for northerly distributed juveniles to retain this distribution throughout their entire life. This shift led to an overall northward shift in the centre of gravity of the species, supporting the contention of Perry *et al.* (2005).

The Thames Estuary fish assemblage is composed largely of juvenile individuals that use the estuary as a nursery habitat (FSBI, 2007). Attrill and Power (2002) demonstrated that patterns in the NAO coincided with variation in the structure of the fish assemblage (explaining 54% of variation), growth of many juvenile residents (76% of variation), and the abundance of the dominant species (69% of variation). Flatfish and "northern" species (e.g. herring) demonstrated a negative relationship between abundance and the NAO, whereas those species considered "southern", e.g. bass (*Dicentrarchus labrax*) and sprat (*Sprattus sprattus*), demonstrated a positive relationship. The abundance of gadoid fish, sole, and estuarine species, e.g. smelt (*Osmerus eperlanus*), pipefish, and pogge (*Agonus cataphractus*), was not related to variation in the NAO (Attrill and Power, 2002).

Climate change has been predicted to lead to changes in local and regional species richness through species extinctions and latitudinal ranges shifts. In the North Sea, species richness of fish fauna increased from 1985 to 2006, which Hiddink and ter Hofstede (2008) suggested was related to large-scale biogeographic patterns and climate change. Eight times as many fish species displayed increased distribution ranges in the North Sea (mainly smaller species of southern origin) compared with those whose range decreased (primarily large and northern species). This increase in species richness can be explained by the fact that fish species richness, in general, decreases with latitude. For marine fish, Macpherson and Duarte (1994) found a decline in species richness of approximately 1% for each degree of latitude for East Atlantic teleosts and elasmobranchs on both sides of the equator, regardless of habitat, and an increase in average maximum length with both depth and latitude.

10.3.4 Baltic Sea

The Baltic Sea is characterized by low salinities and low biodiversity, and by a closed circulation in the central basin. Salinity, temperature, and oxygen content of the different water layers are the factors that determine the distribution and abundance of marine fish in the Baltic Sea. Both water temperature in summer and the extent of ice cover, which reflects the thermal state in winter, exhibit large variations. Winter conditions, which are most severe in the Bothnian Bay and in the easternmost Gulf of Finland, limit the species of marine Boreal origin.

Despite the large number of marine fish found as occasional visitors or strays in the Baltic Sea, successful establishment has been limited. Of approximately 120 marine fish species in the North Sea, fewer than 30 occur permanently and can reproduce in the Bornholm area, and only 6–10 do so in the Bothnian Bay (Zenkevich, 1963; Haahtela, 1974). Marine species such as sole and plaice are common in the Kattegat but become much less common farther south and east–northeast into the Baltic.

The interannual variability of the Baltic Sea is modulated by the NAO and by the inflow of Atlantic Water from the North Sea. In the 1990s, inflow from the North Sea was relatively weak and infrequent. The situation caused a retreat of marine species from the northern and eastern areas and favoured freshwater fauna (Lumberg and Ojaveer, 1991). Fish of marine origin (especially cod, flatfish, herring, and other species that depend mainly on influxes of oxygenated saline water and the accompanying increases in productivity) were affected both by the deterioration in conditions for reproduction and by changes in the abundance and composition of prey (Bagge *et al.*, 1994; Nissling *et al.*, 2002; Ojaveer and Kalejs, 2005).

During periods of low salinity, the abundance and spatial distribution of marine species is reduced. Probable earlier immigrants (e.g. gulf herring) are less dependent on saltwater inflows, but depend more on local processes. The success of marine species in different areas of the Baltic Sea has been variable, and species adaptation, mediated by climate oscillations, has resulted in the formation of distinct local populations (Ojaveer and Kalejs, 2005).

The spatial and temporal distribution of cod in the Baltic Sea varies seasonally and between years. The migrations between spawning, feeding, and nursery habitats demonstrate seasonal and annual changes caused by changes in the physical and/or biological environment (Aro and Plikshs, 2004). By migrating to different areas for purposes such as feeding and reproduction, an individual can optimize its fitness as well as minimize the negative impacts of a fluctuating environment (Aro, 1989). Baltic cod has decreased since 1985, and reached a historical low in 1992. During the past 15 years, only two major inflows have occurred and, consequently, large areas with hypoxic and anoxic conditions have developed. Analyses by Hjelm *et al.* (2004) confirmed that oxygen was the main factor affecting cod density and distribution. Tomkiewicz *et al.* (1998) attempted to explore the oceanographic influences on the distribution of Baltic cod during the spawning season in the Bornholm Basin. Cod distribution, abundance, and population structure were estimated from hydroacoustic and trawl data and related to hydrographic parameters as well as to bottom depth. Salinity and oxygen conditions were found to be the major factors influencing the vertical and horizontal distribution of adult cod. The effect of temperature was minor.

Plaice is a commercially important species in the Kattegat and, to a lesser extent, in the Belt Sea (MacKenzie *et al.*, 2007). Its spatial distribution depends partly on the salinity gradient through the Kattegat–Belt Sea–western Baltic. In addition, interannual variations in juvenile plaice abundance in the Kattegat are at least partly controlled by wind-driven hydrographic transport of eggs and larvae from the Skagerrak (Pihl, 1990; Nielsen *et al.*, 1998). Plaice was common in the central Baltic

(ICES Subdivisions 25–28) in the earlier decades of the 20th century, when it supported directed commercial fisheries (Temming, 1989). The stock declined in the late 1930s–1940s because of recruitment failures associated with recruitment overfishing and unsuitable hydrographic conditions for survival of eggs and larvae (Temming, 1989). Since the mid-1980s, the plaice population has remained small (ICES, 2005b), despite much lesser abundance of an important predator (cod) and lower bycatch mortality in the cod fishery. Presumably, plaice recovery has been delayed because hydrographic conditions (salinity and oxygen levels in deep water) since the early 1980s have generally been unfavourable for fertilization and survival of eggs in this region (Nissling *et al.*, 2002).

The dab (*Limanda limanda*) currently inhabits the Kattegat and the western Baltic. However, historically, the dab also existed in the central Baltic and used the Bornholm Basin as its main spawning area (MacKenzie *et al.*, 2007). Catch statistics and research surveys indicate that the dab stock in the central Baltic collapsed with the plaice stock during the early 1930s–1940s (Temming, 1989). Unlike the plaice stock, the dab stock has never recovered. Compared with other marine species (e.g. plaice, flounder, and cod) in the central Baltic, higher salinities are required for activation of spermatozoa and successful fertilization of eggs (Nissling *et al.*, 2002). Dab eggs are, therefore, less likely to be fertilized and to survive at low salinities than the eggs of other marine species in the Baltic.

The flounder (*Platichthys flesus*) is a third commercially and ecologically important flatfish species in the area. The flounder is able to reproduce (i.e. activation of spermatozoa, fertilization of eggs) at lower salinities than other flatfish in the Baltic and, therefore, its habitat and biomass are much larger (Nissling *et al.*, 2002). Its distributional range extends from the Kattegat into the central–northern Baltic, including low-salinity coastal areas. Catch rates in the eastern and northern areas (e.g. Gulf of Finland) rise 3–4 years after increases in bottom salinity caused by major Baltic inflows and subsequently fall in the period between inflows (Ojaveer and Kalejs, 2005).

Some marine species enter the Baltic seasonally from the Kattegat, North Sea, and open Northeast Atlantic. These species include garfish (*Belone belone*) and mackerel (MacKenzie *et al.*, 2007). Other species (e.g. some herring populations) leave the Baltic on a seasonal basis. The timing of migration to and from the Baltic, as well as the residence time within (or outside) the Baltic, are determined partly by climatic variables, including temperature. For example, the arrival and departure of garfish to and from the Baltic occurred earlier in the warm years during 1986–2005 (Jacobsen, 2006).

10.3.5 Celtic–Biscay Shelf

The Celtic–Biscay Shelf includes the coastal and shelf seas of the northern Bay of Biscay, the Celtic Sea, English Channel, and the Irish Sea, plus the coastal seas west of Scotland and Ireland (Philippart *et al.*, 2007a). This region has a complex topography, with patterns of water movement primarily from the south and west penetrating into the English Channel and the Irish Sea. Water also leaves the region to enter the North Sea from the south and west via the English Channel and from the north and west around Scotland. Observations of sea surface temperatures (SSTs) have been made in the Celtic–Biscay region since the middle of the 19th century (Philippart *et al.*, 2007a). The SSTs reveal that, following a warm period in the 1880s, temperatures cooled until the early 20th century before increasing from around 1920, and remaining warm until the 1960s. A cooler period followed the extremely cold winter of 1962/1963 and continued well into the 1980s. Since then, accelerated warming has been apparent (Southward *et al.*, 2005).

During the warming in the 1930s, the herring fishery in the English Channel collapsed; this was associated with many changes in the rest of the ecosystem, indicating that overfishing was probably not the main underlying cause of the decline. Cold-temperate herring were replaced by warmer-water sardine. These ecosystem-wide changes were subsequently ascribed to climate change (Southward, 1980). Historical research has since demonstrated that such switches in species populations were commonplace and have occurred since at least the 13th century during alternating cold or warm periods (Southward *et al.*, 1988). In the 1960s, there was a switch back to colder conditions, and the planktonic communities returned to their previous colder-water characteristics. Populations of sardine declined again. Herring populations did not recover, however, perhaps because, at that time in the 1970s, stocks were at historically low levels in the eastern English Channel and North Sea, and recolonization was not possible (Hawkins *et al.*, 2003). Sardine are now abundant again and have spread farther north into the Irish Sea, as indicated by higher abundance in annual fish surveys. The warming observed from 1920 to 1960 and the resulting impact on pelagic fish has been related to the Atlantic Multidecadal Oscillation (AMO), which had previously been described as part of the "Russell Cycle".

Abundance of some warm–temperate fish species with southern distributions has exhibited a tendency to increase in southern UK waters during warming periods (1950s, 1980s–2002), whereas declines were apparent during cooling episodes (1920s, 1960–1970s). Analysis of fish taxa in the western English Channel over a 90-year period indicated that 9 of 33 core species (butterfly blenny (*Blennius ocellaris*), dragonet (*Callionymus gardineri*), topknot (*Phrynorhombus norvegicus*), solenette, poor cod, lesser spotted dogfish, greater pipefish (*Syngnathus acus*), thickback sole (*Microchirus variegatus*), and red bandfish (*Cepola rubescens*)) responded strongly to increasing sea temperatures (Genner *et al.*, 2004). A parallel analysis of 33 species from power-station intake screens in the Bristol Channel over 22 years demonstrated similar macroscopic trends, with one species declining in abundance with warming (the sea snail (*Liparis liparis*)), and nine increasing (Genner *et al.*, 2004). Somewhat paradoxically, there was a general lack of increase in Boreal species during cooling periods (and of decrease during warming periods) compared with responses to climate by southern species. The reason for this asymmetry in responses between species of different biogeographic affinity is not known, but complex indirect processes may be involved (Stenseth *et al.*, 2002; Genner *et al.*, 2004).

A study of the changing fish community in the Bristol Channel was published in 2007 (Henderson, 2007) using data derived from the filter screens of Hinckley Point nuclear power station. This study identified two periods of discrete change in the fish community over the past 25 years. The first change occurred in the late 1980s and involved a shift in the relative abundance of the "permanent" members of the community. This abrupt event coincided with observed changes in the plankton of the Northeast Atlantic (Beaugrand, 2004) and was correlated with the winter NAO. A second discrete change, affecting the total species assemblage, occurred in the early 1990s. This was marked by a sudden alteration in the set of "occasionally occurring" species. After 1993, these were dominated by species with distributions centred south of the Bristol Channel, whereas northern cold-water species disappeared. This change was correlated with average seawater temperature (and possibly AMO) rather than

NAO. In addition to discrete changes in community structure, the species richness of fish samples collected from the power station has shown a continuous increase.

Renewed observations of rare fish migrants to UK waters in recent years (Stebbing *et al.*, 2002), following earlier observations (Russell, 1953), may be related to recent sea warming. Sightings of bluefin tuna (*Thunnus thynnus*), triggerfish (*Balistes capriscus*), thresher shark, blue shark (*Prionace glauca*), stingray (*Pteroplatytrygon violacea*), turtles, and seahorses (*Hippocampus* spp.) are all becoming more commonplace (Stebbing *et al.*, 2002), as are ocean sunfish (*Mola mola*; Houghton *et al.*, 2006), although mechanisms and consequences are poorly understood. Swaby and Potts (1999) made the first British record of the sailfin dory (*Zenopsis conchifer*), noting that the species is advancing northwards along the continental shelf west of the British Isles at a rate of 60 km decade^{-1}.

Change in migration phenology has been described for the flounder, which has been demonstrated to undertake a spawning migration 1–2 months earlier when conditions are cooler (Sims *et al.*, 2004). To a large extent, timing of flounder migration is driven by short-term, climate-induced changes in thermal resources linked to negative (cool) phases of the NAO. Hence, short-term climate fluctuations have significant effects on the timing of peak fish abundance in an area, which may have implications for fisheries (Sims *et al.*, 2004).

Many of the species that have expanded in recent years have been non-commercial, planktivorous species, such as the boarfish (*Capros aper*), which has become particularly prevalent in French and UK survey catches (Pinnegar *et al.*, 2002). This phenomenon has been reported elsewhere in the North Atlantic, including the Bay of Biscay (Farina *et al.*, 1997; Blanchard and Vandermeirsch, 2005) and offshore seamounts (Fock *et al.*, 2002). In the past, *C. aper* outbreaks have been linked to storms and variability in offshore climate (Cooper, 1952). Boarfish are now being landed by Irish fishing boats and converted to fishmeal for aquaculture; in excess of 21 584 t were landed in 2008 (Marine Institute, 2009).

Pronounced increases in tropical fish in the Bay of Biscay area have been noted by scientists in France (Quéro *et al.*, 1998). Many fish species are at the southern or northern limit of their distribution range in the Bay of Biscay, where large-scale hydroclimatic changes have occurred in recent decades. Poulard and Blanchard (2005) attempted to identify the impact of such changes on the fish community using data collected during autumn groundfish surveys between 1987 and 2002. Results suggested a trend of increasing abundance with time for fish species having a wide distribution range (mainly subtropical ones), whereas the abundance of temperate and least widely distributed species decreased steadily.

The effects of climate change on elasmobranch fish (rays, skates, and sharks) are poorly understood and contrast to what is known about many important teleost fish. Some elasmobranch fish are extremely sensitive to temperature variation (i.e. as little as 0.001°C; Brown, 2003). Although it is currently unclear how important this sensitivity to temperature might be to their ecology, many elasmobranchs demonstrate complex behavioural trade-offs that are often associated with temperature (Sims, 2003). Cotton *et al.* (2005) demonstrated that a major component of the interannual variation in relative abundance of basking sharks (*Cetorhinus maximus*) off southwest Britain was positively correlated with fluctuations in SST and the NAO. Results of this study indicate that climatic forcing of the copepod *C. helgolandicus* influenced basking shark abundance. At a local scale (0.01–10 km), basking shark distribution and migration was determined by the abundance of adult

C. helgolandicus (Sims, 1999; Sims and Merrett, 1997; Sims and Quayle, 1998), with SST being less important (Sims *et al.*, 2003). However, at larger scales (10–1000 km), SST correlated significantly with basking shark distribution and movement patterns (Sims and Quayle, 1998; Sims *et al.*, 2000). These observations indicate that, although prey density is a key factor in determining short-term distribution patterns, long-term behavioural choices by these ectothermic planktivores may relate more closely to occupation of an optimal thermal habitat that acts to reduce metabolic costs and enhance net energy gain (Crawshaw and O'Connor, 1997; Sims *et al.*, 2003).

10.3.6 Iberian upwelling region

The Iberian coastal area includes the continental shelf region and the oceanic part of the eastern Atlantic Ocean between 35°N and 44°N. A rapid increase (1993–1994) in abundance of the rare, warm–temperate copepod *Temora stylifera* occurred in the Bay of Biscay, which correlated with the decreasing abundance of the coastal *T. longicornis*. Several other organisms of subtropical origin have been detected during recent years (Guerra *et al.*, 2002). There have been changes in species abundance and diversity of intertidal communities (Sánchez *et al.*, 2005) and northward displacement of southern-origin species, i.e. the limpet (*Patella rustica*; Lima *et al.*, 2006). Notably, there have been changes in exploited fish populations such as pilchard (sardine), anchovy, mackerel, and horse mackerel, but it is difficult to differentiate between the impacts of climate and of fishing effects.

Although juvenile nurseries of *Solea solea* and *S. senegalensis* are located inshore, spawning takes place offshore (Russell, 1976; Whittames *et al.*, 1995). Thus, larvae must migrate from the spawning grounds along the continental shelf towards shallow coastal areas, and particularly estuaries. These species are among the most commercially important fish using the Tagus estuary in Portugal. Previous studies in the Tagus estuary have reported trends in the fish assemblage related to climatic change. Although cold-water fish species have been disappearing from the estuary, fish species with tropical affinities have been increasing in abundance (Cabral *et al.*, 2001). Costa *et al.* (2007) reported an important effect of river flow on the fish assemblage of the Tagus estuary. Vinagre *et al.* (2007) demonstrated a positive correlation between river drainage and juvenile densities of both sole species, possibly because of the existence of chemical cues used by larvae for movement orientation. In contrast, no strong correlation was found between the NAO and/or the north–south wind component and sole densities, and it was concluded that the high complexity of the Portuguese upwelling system makes it hard to detect clear causal relationships with the environmental variables tested. Since climate-change scenarios predict a strong decrease in rainfall over the Portuguese river basins, as well as a concentrated period of heavy rain in winter, it was hypothesized that a future decrease in river drainage over much of the year may lead to lower recruitment success for the soles, especially for *S. senegalensis*.

10.3.7 Mediterranean and Black seas

In the western Mediterranean, climate change has been demonstrated to affect the boundaries of biogeographic regions, with some warm-water species extending their ranges and colonizing new areas where they were previously absent (Philippart *et al.* 2007a). The northward migration of species with an affinity for warmer waters has been demonstrated in several regions (Bianchi and Morri, 1994; Morri and Bianchi, 2001). The Ligurian Sea, one of the coldest areas in the Mediterranean, has a smaller number of subtropical species and a higher abundance of species characteristic of cold–temperate waters. The warming of Ligurian waters (Béthoux *et al.*, 1990;

Astraldi *et al.*, 1995) has favoured the penetration of warm-water Atlantic species, including the ornate wrasse (*Thalassoma pavo*), which, from 1985 onward, established large and stable populations (Bianchi and Morri, 1994). Changes in the composition of ichthyofauna have had a considerable impact on local fishing industries (Francour *et al.*, 1994). However, the increase in numbers of tropical Atlantic species found in the northern Mediterranean may result from a combination of anthropogenic and climate factors. Recent studies have identified a correlation between the NAO and the variability of the northwestern Mediterranean zooplankton community (Molinero *et al.*, 2005).

Sabatés *et al.* (2006) analysed the temporal and spatial changes in abundance and distribution of the warm-water species round sardinella (*Sardinella aurita*) in the western Mediterranean over the last decades in relation to seawater temperature. In the western Mediterranean basin (1950–2003), a significant positive relationship was found between round sardinella landings and temperature anomalies. Along a latitudinal gradient off the Mediterranean Iberian coast (1989–2004), a gradual increase in species abundance was observed from south to north, with a certain northward time-lag, associated with the increase in seawater temperature. The abundance of round sardinella in the two warmest and southernmost areas was positively and significantly correlated with SSTs registered during the start of gonad maturation the previous year. In addition, the positive relationship established between water temperature and abundance of round sardinella in the coldest and northernmost study area demonstrates that there is a temperature limit for the distribution of this species in the western Mediterranean.

Tsikliras (2008) also commented on the expanding distribution of round sardinella throughout the Mediterranean. For many years, its distribution in the Aegean Sea was confined to the southern part because of its preference for warmer waters. Recently, the geographic distribution of round sardinella, as reflected in purse-seine catches, has gradually expanded northwards. This northward expansion is directly related to the sea warming observed in the northern Aegean Sea. In addition to this distribution extension, the population of round sardinella in the northern Aegean Sea exhibited a 30-fold increase since the early 1990s and demonstrated a positive correlation with SST. Distributional changes and population explosions may have detrimental ecological effects on the community and ecosystem, but they may also affect the local fishery economics by altering the composition and amounts of catches.

Most information dealing with climate-change impacts in the central part of the Mediterranean are associated with the Adriatic Sea. During the past 30 years, warm-water species of ichthyofauna have increased in the Adriatic Sea (Dulčić and Grbec, 2000), and there are also some examples of the disappearance or increasing scarcity of species. Fish and zooplankton species that were previously rare are becoming more abundant, whereas artificially introduced species are also being recorded (Dulčić and Grbec, 2000; Kamburska and Fonda-Umani, 2006). These observations are related to increasing temperatures and salinity variations, which intensified in the Adriatic Sea after 1988 (Russo *et al.*, 2002).

The opening of the Suez Canal in 1869 allowed the entry of Indo-Pacific and Red Sea biota into the eastern Mediterranean, where these so-called "Lessepsian migrants" now dominate the community structure (50–90% of fish biomass). For many decades, this migration was very limited, partly because of the extremely high salinity within the Suez Canal, where dry salt valleys had existed previously; however, the process has accelerated in recent years, associated with a warming trend of the seawater and a significant drop in the canal's salinity to "normal" marine levels (Mavruk and Avsar, 2007). Record numbers of newly discovered, non-native species have been observed, leading to the creation of what has come to be called a "human-assisted" Erythrean (Red Sea) biotic province in the eastern Mediterranean (Goren and Galil, 2005). The list of exotic animals and plants that have invaded the Mediterranean, and particularly the eastern Mediterranean, continues to grow. Not only are more species coming through the Suez Canal, but also, with warmer seawater temperatures, it is becoming easier for exotic species to spread and establish viable populations.

Species movements in relation to global warming may increase the spatial overlap between exotic and endemic species, which is a critical issue for the conservation of biodiversity. Recent records of Lessepsian fish species in the Sicily Channel and the southern Tyrrhenian Sea (Castriota and Andaloro, 2005) demonstrate that these alien species are spreading throughout the Mediterranean. The alien Erythrean goldband goatfish (*Upeneus moluccensis*) was first recorded in the Levant in the 1930s, and has since established populations from Rhodes to Libya. By the late 1940s, it made up 10–15% of the total mullet catches off the Israeli coast (Wirszubski, 1953). Following the exceptionally warm winter of 1954–1955, its percentage increased to 83% of the catch, replacing the native red mullet (*Mullus barbatus*) in commercial fisheries (Perlmutter, 1956).

Ben Rais Lasram and Mouillot (2009) attempted to quantify (i) the increasing invasion of southern exotic species (either arriving from the Red Sea or Atlantic Ocean), and (ii) the spatial overlap between exotic and endemic Mediterranean fish fauna that are coming under increasing pressure as a result of global warming. The rate of Lessepsian fish introduction during 2000–2006 was threefold higher than during the preceding decade, representing the highest value since the opening of the Suez Canal. These observations are associated with the highest seawater temperatures recorded in the Mediterranean since 1810, when records began.

After the 1980s, some exotic fish reached the coldest areas of the Mediterranean Sea, e.g. the Adriatic Sea, which is a major hot spot of endemism. The number of exotic species in the Mediterranean is now 98.4% larger than it was 20 years ago; the number of invasive species has risen from 64 in the 1980s to 127 in 2006. The authors predict that the risk of future invasion by fish from the Red Sea is potentially very high, and that the magnitude of the phenomenon may accelerate with sea surface warming (+3.1°C for the surface and +1.5°C for the deeper layers before 2100, following Somot *et al.*, 2006). The prediction of such phenomena and the identification of fish species from the Red Sea that are more likely to invade the Mediterranean are critical areas for further research.

Changes have also been reported in the reproductive distribution of Black Sea anchovy, as may be inferred from the long-term distribution of the early life stages. In contrast to earlier studies, numbers of eggs and larvae in the southeastern Black Sea in recent years are higher than in the northwestern region (Niermann *et al.*, 1994; Kideys *et al.*, 1999), which was formerly the main spawning area (Ivanov and Beverton, 1985). Recent studies confirm that the main spawning areas have become established along the Turkish coast in the southern Black Sea (Kideys *et al.*, 1999). Niermann *et al.* (1994) and Kideys *et al.* (1999) suggested notably increased eutrophication in the northern part of the sea, possibly associated with recent climate change, as a possible cause. The reporting of the change corresponded to a great reduction in anchovy biomass resulting from overfishing and expansion of an alien ctenophore (*Mnemiopsis leidyi*), which might also have influenced the shift in spawning locations (Daskalov, 2002).

10.4 Perspectives

As we have demonstrated, a wide range of species has demonstrated distribution changes in each of the larger areas of the Northeast Atlantic. Whereas some of these changes can be related at least partly to fishing impacts, there is a broad body of evidence that climatic fluctuations are playing an important role. During warmer periods, "southern" species have tended to become more prominent and "northern" species less abundant, and vice versa, but there appear to be important differences between various regions. For example, in the Celtic–Biscay Shelf, there appears to be an asymmetric response to climate variations: southern species have tended to become more abundant in warmer periods, but the opposite appears not to be necessarily true for colder periods (corroborated by herring not returning to the region during the relatively cold 1960s to 1970s).

Much of the available evidence is circumstantial or correlative in nature. Very little is understood about the physiological processes and precise mechanisms that link climate change and fish distribution patterns. This is particularly true for non-commercially important fish species. Most of our conclusions regarding the response of fish and fisheries to climate change are assembled from fragmentary information from surveys and commercial landings. However, recent studies, using data-storage tags, genetics, and analyses of otolith microstructure and chemistry, have begun to unravel the behavioural and physiological processes that dictate the distribution and production of fish species in the Northeast Atlantic. These types of study seem to offer the most promising way of diagnosing the reactions of fish to changing climate conditions in sufficient detail for us to predict responses in future. Areas where data are lacking include:

- "real" information about the connectivity between spawning grounds, the distribution of larval fish (their survival and feeding), nursery grounds, and climate change;
- information about migration routes and timing;
- predictive studies that attempt to estimate changes in fish distributions, interactions between fish species, and the ecological role of incoming species;
- information on how changes in the behaviour of commercially important fish species might affect the catchability of fishing fleets.

11 Anchovy

Pierre Petitgas

11.1 Introduction

This section reviews knowledge of the European anchovy (*Engraulis encrasicolus*; order Clupeiformes, family Engraulidae), with particular reference to the population in the Bay of Biscay. Life-history traits, life-cycle organization, fisheries, and patterns of change, together with their link to climate, are also reviewed. Potential climate-change effects on the anchovy in Biscay are suggested, together with the appropriate individual-based modelling tools for predicting future responses of the exploited population.

11.2 General biology

The European anchovy, which is the only representative of the Engraulidae family in the Northeast Atlantic and Mediterranean, is generally regarded as a species with subtropical affinity. In Europe, populations of anchovy are present in the Mediterranean and Black seas, and in the Atlantic around the Iberian Peninsula, the Bay of Biscay, the English Channel, and the Irish, North, and Baltic seas. The species tolerates a wide range of temperature (6–29°C) and salinity (4–41 psu), as demonstrated by its wide distribution, but spawning is generally restricted to warm summer months (Ré, 1996).

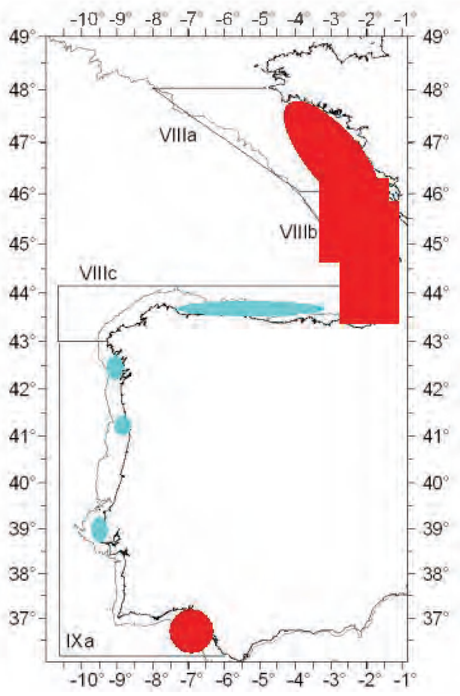


Figure 11.1 Schematic localization of current anchovy populations in ICES Areas VIII and IXa. Red = main populations with developed fisheries; blue = residual populations with sporadic fisheries (ICES, 2004c).

Fage (1911) documented the general traits of the European anchovy. Populations in different localities demonstrate different morphometric and meristic characteristics. Anchovy abundance is high in many areas, but also exhibits large fluctuations, both seasonally and interannually. Many anchovy populations demonstrate a coastal fraction associated with river plumes, with part of the life cycle being marine. Anchovy appear at the surface in warm months (coinciding with the spawning period) and are absent from surface waters at other times, when they probably migrate to greater depths on the shelf. In this review, we focus on the Bay of Biscay anchovy population (ICES Subarea VIII, Figure 11.1), which has supported valuable fisheries. Since the end of the 1990s, anchovy have again been reported in the North Sea after a long absence (Beare *et al.*, 2004; Alheit *et al.*, 2007). This recent expansion in the North Sea will be discussed and contrasted to the situation in the Bay of Biscay.

11.2.1 Life history

The anchovy is a short-lived species (five years maximum), with high rates of natural mortality and high fecundity. In the exploited population of the Bay of Biscay, anchovy aged >3 years are rare. Egg development is rapid, eggs hatch within 3–5 d. The size of the larvae at first feeding is 3–5 mm and the larval growth rate is 0.4–1.1 mm d^{-1} (Garcia and Palomera, 1996). The size at metamorphosis is ca. 40 mm and the larval duration period varies within 30–60 d (La Mesa *et al.*, 2009, and references therein). Most of the growth takes place during the first months of the juvenile stage, before the first winter. Anchovy are fully mature and reproduce at age 1 during their first spring. The annual natural mortality rate of ages 1–3 is high and variable, ranging from 0.7 to 2.0 (Uriarte *et al.*, 1996). The ICES Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy uses an average value of 1.2 (ICES, 2007i). Annual fishing mortality, as estimated by ICES, ranges from 0.4 to 1 (Uriarte *et al.*, 1996). Annual total mortality estimated by cohort analysis using abundance-at-age in the French acoustic surveys was 1.6 in the period 2000–2005 (unpubl.).

Juvenile growth rates are rapid, with most of the growth taking place during the first months after metamorphosis. The value of the von Bertalanffy parameter K ranges from 1.0 to 1.4 (unpubl.; see Section 11.2.5). For sustainable populations to have a total mortality value of 1.6, the von Bertalanffy parameter K would have to be ca. 1.4, according to the model of Chen and Watanabe (1989), which relates rates of mortality to growth.

Larval survival is on the order of 10–5 (Allain *et al.*, 2007). Reported daily egg mortality in May ranges from 0.11 to 0.30 and depends on temperature (Somarakis *et al.*, 2004). Juvenile mortality rate is unknown, but can be predicted as a decreasing function of age by using a Pareto function (Lo *et al.*, 1995), and egg, larval, and adult mortality values.

The average total number of eggs spawned during the season ranges from 110 000 to 350 000 eggs $female^{-1}$ (Motos, 1996), depending on the weight of the female.

Recruitment (estimated by ICES as abundance at age 1 by 1 January) demonstrated no relationship with adult stock size in the period 1987–2005 and ranged from 50 000 to 130 000 t (Figure 11.2). For this short-lived species, variation in stock size reflects variation in recruitment and growth.

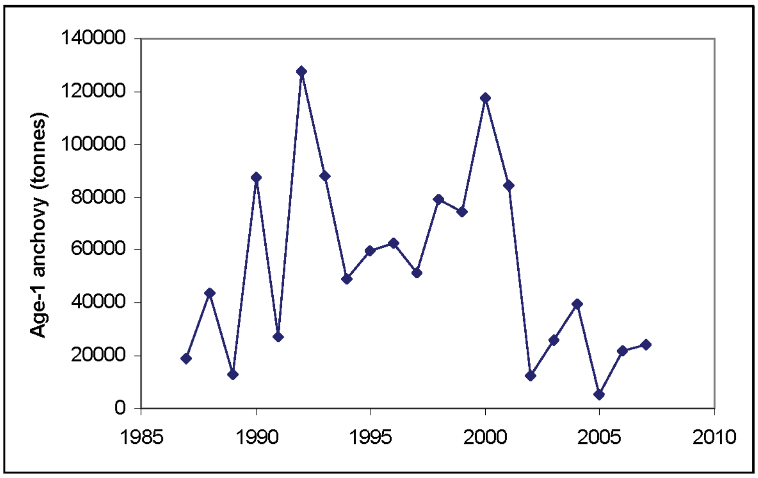


Figure 11.2. ICES recruitment series for European anchovy in ICES Areas VIIIa, b, and c: tonnes of age-1 fish on 1 January (ICES, 2007i).

11.2.2 Life cycle, habitats, and migrations

In ICES Division VIIIc along the Spanish north coast, the abundance of anchovy has progressively declined from west to east (Junquera, 1984) since the 1970s. We will, therefore, only describe features of the life cycle of the population inhabiting Area VIIIa, b, and c, east of 5°W (Figure 11.3). The ICES Study Group on Regional Scale Ecology of Small Pelagic fish (ICES, 2004c) documented the anchovy life cycle in that area and its relationship with oceanographic features. Recent juvenile acoustic surveys in autumn (since 2003) provided additional information on juvenile habitats and behaviour as well as life-cycle closure (e.g. Petitgas *et al.*, 2004; Annex 10 in ICES, 2007m). Spawning takes place predominantly in the southeastern corner of the Bay of Biscay (south of 46°30N) in spring (April–July), where the population aggregates. Spawning habitats have been documented and mapped using egg and acoustic survey data. The anchovy spawning (May–June) spatial distribution is length-dependent; smaller fish are more coastal and larger fish more offshore (Petitgas *et al.*, 2003). Major spawning grounds of smaller fish are associated with river plumes (Gironde and Adour), whereas those of larger fish are distributed on the outer shelf and shelf break (Motos *et al.*, 1996). The fish form small schools near the bottom during the day and disperse during the night, when they come to the surface layers (0–20 m) for spawning and/or feeding. Differences have been reported between anchovy school types in coastal and offshore habitats (Massé, 1996).

After spawning (July–November), adult fish disperse north and potentially also west. Small fish are expected to be more stationary, utilizing their coastal nursery habitats. The northward migration has been documented by analysis of the fishing activity of French trawlers that exploit the anchovy (Uriarte *et al.*, 1996). The northern feeding grounds are located off southern Brittany (48°–46°30′N) on the inner part of the shelf (20–120 m depth). During the day, most fish schools are close to the bottom, similar to the spring schools (Petitgas, 2005). Winter distribution is less well documented. Fage (1911) reports the anchovy as a demersal fish that is caught by bottom trawlers. In early spring, anchovy aggregate in their spawning habitats in the southeastern part of the Bay of Biscay.

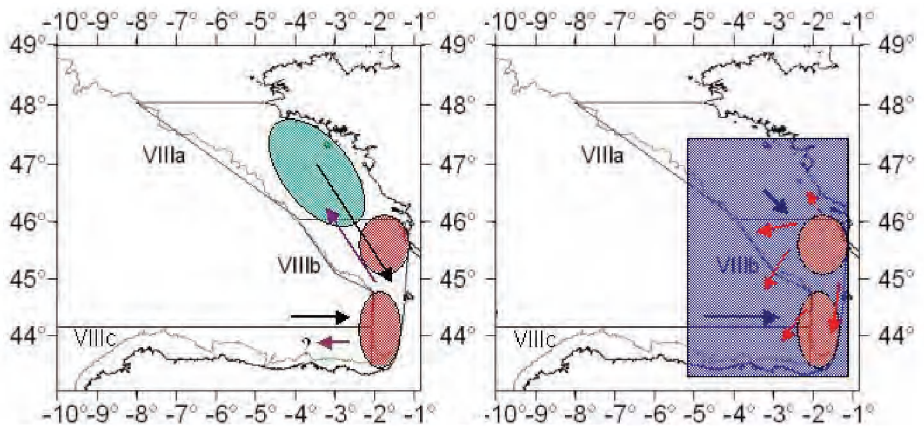


Figure 11.3. Schematic drawing of the life-cycle organization of the current anchovy population in ICES Area VIIIa, b, and c. Left: spring spawning grounds (red) and autumn feeding grounds (green); summer migration (purple arrows) and early winter migration (black arrows); wintering grounds are supposed to be at similar locations as the spring spawning grounds. Right: spring spawning grounds (red) and area containing autumn juvenile habitats (blue); summer larval drift (red arrows) and early winter juvenile arrival to the coast (blue arrows); winter juvenile habitats are coastal. (Redrawn from ICES, 2004c.)

From the major spawning grounds on the French shelf, the larvae drift and disperse predominantly southwestwards, offshore in the central part of the Bay of Biscay and towards the Spanish coast (Allain *et al.*, 2007). The larval drift depends on the seasonality of the flowfield, which depends on the seasonality of the winds and river discharges. When peak spawning occurs in May–June, the drift is southwestwards, but earlier spawning results in a more northward drift (Huret *et al.*, In press).

After the larval drift, 4–8 cm juveniles are found predominantly in small schools in the surface layers (0–20 m) during the day and at night in the southern part of the Bay (Petitgas *et al.*, 2004). Afterwards, juveniles progressively colonize coastal habitats and recruit to the adult stock (October–December). The area off the Gironde estuary is a major nursery ground. It is striking that coastal colonization is seen on the French coast, but not on the Spanish coast, where most of larval drift ends. The area off the Gironde estuary (Figure 11.3) corresponds to the major nursery ground in autumn and winter and to the major spawning ground in spring. This area has been demonstrated to be an essential fish habitat for the long-term population viability (Vaz and Petitgas, 2002). It has been suggested that the area be closed to fishing for conservation purposes (STECF, 2005a).

11.2.3 Trophic position

The anchovy plays a critical role in the transfer of energy from lower trophic levels (zooplankton) to higher trophic levels (fish) and is, hence, a typical "wasp-waist" species (Cury *et al.*, 2000). Uriarte *et al.* (1996) report that, in the Bay of Biscay, the anchovy is strongly preyed on, in particular by hake, tuna, mackerel, and shad during different stages of its life cycle. The anchovy is reported to be a strict mesozooplankton feeder during the adult stage (active feeding mainly on copepods and crustacean larvae; Plounevez and Champalbert, 1999). Anchovy larvae have been reported to feed on microzooplankton (Garcia and Palomera, 1996), with early larvae feeding on organisms in the size range of 50–100 μm.

11.2.4 Ecophysiology

Spawning is timed to the seasonal warming and occurs above a temperature threshold close to 14°C (Motos, 1996). Sea surface temperature (SST) and water column stratification are major predictors of egg presence (Planque *et al.*, 2007). Egg and larval-stage duration is temperature dependent, and relationships have been modelled using power functions (Lo, 1985; Regner, 1996).

The energy density (kJ g^{-1}) of adult and juvenile anchovy has been estimated from field samples (Tirelli *et al.*, 2006; Dubreuil and Petitgas, 2009). The energy density varies seasonally, being highest at the end of the feeding season (autumn) and lowest in late winter. In winter, anchovy lose weight, which is partly replaced by water, and, hence, the energy content decreases. Using a bioenergetics model, Pecquerie (2007) found, by simulations, that adverse winter conditions could decrease the subsequent total realized fecundity.

Anchovy continue to feed during the spawning season (Plounevez and Champalbert, 1999), a feature typical of fish with indeterminate fecundity. The energy required for spawning is available from two sources: (i) energy reserves are accrued during the previous year's feeding season and allocated to gonadal (reproductive) tissues; and (ii) energy obtained from feeding during the current spawning can be used to prolong the reproductive season. Hunter and Leong (1981) estimated that two-thirds of the total energy content in the spawned eggs came from the previous feeding season and one-third from food intake during that spawning season. It may therefore be assumed that the start of the spawning season is temperature-dependent, whereas the end of the spawning season depends on plankton production (food intake), resulting in a spawning window that varies with environmental conditions.

11.2.5 Growth

The growth of anchovy in the Bay of Biscay is rapid, and most of it takes place before the first winter. Juvenile fish are located above the thermocline in the upper layer by day and by night in summer and autumn (Petitgas *et al.*, 2004), thus benefiting from the high temperatures (>20°C). This situation inevitably affects growth and may explain the fast growth during the first months of life.

The average length-at-age in the spring acoustic surveys for the period 1987–2006 is 12.7 cm (age 1), 16.9 cm (age 2), and 18.2 cm (age 3; unpublished data reported to ICES annually). Von Bertalanffy growth curves, estimated from adult anchovy data only (Cendrero *et al.*, 1981), resulted in underestimation of the parameter K and a correlative overestimation of the parameter L_∞. Data from recent surveys of juveniles in the Bay of Biscay was used to revise the growth-curve parameters, suggesting that K is on the order of 1–1.4 and L_∞ the order of 17–19 cm. As the estimation of K and L_∞ is correlated and as length-at-age and annual mortality in the data are variable, it is difficult to ascertain whether or not total mortality in recent years could be sustained by growth (the stock collapsed in 2005). A striking characteristic of the growth curve is the large variability in length-at-age and the subsequent large overlap in size between ages. This may be explained by the long spawning season and individual fish histories.

From otolith analysis, total growth during age 1 has been demonstrated to be inversely related to total growth at age 0 (Petitgas and Grellier, 2003). A fish close to its L_∞ at the end of its first winter (end of age 0) will therefore grow little in its subsequent year (its first year of spawning) and may have a longer spawning period than a smaller fish of the same cohort. Growth is related to mortality in different ways and at different stages of the life cycle. For the larval stage, Allain *et al.* (2003) demonstrated that faster-growing larvae survived to juveniles. For the adult stage, Petitgas and Grellier (2003) observed that small-at-age anchovy selectively survived into the next year. This may be the result of fishing practices targeting large individuals.

11.2.6 Maturation, spawning, and fecundity

Motos (1996) reviewed the reproductive biology of anchovy in the Bay of Biscay. The anchovy has an indeterminate fecundity: oocytes continuously differentiate in the ovary during the spawning season. The anchovy is sexually mature at age 1, during its first spring. Spawning takes place from mid-April to mid-August, with a peak in May–June. In the Bay of Cadiz, Millán (1999) reported that smaller anchovy start spawning later and end spawning earlier than the larger fish. In the Bay of Biscay, Motos (1996) also documented an earlier start of spawning for larger fish. Spawning occurs at night in the surface layers (0–20 m), where early-stage eggs can be found. Goarant *et al.* (2007) demonstrated that egg buoyancy is regulated at spawning to match local sea surface hydrological conditions, thus ensuring that early ichthyoplankton stages are maintained above the thermocline. The anchovy is a batch spawner. The spawning rate (inverse of daily spawning fraction estimated from gonad histology) ranges from 0.2% to 0.25% of females. Each female therefore produces a batch of eggs every 4–5 nights, resulting in an average of 20 batches female^{-1} during the spawning season (2–4 months). The spawning rate is not affected by fish size. Batch fecundity is linearly related to gonad-free wet weight. Batch fecundity and spawning fraction are nearly constant over years (Somarakis *et al.*, 2004). Therefore, variation in total realized fecundity will depend on fish growth and spawning duration, which, in turn, vary according to environmental history over several months (temperature and food intake during the spawning season and during the previous feeding season, and winter conditions).

11.3 Fisheries

The fishery has been documented by Uriarte *et al.* (1996), and annual updates (e.g. ICES, 2007i) can be found in the reports of the ICES working groups (Working Group on the Assessment of Horse Mackerel, Sardine and Anchovy (WGHMSA), Working Group on Anchovy (WGANC), Working Group on Anchovy and Sardine (WGANSA)). The main fisheries are located on the spawning grounds south of 46°30N and east of 5°W in spring (April–June), and on the feeding grounds between 48°N and 46°30′N in autumn (September–November). Two fleets exploit the anchovy: purse-seiners that operate on surface fish aggregations and pelagic pairtrawlers that can operate at any depth on any type of fish aggregation. The population abundance index is better correlated with the catches of the pairtrawlers than with those of the purse-seiners (Villamor *et al.*, 2007), probably because of a difference in catchability between the two fishing techniques.

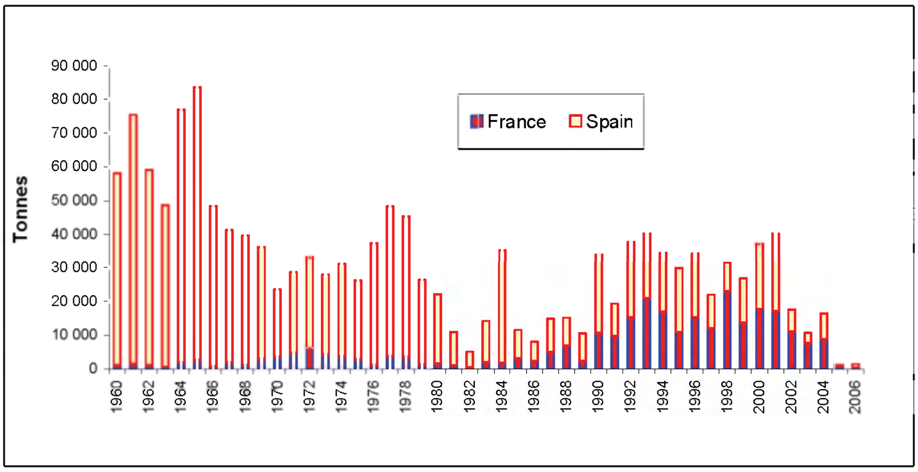


Figure 11.4. Long-term series of the landings by country for European anchovy in ICES Area VIIIa, b, and c (Villamor *et al.*, 2007).

The Spanish fleet consists only of purse-seiners, whereas French vessels comprise pairtrawlers as well as purse-seiners. Pair trawling developed in the mid-1980s, and the majority of the French catch has been taken by this technique since 1990. Since 1992, fishing activity is managed in space and time following an agreement between Spain and France: fishing is restricted to Spanish purse-seiners during March–June, after which fishing is also opened to the French fleet. The Spanish catches are therefore predominantly made in spring on the southern spawning grounds, and the French catches in autumn on the northern feeding grounds. The annual catch of each country has been approximately 15 000 t since 1990 and prior to the collapse in 2005 (Figure 11.4).

Length in the catches ranges from 10 to 19 cm, representing all age classes from 1 to 3+. A fraction of the large age-0 fish (>10 cm) may also be caught prior to its first spawning in autumn and early spring. The average demography in the survey data is approximately 75% at age 1 and 20% at age 2, with the balance at age 3+. The fishery is therefore mainly exploiting the recruitment.

The Spanish purse-seiners also exploit small anchovy (6–10 cm), including age-0 fish, in summer and autumn (July–October) for live bait in the tuna fishery. The live-bait fishery operates in the Gironde area and in all of the southern part of the Bay, when age-0 aggregations are accessible in the surface layers. The live-bait fishery is not regulated and its impact on stock dynamics is not explicitly documented. Live-bait catches have not been reported to ICES since 1999. The catch is expected to be on the order of 2 t wk^{-1} vessel^{-1}.

Recruitment (age-1 abundance at 1 January estimated by ICES) demonstrates no relationship with the parental stock size (ICES, 2007i). The ICES recruitment series has been tentatively correlated with a number of indices characterizing the environment in spring and summer. Borja *et al.* (1998) proposed a correlation model, with an upwelling index based on winds in spring, in which upwelling favoured recruitment. Allain *et al.* (2001) proposed a correlation model with two explanatory variables derived from hydrodynamic model outputs: a spring upwelling index, which also had a positive effect, and a water-column summer stratification breakdown index, which had a detrimental effect on recruitment. Since spring–summer 2002, these correlative models have lost their capability to predict recruitment in the subsequent year.

11.4 Changes in production and distribution

Junquera (1984) documented changes in the distribution and catches of the fishery during the 1970s, and ICES (2004c) reported changes that occurred during the 1980s and 1990s. During the 1960s and 1970s, the fishery was productive and mainly distributed in ICES Divisions VIIIc and VIIIb in the southern part of the Bay of Biscay and along the Spanish coast (Figure 11.1). At the end of the 1970s, this southern fishery collapsed. There was a progressive geographic reduction in the fishing area from west to east in both spring and autumn catches. The fishery west of 5°W in Division VIIIc is now sporadic and has not recovered. During the mid-1980s, pair trawling developed, and by the beginning of the 1990s, a stabilized pair trawling fishery had been operating, mainly as an autumn fishery on the northern feeding grounds in ICES Divisions VIIIa, which had not been exploited before. During the 1970s, the fishery was located in Divisions VIIIb and c. Since the 1990s, it shifted to Divisions VIIIa and b. Anchovy were known to be present in Division VIIIa in the 1970s, but were not exploited (J. Massé, pers. comm.). Fage (1911) reported that anchovy were abundant seasonally in that area, but that fishers exploited sardine rather than anchovy. In spring 2005, the VIIIa and b fishery collapsed, and recruitment has stayed low since. In the 2000s, prior to the collapse, the weight-at-age in the catches increased slightly over the mid-1990s (Figure 11.5).

Using survey data, Bellier *et al.* (2007) compared the spring egg-distribution pattern in the early 1970s (Arbault and Lacroix, 1971) with that in the 2000s. Slight differences were observed: spawning in the recent period was less coastal and slightly more to the north.

The application of the Bay of Biscay potential spawning model of Planque *et al.* (2007) to the hydrological parameters of the North Sea revealed that, since the end of the 1990s, spawning windows had potentially opened for anchovy in the North Sea as a consequence of higher summer temperatures (ICES, 2007k). This prediction has been ground-truthed, because anchovy eggs and larvae have been found on the German Bight in 2004 at a location similar to that in historical records of 1953 (Alheit *et al.*, 2007). Beare *et al.* (2004) demonstrated an increase in the occurrence of anchovy in the North Sea International Bottom Trawl Survey series at the end of the 1990s. The length structure in the dataseries supports the hypothesis that the increase in abundance of anchovy in the North Sea is the result of high recruitment from local relict coastal populations (ICES, 2007i).

11.5 Processes underlying observed changes

11.5.1 Growth

Most growth takes place at age 0, before the first winter, and no historical reference exists for that life stage. The age-0 growth depends on summer SSTs, and these have increased in Biscay (Koutsikopoulos *et al.*, 1998). Variation in growth will affect the spatial distribution, because larger fish occur more offshore, as well as the realized total fecundity, because batch fecundity is related to length. Adverse winter conditions (low food, low temperature) are also potentially a source of concern, because they may increase juvenile mortality and also affect total realized fecundity.

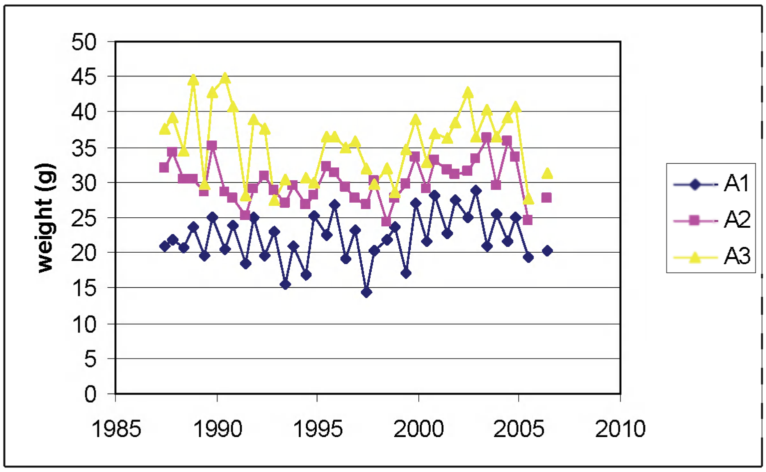


Figure 11.5. Time-series of the mean weight-at-age in the catches of European anchovy in ICES Area VIIIa, b, and c (ICES, 2007i).

11.5.2 Recruitment

No obvious change in the environment could explain the fishery collapses during the late 1970s and in 2005. Junquera (1988) found no convincing evidence for a regional environmental signal explaining recruitment failure in the 1970s in Division VIIIc. Likewise, in recent years, no obvious change in the environment has been found to explain the low recruitment levels since 2003 (ICES, 2007i). In the absence of an environmental cause, biological explanations have been suggested: a top–down control with increased predation on the larvae (Irigoien *et al.*, 2007), and/or a change in the aggregation pattern of adults during spawning (ICES, 2007m). Change in the spawning-time window, as a result of a change in growth or energy content, could also be added to the list of working hypotheses. The larval-dispersal kernel was demonstrated to depend on spawning location and date (Huret *et al.*, In press). Therefore, a change in the spawning window, resulting from a change in growth, could affect recruitment. Crucial questions to be answered include: prior to the collapse, was there a detrimental interaction between climate, population status, and fishing (e.g. hot summer, cold winter, heavy fishing), and is the repeat recruitment failure the result of direct environmental forcing or trophic interactions?

11.5.3 Mortality

There is no evidence for change in adult natural mortality in recent years and since the fishery closure. Larval and juvenile mortalities are not monitored and can only be estimated by the use of models (e.g. Allain *et al.*, 2007; Pecquerie, 2007). Progress in the development of larval-drift and survival models, as well as bioenergetic models, is essential if we are to increase our insight into these early life stages, which are crucial to assessing the anchovy population status.

11.6 Conclusion on climate effects

In the North Sea, temperature can be assumed to have been a limiting factor for anchovy spawning. In recent years, this factor would no longer have been limiting, and new spawning windows would have been opened, resulting in increased recruitment. Physical conditions in the German Bight (low salinity, high temperature, and high productivity of phyto- and zooplankton) appear appropriate to adult spawning and survival of early life stages. In contrast, the situation in the Bay of Biscay seems more complex.

Climate change can potentially affect anchovy at different stages of its life cycle, in particular, the larval-dispersal kernel, age-0 growth, and the spawning windows in space and time. However, long-term and recent changes observed in the Bay of Biscay anchovy population cannot be directly related to climate change. Therefore, the situation is thought to be one of complex interactions between fishing effects, trophic effects, and climate effects.

The Bay of Biscay is a mosaic of physical features, each with a potential impact on the anchovy life cycle (Koutsikopoulos and Le Cann, 1996). The impact of one factor is, therefore, not expected to override the others. Planque *et al.* (2003a) documented variability rather than change and argued that the Bay of Biscay oceanographic regime was complex because, being situated between the North Atlantic and subtropical meteorological systems, it takes influences from both. Borja *et al.* (2008) argued that the meteorological condition over the Bay of Biscay was related to the eastern Atlantic pattern and not to the North Atlantic Oscillation. In particular, the eastern Atlantic pattern relates to northeasterly winds that produce upwelling in Biscay. However, interannual variability is high. Changes in the environment in the Bay of Biscay have been reported: increased surface temperature (Koutsikopoulos *et al.*, 1998), increased surface and bottom temperature and picnocline depth, and fluctuations in river discharges (Woillez *et al.*, 2009).

The suggested approach is to construct a list of potential impacts at different stages during the life cycle and to identify which of these is active under which conditions. In terms of the development of working hypotheses, two topics are worth considering: (i) the establishment of long-term series of fish biological parameters (e.g. using catches) and of the environment, e.g. using realistic hydrodynamic and nutrient–phytoplankton–zooplankton–detritus (NPZD) model re-analyses; and (ii) the use of larvae individual-based models (IBMs) and bioenergetics fish models should allow an investigation of the complex interactions that cannot be done using simple correlative (statistical) methods. For instance, Struski *et al.* (2009) found that the area of unsuitable winter habitats had decreased as a consequence of the increase in temperature. Huret *et al.* (2009) tested the impact on the larval-dispersal kernels of climate-change scenarios and concluded that an increase in temperature decreased larval duration and, thus, dispersion around spawning grounds, but that a change in spawning location and time resulted in importance changes in larval dispersal.

The response of fish populations to climate requires the integration of different responses at different life stages. Furthermore, the response is expected to depend on population status and, in particular, the size structure and habitats occupied. It may also be necessary to add trophic interactions to this complexity. Fishing may change a population response to climate by modifying abundance, demography, length-at-age, and patterns of spatial distribution. Therefore, in order to investigate climate impacts on the anchovy, an analysis of the interactions between different scenarios of climate and population status (sizes and habitat occupation) is needed. The use of IBMs seems appropriate in order to formulate interactions and integrate them in space and time. These interactions would use the links between growth and reproduction and temperature and lower trophic levels. Detrimental as well as favourable scenarios could then be documented.

12 Herring

Mark Dickey-Collas, Georg H. Engelhard, and Christian Möllmann

12.1 Introduction

This section investigates what is known about herring (*Clupea harengus*; order Clupeiformes, family Clupeidae) in relation to climate change. Most of the work is drawn from our understanding of herring in three systems: the North Sea, Baltic Sea, and Norwegian/Barents seas. The section concludes with what is and is not known about the productivity of herring in relation to climate.

12.2 General biology

The Atlantic herring is a species of great commercial importance. It is a pelagic, ocean- and coastal-dwelling species, covering a depth range of 0–200 m (Geffen, 2009). Atlantic herring are found across the North Atlantic. In recent years, the herring fishery has been among the world's five largest fisheries by biomass (FAO statistics). The herring is considered a temperate fish species that inhabits the western and eastern Atlantic and the Baltic Sea, and has Boreal biogeographic affinities (Ellis *et al.*, this volume, Section 2). The Baltic herring is considered a separate subspecies (*Clupea harengus membras*) and is somewhat smaller and shorter lived. A closely related species, the Pacific herring (*Clupea pallasi*), inhabits the North Pacific (Haegele and Schweigert, 1985; Hay *et al.*, 2001).

In the fully marine environment, there is little genetic differentiation between the main Northeast Atlantic herring populations. However, once salinity starts to fall below 30, genetic differentiation becomes more pronounced (Ruzzante *et al.*, 2006; Reiss *et al.*, 2009), resulting in fairly ambiguous stock integrity in many areas (King, 1985; Hatfield *et al.*, 2007). Norwegian spring-spawning herring and North Sea herring are the biggest stocks within the ICES Area (Holst *et al.*, 2004; ICES, 2007e). Like other pelagic fish, extensive migrations are a characteristic feature of the herring's life strategy (Blaxter, 1985). Large migrations between spawning and feeding areas often occur, and clear overwintering areas exist for some stocks (Blaxter and Hunter, 1982; Holst *et al.*, 2002).

The high phenotypic plasticity of herring (Jennings and Beverton, 1991; Dickey-Collas *et al.*, 2009a) means that the environment has a fairly strong influence on most biological characteristics (Cushing, 1967). It also results in many stock components (Kell *et al.*, 2009). This substock structure is typified by the components of the North Sea herring, i.e. Orkney, Buchan, Banks, and Downs (Heincke, 1898; Redeke and van Breemen, 1907; Cushing, 1955; Zijlstra, 1958; Baxter and Hall, 1960; Bridger, 1961). These herring interact with each other and are influenced in different ways by the environment (Wallace, 1924; Anthony and Fogarty, 1985; Hulme, 1995; Schmidt *et al.*, 2009). In the Baltic Sea, there are a number of spring-spawning substocks that experience different environments in terms of hydrography and ecosystem structure (Parmanne *et al.*, 1994). Autumn-spawners have been historically important in the Baltic Sea, but are now absent, for reasons that are unclear (Parmanne *et al.*, 1994). In Norwegian spring-spawning herring, no clear evidence of substocks exists other than a north–south gradient in morphometrics, growth, and maturation (de Barros and Holst, 1995; Husebø *et al.*, 2007), on top of interannual and long-term variability in both these traits (Engelhard and Heino, 2004a) and a north–south gradient in genetics (Shaw *et al.*, 1999).

It has become clear that the life strategy or "spawner type" (e.g. autumn, winter, spring, or summer) is an expression of a cline across populations, not a discrete class. Spawning type may be fixed for an individual fish, but the designation is characteristic more of growth and association with other fish of the same type than of the actual spawning time (McQuinn, 1997; Corten, 2002; Engelhard *et al.*, 2003; Melvin *et al.*, 2009), and physiologically, there are very few differences between types (van Damme *et al.*, 2009). The interaction of growth, learned behaviour, and population size leads to a range of between- and within-population structures.

There are also strong density-dependent effects in the population characteristics (Cushing and Bridger, 1966; Hubold, 1978; Winters and Wheeler, 1987; Toresen, 1990; Engelhard and Heino, 2004b; Melvin and Stephenson, 2007). The lifespan of herring is between 17 and 20 years (38–40 cm length), although, as most species are heavily fished, they rarely live this long. Herring in the Baltic are generally smaller, with similar pronounced differences between stock components (Parmanne *et al.*, 1994; Cardinale and Arrhenius, 2000).

Atlantic herring spawn demersal eggs that stick to the substratum or to each other (Blaxter and Hunter, 1982; McPherson *et al.*, 2003). In the North Sea, herring spawn in gravel beds that are generally 20–40 m in depth (Cushing and Burd, 1957; Parrish *et al.*, 1959); in other areas, seaweed or other substrata may also be used. In thicker egg mats, mortality attributable to oxygen deficiency can be high (Parrish *et al.*, 1959). In the Baltic Sea, eutrophication has been demonstrated to cause egg mortality as a result of oxygen deficiency and changes in the spawning substratum (Aneer, 1985).

The main feeding time of herring is spring (i.e. April–June; Hardy, 1924; Savage, 1937). Feeding intensity reduces during the build-up to spawning, and little feeding occurs during winter (Hardy, 1924). Herring with different spawning times exhibit different energy strategies; so, the ecological impact may vary with spawning time, for example, in autumn-spawning and spring-spawning herring (Iles, 1984; Winters and Wheeler, 1996; Slotte, 1999; van Damme *et al.*, 2009).

The prey of herring varies according to location (Savage, 1937), season (Hardy, 1924), and year (Last, 1989). Larvae feed on copepod nauplii and microzooplankton (Bowers and Williamson, 1951; Checkley, 1982), juveniles move onto *Pseudocalanus*, *Paracalanus*, and *Temora* copepodites and small meroplankton, and adults feed on *Calanus*, *Temora*, *Oikopleura*, Schizopoda, amphipods, mysids, and young fish, such as juvenile sandeel (*Ammodytes* spp.; Hardy, 1924; Savage, 1937; de Silva, 1973a; Last, 1989; Dalpadado *et al.*, 2000; Möllmann *et al.*, 2004). In the North Sea, fish eggs are present in the diet of herring in the very early spring (when the feeding rate is low: Daan *et al.*, 1985; Segers *et al.*, 2007) and in June (Savage, 1937), whereas in the Baltic, they are also found in summer (Köster and Möllmann, 2000b). It is clear that the distribution of feeding schools is correlated with plankton abundance; herring schools are rarely found near diatom blooms (Savage and Wimpenny, 1936), whereas feeding is invariably associated with zooplankton abundance (Maravelias and Reid, 1997; Maravelias, 2001; Nøttestad *et al.*, 2007). Variability in the spatial structure of these schools tends to be at a scale of 6.5–20 nautical miles (Maravelias *et al.*, 1996), ignoring the unresolved small-scale variability. In the North Sea, the distribution of feeding herring demonstrates very strong affinity with the annual southern incursion of *Calanus* and *Limacina* (Bainbridge and Forsyth, 1972), which is influenced by the Atlantic inflow. In years when the *Calanus* peak is farther north, herring catches are also farther north (Corten, 2001a). The ratio between zooplankton production in the Buchan area off northeast Scotland and in the northeastern North Sea is also thought to influence where herring feed (Bainbridge and Forsyth, 1972), because years with poor zooplankton production in the Buchan area were also years when herring moved farther north (as determined by catches). Herring feeding schools are often associated with feeding mackerel (*Scomber scombrus*; Holst *et al.*, 2004).

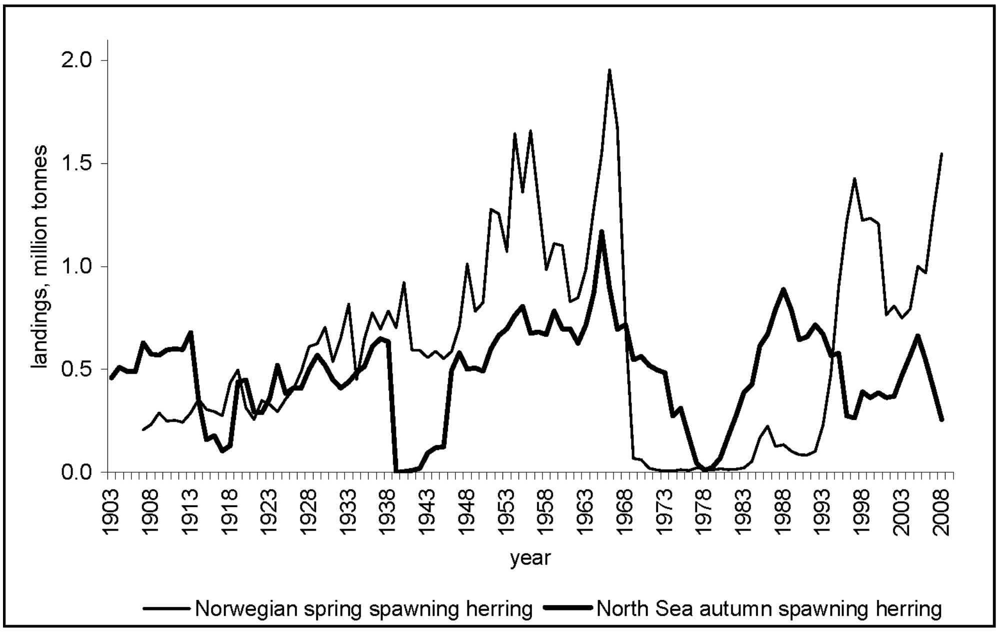


Figure 12.1. Landings of Norwegian spring-spawning and North Sea autumn-spawning herring from the beginning of the 20th century to 2008.

12.3 Herring fisheries and climate

Atlantic herring support one of the biggest fisheries in the world. Approximately 2 million t are fished every year (FAO statistics). Currently, the two largest fisheries are on Norwegian spring-spawning and North Sea autumn-spawning herring (Figure 12.1). Most stocks maintain a fishery. Herring is mainly exploited in fisheries directed at human consumption and by a variety of fleets, ranging from fixed gears, purse-seiners, and pelagic trawlers (often using refrigerated seawater (RSW)), to freezer-trawlers (see Borges *et al.*, 2008). Herring is traded fresh, pickled, frozen, smoked, and canned. Sizable industrial fisheries also take herring as a bycatch in the Northeast Atlantic. Herring are often caught together with mackerel and sprat (*Sprattus sprattus*).

Herring are very sensitive to overfishing, and collapses of stocks have occurred across the Atlantic (Figure 12.2), e.g. North Sea herring (Nichols, 2001; Simmonds, 2007; Nash *et al.*, 2009; Dickey-Collas *et al.*, 2010), Norwegian spring-spawning herring (Dragesund and Ulltang, 1978; Toresen and Jakobsson, 2002), and Icelandic summer-spawning herring (Jakobsson and Stefansson, 1999).

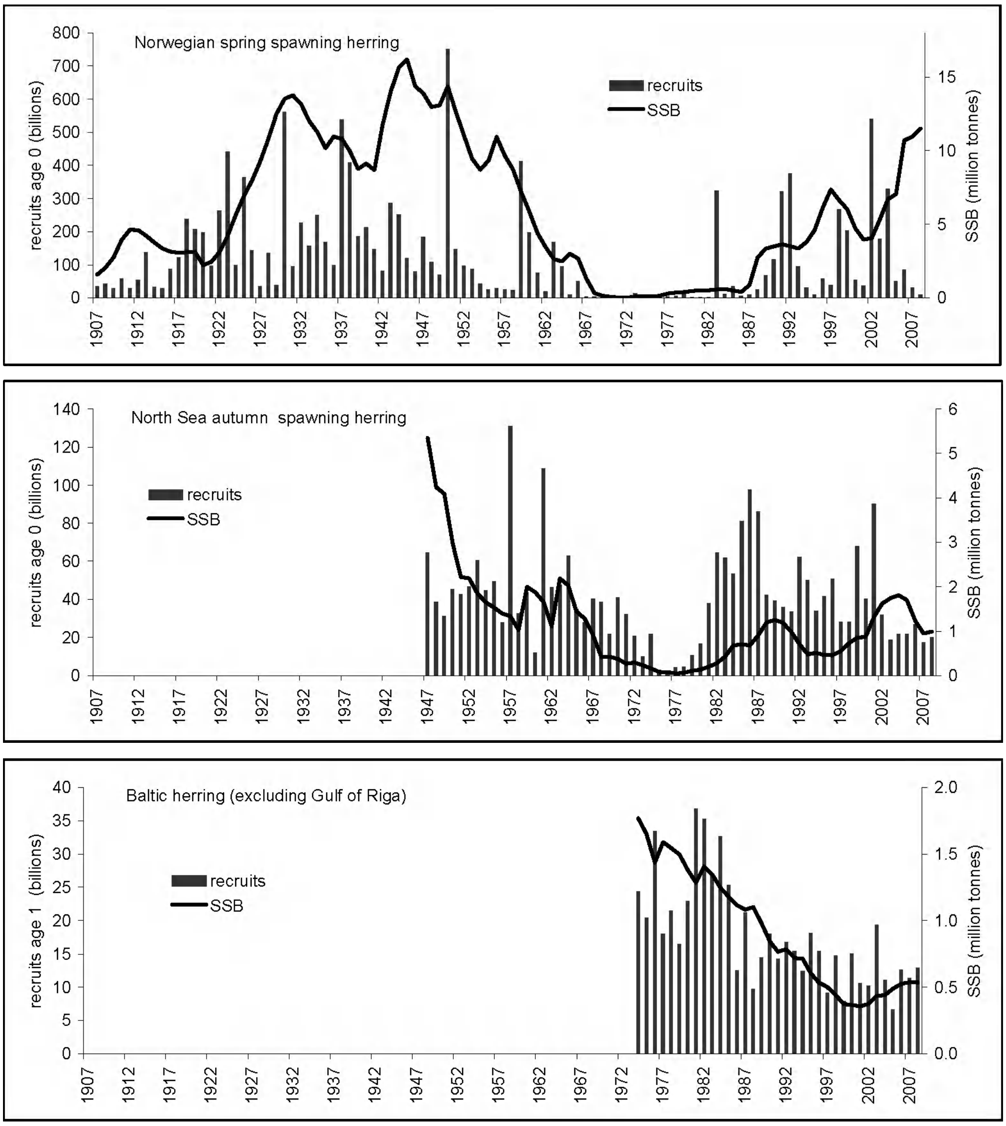


Figure 12.2. Population dynamics of Norwegian spring-spawning herring, North Sea autumn-spawning herring, and Baltic herring. (From ICES Fisheries Statistics.)

12.4 Observed changes in productivity

Herring stocks are well known to exhibit substantial fluctuations in productivity (Toresen, 2001), and herring fisheries have always been highly variable in terms of catch (Mitchell, 1864). In the 18th century, this variability led to the naive idea that all herring were part of one "megastock" that would migrate to the Arctic in winter, with a variable portion of the megastock returning each year to the North Sea (Heincke, 1898; Sinclair, 2009). This idea was disproved by several pioneering studies in fishery science, notably early research on annual growth layers in herring scales by Hjort (1914) and Lea (1911), which first demonstrated the marked interannual variability of herring year-class strength as an important driver of population fluctuations.

The variability in catches has allowed productivity to be compared with climate variability (Toresen and Østvedt, 2000; Poulsen *et al.*, 2007), and there are several well-known examples of changeable local productivity in herring stocks. In the western English Channel, the so-called "Russell Cycle", which comprises alternating periods of high abundance of herring and sardine (*Sardina pilchardus*), has had profound effects on the local fisheries (Southward *et al.*, 1988, 2005; Alheit and Hagen, 1997). In the North Sea, the Bohuslän herring periods were historical periods, lasting several decades, in which autumn-spawning herring catches in the easternmost Skagerrak could be extremely high (notably off the Bohuslän province of Sweden); these productive periods alternated with periods of near-absence of herring in the same locations (Corten, 1999a). There seems to be a very clear link between herring productivity and temperature, and this has been described by many studies (e.g. Toresen, 2001; Axenrot and Hansson, 2003; Cardinale *et al.*, 2004; Brunel and Boucher, 2007; Gröger *et al.*, 2010). Growth of the central Baltic herring stock has demonstrated a pronounced variability during recent decades, which has been confirmed to be the result of climate-induced changes in the zooplankton community and competition with sprat (Möllmann *et al.*, 2005; Casini *et al.*, 2006). Recruitment of Baltic herring stocks is substock-specific, with the gulf herring stocks demonstrating a generally positive response to increased temperatures, but with recruitment of central Baltic herring suffering from reduced food supply and, consequently, bad condition (Cardinale *et al.*, 2009).

The variability in recruitment and growth often differs between stocks, e.g. year-class strength in the North Sea is less variable than in the Baltic (Cushing, 1996; Myers, 2001). The recruitment patterns from subcomponents of stocks are also different (Bjerkan, 1917; Cushing, 1992; Oeberst *et al.*, 2009). It is widely accepted that the recruit-to-stock relationship is domed for herring, and that productivity per spawner is impaired at high spawning biomasses (Anthony and Fogarty, 1985; Zheng, 1996; Fox, 2001). However, overall stock size or area size may influence this density-dependent effect (Winters and Wheeler, 1987; Corten, 2002). The effect of collapse and recovery may also affect the characteristics of production (Engelhard and Heino, 2004a; Melvin and Stephenson, 2007; Nash *et al.*, 2009) because of density effects (Burd, 1984). Recruitment overfishing is a common feature in herring, and it is considered that this has often had as large an effect on productivity as the environment (Hodgson, 1936; Cushing and Burd, 1957; ICES, 1965a; Burd, 1978, 1985; Cushing, 1992; Nichols, 2001; Simmonds, 2007; Payne *et al.*, 2009).

12.5 Observed changes in distribution

Corten (2001b) suggested that many of the fluctuations in the distribution of North Sea herring are driven by stock increase, changes in zooplankton production, and variability in the Atlantic inflow by the Fair Isle Current. The interaction of year-class strength and environmental signals (combined with imprinting effects on individuals, and hence lag effects on the population) may make the interpretation of the influence of environment difficult (Corten, 2001b; Huse *et al.*, 2010). There appears to be a relationship between the changes between years in the distribution of overwintering herring and the North Atlantic Oscillation (NAO) and the location of the feeding grounds in relation to areas of high zooplankton abundance (Section 12.2). However, this is also complicated by a multidecadal effect, such as that seen in Bohuslän periods (also called the open Skagerrak periods; Alheit and Hagen, 1996, 1997; Corten, 1999b; Figure 12.3).

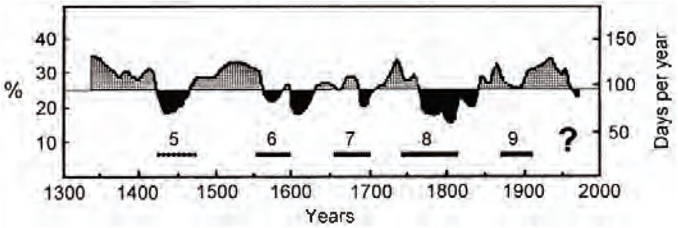


Figure 12.3. Frequency of southwesterly surface winds in England over the period 1340–1978 and the numbered Bohuslän herring periods. (From Alheit and Hagen, 1997.) The question mark denotes that the authors were uncertain whether or not another Bohuslän herring period was about to begin.

An attempt to consider the spatial nature of North Sea herring dynamics was begun relatively successfully by Heath *et al.* (1997). Overall, the evidence suggests that changes in the abundance of horse mackerel (*Trachurus trachurus*) and sandeel, as well as of *Calanus*, *Temora*, and *Pseudo/Paracalanus* production (Beaugrand, 2003; Reid *et al.*, 2003) will affect herring production and distribution (Bainbridge and Forsyth, 1972), and vice versa in the North Sea. The increased abundance of herring, combined with a reduction in zooplankton, will increase the impact of herring on the egg survival of plaice (*Pleuronectes platessa*) and cod (*Gadus morhua*; Daan *et al.*, 1985; Ellis and Nash, 1997; Segers *et al.*, 2007; Dickey-Collas *et al.*, 2010). Sprat and herring appear to have a complex relationship with some sympatric signals (Torstensen and Gjøsæter, 1995) and divergent signals in other areas (Corten, 2001b). There may also be a link with the abundance of Norway pout (*Trisopterus esmarkii*; Huse *et al.*, 2008).

Norwegian spring-spawning herring have demonstrated particularly marked changes in distribution over the past 50 years (reviewed by Dragesund *et al.*, 1997; Holst *et al.*, 2002), and these may be linked to a combination of climate variability and the (mainly fishery-induced) collapse of the stock in the late 1960s (Engelhard and Heino, 2004a). The most pronounced of these distribution changes concerns the extensive summer feeding migrations. Before the 1960s, when the stock was very abundant, its feeding areas were in an extremely productive area in the central Norwegian Sea, close to the Arctic Polar Front. However, when the stock began to decline in the 1960s, progressively fewer fish visited this productive area in summer, until it was completely abandoned around 1970 (Holst *et al.*, 2002). From the 1970s to the mid-1980s, the remaining stock foraged only in a narrow area close to the Norwegian coast. When the stock recovered, as a result of the recruitment of the very strong 1983 year class, the herring resumed their historically extensive feeding migrations, albeit shifted somewhat farther eastwards than the previous situation.

However, the overwintering and spawning areas have also differed over time. Until the mid-1960s, virtually the entire stock is thought to have overwintered in a small area off east Iceland, but by then, a strong, new year class established an entirely new overwintering site north of the Lofoten Islands. Around 1970, the collapsed stock also abandoned this area and established yet another overwintering site in Norway's Vestfjord. This, and a few nearby fjords, remained the overwintering area for the following three decades, even when the stock had fully recovered (Holst *et al.*, 2002; Figure 12.4). Most recently, a new shift has occurred. The herring are now overwintering in the Norwegian Sea north of Lofoten (Engelhard and Toresen, in press). Over the years, many different spawning sites along the Norwegian coast have been used at various periods, and one "core spawning site" off Møre (west Norway) has been occupied at all times. However, the southernmost sites, where larval survival appears to be greatest, have only been used in periods of high stock, when there were many large adult herring around (Johannessen *et al.*, 1995; Slotte, 1999) that were capable of performing the extensive spawning migrations to these most distant spawning sites (Slotte and Fiksen, 2000).

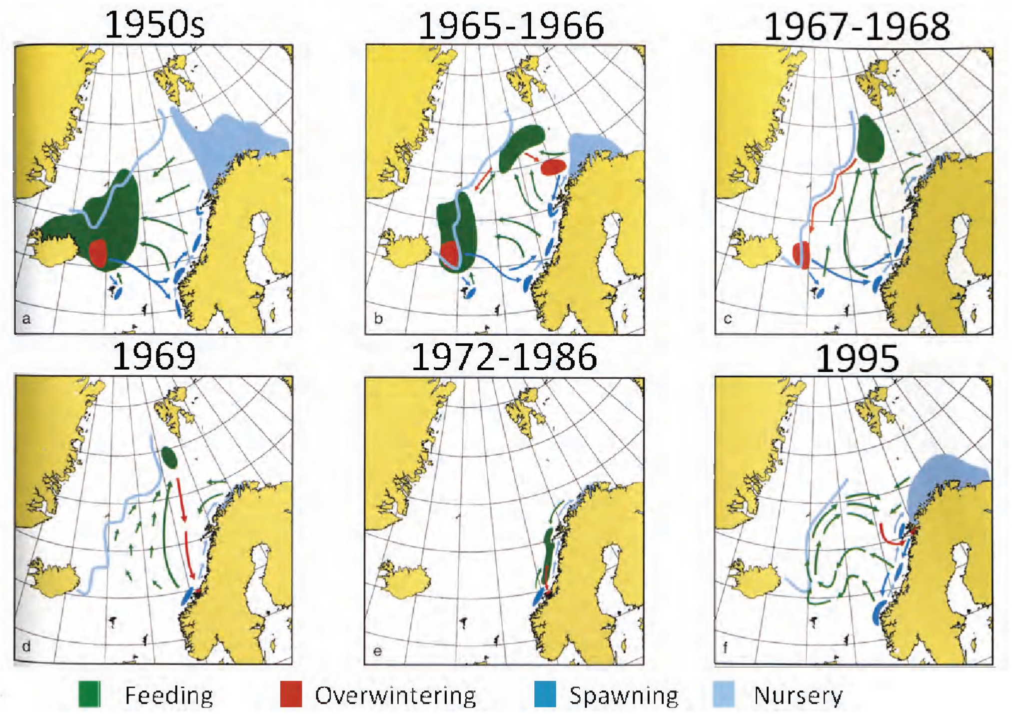


Figure 12.4. Main migration patterns of adult Norwegian spring-spawning herring during the 1950s–1990s. The light blue line is the 2°C isotherm at 50 m depth. (Based on Vilhjálmsson, 1997.)

12.6 Processes underlying observed changes

Variability in productivity and distribution in herring appears to exhibit multidecadal cycles, which may be associated with climatic cycles, such as the Atlantic Multidecadal Oscillation (AMO; Knight *et al.*, 2006; Lehodey *et al.*, 2006; Gröger *et al.*, 2010). The mechanism by which temperature is associated with recruitment is still unclear, and more study is required into the impact of temperature on growth and recruitment (Brunel and Dickey-Collas, 2010).

Interestingly, in the Norwegian spring-spawning herring population, climate change may have opposite effects on the juvenile and adult components of the stock (Heino and Engelhard, 2006). In this stock, the juveniles and adults differ in their main distribution areas: adults are distributed in the Norwegian Sea, while the most important nursery areas for juveniles are in the Barents Sea (with much smaller numbers of juveniles occurring in Norwegian coastal fjords). Toresen and Østvedt (2000) demonstrated that warmer climatic conditions (measured as the Kola temperature in the Barents Sea) are positively related to year-class strength. Hence, overall abundance of this stock is related to temperature. Food availability is a likely mechanism: in the Barents Sea, *Calanus* abundance is thought to be positively related to the Kola temperature, because warmer temperatures are associated with increased influx of copepod-rich waters from the Atlantic (Aksnes and Blindheim, 1996). In contrast, Engelhard and Heino (2005, 2006) suggested that warmer temperatures are negatively linked to condition in the adult component of the stock, which may lead to skipped spawning. Indeed, in the Norwegian Sea, there is an inverse relationship of *Calanus finmarchicus* abundance with the NAO and sea surface temperatures (Fromentin and Planque, 1996). In colder years, better feeding conditions for herring during summer are likely to improve survival and lead to higher participation in reproduction during winter immediately after and with a delay of one year.

In the case of Norwegian spring-spawning herring, three mechanisms have been put forward to explain the notable changes in distribution and migration patterns of this stock over the years (e.g. Dragesund *et al.*, 1997; Fernö *et al.*, 1998; Holst *et al.*, 2002; Huse *et al.*, 2002; Engelhard and Toresen, in press).

i) Oceanographic shifts may affect the location of productive areas, causing changes in feeding areas and, indirectly, in overwintering and spawning areas. The position of the current feeding ranges, which are farther east than the precollapse feeding range, may be explained by a shift in the position of the Arctic Polar Front, which, in the 1950s, was farther west than it is now.

ii) Herring migrations are often density-dependent, because individuals in a population appear to follow the adopted-migrant hypothesis (McQuinn, 1997; adapted from the Sinclair and Iles (1989) member-vagrant hypothesis). According to this, core areas of the stock are likely to be visited during both high and low stock concentrations, whereas more marginal areas will only be visited during high stock periods (Holst *et al.*, 2002). This interpretation is similar to the "numerical dominance" hypothesis (Corten, 2002; Huse *et al.*, 2002). This is confirmed by the observation that each of the very strong year classes of 1959, 1983, and 1991 – which followed fairly long series of weak year classes – established changes in migration patterns (Huse *et al.*, 2002; Huse *et al.*, 2010).

iii) Migratory behaviour might be partly genetically determined; to some extent, selective removal of fish exhibiting certain behavioural patterns by the concentration of fisheries in specific areas may have affected the migration patterns (Engelhard and Heino, 2004b).

Productivity changes in Baltic herring are thought to be a result of environmental variability (MacKenzie *et al.*, 2007), which is affected by climate change. Growth changes occurred mainly as a result of changes in the zooplankton community caused by changes in salinity (Möllmann *et al.*, 2003a; Rönkkönen *et al.*, 2004). Additionally, competition with sprat (Köster *et al.*, 2003b) has contributed to reduced herring growth and condition (Möllmann *et al.*, 2005; Casini *et al.*, 2006). The effect of climate on herring recruitment appears to be different between substocks (Cardinale *et al.*, 2009). Although, for the shallower gulf stocks, the direct effect of temperature on physiology and the indirect effect on increased zooplankton production resulted in increased recruitment success, the open-sea stock suffered from reduced food supply and worsened condition (Cardinale *et al.*, 2009).

In the North Sea and west of the British Isles, very little study and synthesis of the processes that determine variability in production appear to have taken place. The recent poor recruitment (from 2002 to the present day) has been attributed to changes in the environment of the North Sea, linked to warming (ICES, 2006o, 2007e; Payne *et al.*, 2009; Dickey-Collas *et al.*, 2010). Recruitment strength in North Sea herring is determined just prior to metamorphosis of the larvae (Nash and Dickey-Collas, 2005), but the environmental variability at hatching time on the northern spawning components is different from that of the southern spawning components (Hjøllo *et al.*, 2009; Petitgas *et al.*, 2009). Time-series analysis suggests that changes in hydrography and zooplankton community (described as a regime shift; Edwards *et al.*, 2007), and perhaps transport of larvae, occurred at the same time as the change in recruitment productivity (Dickey-Collas *et al.*, 2009b). However, the processes involved have yet to be identified, despite in-depth analysis of time-series of biological processes, productivity, and environmental variability (T. Brunel, IMARES, unpublished data).

12.7 Herring and climate change

It is often stated that pelagic fish are the most likely fish in which to detect responses to climate in the short term (Lehodey *et al.*, 2006). From the evidence available, it appears that the plasticity of herring makes them very responsive and perhaps sensitive to environmental and, thus, climatic variability. Within their physiological limits, herring are adaptive to their environment. The systems that have been well studied (Norwegian and Baltic seas) highlight the importance of prey, competition, and temperature on the productivity of herring. In systems that are less well studied (North Sea, west of the British Isles), it is likely that these factors are equally important to the productivity of herring. Therefore, if climate change affects these factors (as it will), it is likely to affect herring productivity through a combination of growth, recruitment, migrations, distribution, and competition for prey and physiological habitat.

It is clear from this review that little synthesis of process understanding, relating North Sea herring production to climate, has taken place. Therefore, if the impact of climate change on the second most important herring fishery in Europe is to be fully understood and accounted for within management, further work on understanding the dynamics of the North Sea system, and the role of herring within it, needs to be carried out.

13 Sprat

Christian Möllmann and Myron A. Peck

13.1 Introduction

This section reviews knowledge of the sprat (*Sprattus sprattus*; order Clupeiformes, family Clupeidae), with particular reference to the effects of factors influencing productivity in the Baltic Sea and elsewhere. An overview of the general biology and ecology of the species is provided to help understand the main climate-driven processes acting to cause changes in this species' distribution and productivity within European waters.

13.2 General biology

The European sprat is a small-bodied, pelagic, schooling, zooplanktivorous species that occurs over a broad geographic range, from the Black and Mediterranean seas in the south to the European Atlantic shelf, including the North and Baltic seas in the north (Muus and Nielsen, 1999). Three subspecies have been defined (Whitehead, 1985): *S. sprattus sprattus* in the Northeast Atlantic and North Sea, *S. sprattus balticus* in the Baltic Sea, and *S. sprattus phalericus* in the Mediterranean and Black seas. Growth rates in sprat are notoriously variable within and between age groups, areas, and years. Sprat are short-lived and rarely reach an age of >5 years (Bailey, 1980) or a length of >16 cm (Whitehead, 1985). The species is characterized by a tolerance of a wide range of salinities and, because of this, is also abundant in estuarine habitats.

In the ecological context, *S. sprattus* is a key "wasp-waist" species (e.g. Cury *et al.*, 2000) and plays a major role in the ecosystem, both as an important food resource for many top predators, such as piscivorous fish, marine birds, and mammals (Bagge *et al.*, 1994; Sparholt, 1996), and as a significant predator on the zooplankton community (Arrhenius and Hansson, 1993; Rudstam *et al.*, 1994; Möllmann and Köster, 2002). Sprat are zooplanktivorous in all exogenously feeding life stages and, as adults, feed mainly on calanoid copepods (e.g. de Silva, 1973b; Arrhenius and Hansson, 1993; Voss *et al.*, 2003; Möllmann *et al.*, 2004; Dickmann *et al.*, 2007). They can have an important impact on their prey species, and this is especially apparent in the Baltic Sea, where food competition with herring (*Clupea harengus*) has led to growth changes in both species (Möllmann *et al.*, 2005; Casini *et al.*, 2006). Furthermore, the Baltic sprat has been demonstrated to limit the recruitment success of its predator, the cod (*Gadus morhua*), by egg predation (Köster and Möllmann, 2000b) as well as regulating its own stock size through egg cannibalism (Köster and Möllmann, 2000a).

The sprat is a classical *R*-selected species (e.g. short lifespan, early reproduction, low biomass) and a multiple batch spawner, with females repeatedly releasing eggs throughout the spawning season (up to 10 times in some areas; George, 1987). A single female can produce between 100 and 400 eggs g^{-1} body weight (Alheit *et al.*, 1987), equivalent to 1500–6000 eggs $batch^{-1}$ for a 2-year-old female weighing 15 g (Bailey, 1980), and spawn a total of 6000–14 000 eggs $season^{-1}$ (Muus and Nielsen, 1999). Spawning occurs in both coastal and offshore waters (Whitehead, 1985), and the timing of peak spawning, relative fecundity, and batch fecundity vary significantly between years and regions (Alheit *et al.*, 1987). In northern European waters (North and Baltic seas), peak spawning occurs between May and August, depending on water temperature (Wahl and Alheit, 1988). In southern European waters (e.g. Adriatic Sea), sprat generally spawn during winter months

(November–April), at water temperatures of 9–14°C (Dulčić, 1998). Adults are generally mature at 2 years of age, though a small proportion of the population may spawn as 1-year-olds (Bailey, 1980). In most regions, spawning generally takes place at night (Alheit *et al.*, 1987) within surface waters. Waters colder than 5°C cause significant mortality in sprat eggs (Nissling, 2004). Sprat eggs and larvae are pelagic (Russell, 1976; Moksness and Torstensen, 1985).

In the North Sea, sprat eggs are distributed in waters with a salinity of 30–33 psu, whereas larvae are likely to occur over a similar or slightly higher range of salinities (Moksness and Torstensen, 1985). The inner German Bight, the British coast from Scotland to the English Channel, and the northwest coast of Jutland were identified as three main spawning areas for sprat in the North Sea (Aurich, 1941). In the German Bight, peak spawning is observed generally from May to August (Alheit *et al.*, 1987; Alshuth, 1988), and high egg and larval abundance has been found within tidal fronts in this region (Valenzuela *et al.*, 1991; Munk, 1991, 1993). Water circulation in the North Sea transports eggs and foraging larvae from a large catchment area into the German Bight (Bartsch and Knust, 1994a, 1994b), where enhanced larval growth rates have been related to specific frontal areas, with peaks in chlorophyll and secondary production (Munk, 1993). Other authors have reported similar larval growth rates, but found little spatial variability (e.g. Valenzuela and Vargas, 2002). Recent modelling studies suggest that vast areas of the German Bight support high growth rates for young larvae (Kühn *et al.*, 2008).

It is generally assumed that sprat in the North Sea undertake large seasonal migrations. The location of traditional winter fisheries indicates migrations towards inshore waters for overwintering along the British coast and in the central North Sea, although older fish are likely to remain offshore (Bailey, 1980). In spring, sprat leave the inshore areas and disperse into offshore spawning areas during summer, then return, along with the incoming age-0 recruits, to overwintering areas in autumn (ICES, 1990a). Although peak spawning is thought to occur in late spring and early summer, sprat larvae produced in late summer or autumn may overwinter in the larval phase and contribute to recruitment during the following year, but more work is needed to clarify the stock structure and whether this autumn spawning contributes substantially to the stock dynamics (ICES, 2006e).

The sprat population in the Baltic Sea exists at the northern limit of the latitudinal range of this species. Nevertheless, the sprat is highly successful in the Baltic Sea, and abundance has increased dramatically since the mid-1990s. The Baltic sprat is known to spawn over an extended period from March/April to July/August (Grimm and Herra, 1984; Karasiova, 2002). Spawning takes place from the Kiel and Mecklenburg bays in the west to the major basins (Arkona, Bornholm, and Gotland basins and the Gdańsk Deep) in the central and eastern Baltic (Grauman, 1974; Grauman and Krenkel, 1986). During late spring/early summer, adult sprat migrate from basin spawning grounds to coastal feeding grounds. In winter, sprat migrate into deeper areas of the Baltic Sea and overwinter in relatively warmer water layers below the halocline (Stepputtis, 2006). Sprat eggs are spawned in the surface layer, but thanks to their specific gravity, they sink below the low-salinity surface waters down to intermediate water depths 30–60 m below the thermocline (Wieland and Zuzarte, 1991). The temperature of intermediate water in the Bornholm Basin appears to remain relatively constant over the spawning season, ranging from 4.7°C in April and 5.2°C in June to 6.5°C in July. Sprat eggs incubated below 5°C were significantly less viable (Nissling, 2004), which led to the hypothesis that early spawning after cold winters could induce substantial egg and early larval mortality and, therefore, result in relatively weak year classes (Parmanne *et al.*, 1994), whereas warmer years and a warmer intermediate layer lead to higher recruitment success (Köster *et al.*, 2003b). After hatching and during or shortly after the yolk-sac stage, sprat larvae migrate into the warmer, more productive surface waters (Voss *et al.*, 2003; Dickmann *et al.*, 2007), where larval drift is influenced primarily by wind-driven, surface currents (Baumann *et al.*, 2006).

13.3 Fisheries

In the North Sea, increases in fishing pressure on sprat and a few successful year classes helped fuel an increase in landings during the mid-1970s. Catches declined subsequently and increased again in the mid-1980s, reaching a peak in 1994/1995 (ICES, 2007e). Within Mediterranean waters, the sprat ranks third in commercial value behind the sardine (*Sardina pilchardus*) and the anchovy (*Engraulis encrasicolus*; Dulčić, 1998; Tičina, 2000).

The most thorough stock assessment is for sprat in the Baltic Sea, covering ICES Subdivisions 22–32 (ICES, 2007f). In the last two decades, abundance and annual landings of Baltic sprat have increased dramatically, although they decreased by 13% (in 2006) and 35% (in 2005) compared with peak landings (>500 000 t) reported in 1997 (Figure 13.1).

In the Baltic, the main part of the sprat catch is taken primarily by pelagic single trawls and pair trawling (using a 16 mm mesh in the codend). The sprat fishery is year-round and, in most countries, the main fishing season is during the first half of the year. The fishery consists mainly of two types of fleets: small cutters (17–24 m in length, with an engine of up to 300 hp), and medium-size cutters (25–27 m in length, with an engine of up to 570 hp). Occasionally, larger vessels (over 40 m in length, with an engine of 1050 hp) are used; these have a high vertical trawl opening and operate in areas deeper than 50 m. According to national regulation (e.g. in Russia), these larger vessels are obliged to use sorting machines to separate herring from sprat. In most countries, the annual sprat quota has never been fully utilized, in contrast to the relatively low herring quota; this created a strong incentive to misreport herring as sprat.

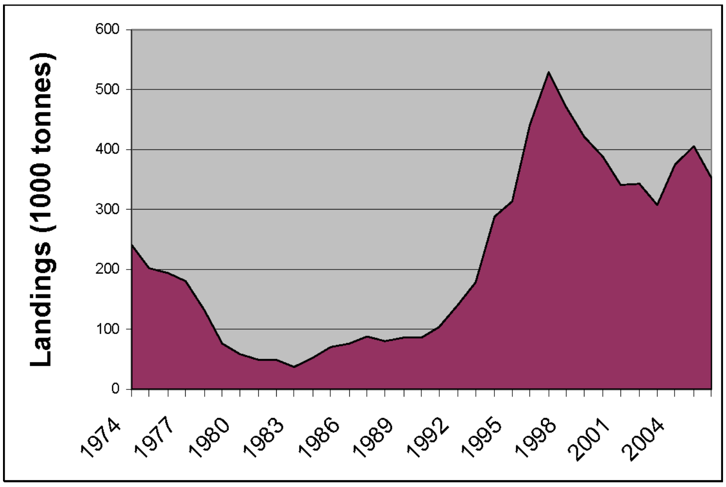


Figure 13.1. Trends in total landings of Baltic sprat in ICES Subdivisions 22–32 during 1974–2007.

13.4 Observed changes in production

Although time-series analysis indicates that the North Sea spawning stock appears to have more than doubled in size in the 1980s, the absolute stock size is unknown (ICES, 2007e). The spawning-stock biomass seems to have increased in recent years. Since 1996, egg abundance has increased (von Westernhagen *et al.*, 2002), and an increase in the standing stock was observed in the 1990s (Dornheim and Wegner, 1998).

The abundance of Baltic sprat increased dramatically during recent decades, peaked in 1997, and is now slightly lower (ICES, 2007f). The increase in stock size is mainly the result of reduced predation pressure by the depleted cod stock and high reproductive success (Köster *et al.*, 2003b; Möllmann *et al.*, 2008). In parallel with the increase in stock size, there was a decrease in the growth and condition of individual sprat (Möllmann *et al.*, 2005; Casini *et al.*, 2006).

Black Sea sprat stocks have increased since the 1950s, especially during the 1970s and 1980s (Daskalov, 2003), but collapsed during the 1990s (Daskalov *et al.*, 2007).

13.5 Processes underlying observed changes

13.5.1 Productivity and recruitment

The major processes governing the production of the North Sea stock remain unknown (ICES, 2007e). Recent otolith analyses of sprat in the southern North Sea suggest that substantial mixing of cohorts occurs during the first year of life (Baumann *et al.*, 2009). The results of biophysical, individual-based model simulations suggest no evidence for climate-driven mismatch with prey during the larval period in the southern North Sea (Daewel, 2008). However, production (survival) of larvae is limited to this region and coastal areas of the UK; zooplankton are not expected to be abundant enough to support larval survival during spring and summer in the central and northern areas of the North Sea (Daewel *et al.*, 2008b).

The increase in Baltic sprat is thought to result from a release in predation pressure by the depleted cod stock as well as from climate-induced changes in recruitment (Köster *et al.*, 2003b; Möllmann *et al.*, 2008). The climatic conditions during the 1990s, with mainly high values of the North Atlantic Oscillation (NAO), resulted in above-average water temperatures in the Baltic Sea (e.g. Matthäus and Nausch, 2003). Warmer temperatures are directly favourable for egg and larval survival of Baltic sprat (Nissling, 2004). Indirectly, warmer temperatures have resulted in an increasing availability of the copepod *Acartia* spp. (Möllmann *et al.*, 2003b), the major food of Baltic sprat larvae (Voss *et al.*, 2003; Dickmann *et al.*, 2007). Additionally, climate-related drift into favourable nursery grounds has been demonstrated to be important for recruitment success (Baumann *et al.*, 2006). The larger adult stock resulting from reduced cod predation pressure and the prevailing warm-water temperatures during the 1990s eventually resulted in a series of large sprat year classes, leading to the observed stock increase (Köster *et al.*, 2003b; MacKenzie and Köster, 2004; Möllmann *et al.*, 2008). At high stock sizes, Baltic sprat may suffer from density-dependent food limitation, particularly during the post-larval/early juvenile period in warm coastal waters (Baumann *et al.*, 2006).

The increase in the sprat stock is part of a major reorganization of the central Baltic ecosystem during the early 1990s (Alheit *et al.*, 2005; Möllmann *et al.*, 2006). The differing recruitment success of the two major fish species, in combination with the high fishing pressure on cod and low predation pressure on sprat by cod, caused a regime shift from a cod- to a sprat-dominated system (Köster *et al.*, 2003b; Möllmann *et al.*, 2008). Clearly, the ecosystem of the central Baltic Sea changed from a state of high productivity for the cod stock, characterized by high-salinity/-oxygen conditions and relatively low temperatures, to a state of high productivity for the sprat stock, characterized by low-salinity/-oxygen conditions and relatively high temperatures. This demonstrates that the carrying capacity of the system for both species changes, depending on the environmental state, and implies changing potentials for recovery and changing long-term sustainable yield for both species.

Similar to the Baltic Sea stock, temporal trends in the Black Sea sprat population have been influenced by climate-related temperature changes and overfishing. During the 1970s and 1980s, increased temperatures caused increased plankton productivity and, hence, increased fish production (Daskalov, 1999, 2003). During the 1990s, overfishing drastically reduced the sprat stock, contributing to a major reorganization of that ecosystem and resulting in a trophic cascade (Daskalov *et al.*, 2007).

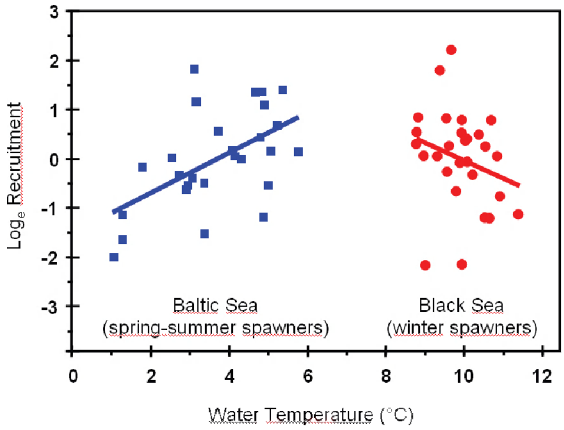


Figure 13.2. Water temperature at the time of spawning vs. sprat recruitment in the Baltic Sea (blue squares) and Black Sea (red circles). A direct comparison of these two populations suggests a temperature "optimum" for recruitment at spawning temperatures between 5 and 9°C. (Data digitized from Figure 2 in MacKenzie and Köster, 2004.)

13.6 Conclusion

In general, knowledge of the dynamics of sprat stocks within European waters is rudimentary, with the exception of sprat in the Baltic Sea. The effect of climate depends on geographic location; although warming has positive effects on recruitment in the Baltic, too much warming might impair recruitment in southern areas, such as the Black Sea (Figure 13.2). As for other stocks, direct and indirect effects of fishing modify the response of the sprat stocks to climate. In the Baltic, the overfishing of cod has released predation pressure on sprat and, hence, amplified the climate-related increase caused by enhanced recruitment (Möllmann *et al.*, 2008). In contrast, Black Sea sprat exploitation caused a stock collapse (Daskalov *et al.*, 2007). In both ecosystems, however, sprat is a major ecosystem player, mediating climate and fishing effects between trophic levels.

14 Mackerel

Christine Röckmann and Mark Dickey-Collas

14.1 Introduction

This section reviews knowledge of the mackerel (*Scomber scombrus*; order Perciformes, family Scombridae) in relation to the effects of climate change on the distribution and the production of the stocks, and focuses on observed changes as well as underlying mechanisms.

14.2 General biology

The mackerel is a species of commercial importance and also a game fish. A pelagic, ocean- and coastal-dwelling species, it has a depth range of 0–1000 m. Occurring between 25°N–70°N and 77°W–42°E, the mackerel is considered a temperate fish species that inhabits the eastern Atlantic, southwestern Baltic Sea, Mediterranean and Black seas, and the western Atlantic from Labrador to Cape Lookout (North Carolina). Mackerel are abundant in cold and temperate shelf areas, forming large schools close to the surface. They overwinter in deeper waters, but move closer to shore in spring, when water temperatures range between 11 °C and 14 °C (FishBase, 2007; Muus *et al.*, 1997; Muus and Nielsen, 1999).

ICES currently uses the term "Northeast Atlantic mackerel" to define the mackerel present in the area extending from ICES Division IXa in the south to Division IIa in the north, including mackerel in the North Sea and Division IIIa. Mackerel migrate extensively between their winter feeding grounds and more southern spring and summer spawning grounds. The spawning areas of mackerel are widespread, but only the stock in the North Sea is sufficiently distinct to be clearly identified as a separate spawning component. In order to keep track of the development of the spawning biomass in the different spawning areas, the Northeast Atlantic mackerel stock is divided by area into three components: the western spawning component, the North Sea spawning component, and the southern spawning component (Table 14.1). In parts of the year, the three components have overlapping distributions, and a part of the southern component is fished in the northern area.

Table 14.1. Northeast Atlantic mackerel: ICES stock divisions. (Source: ICES, 2007c.)

NORTHEAST ATLANTIC MACKEREL			
Distributed and fished in ICES Subareas and Divisions IIa, IIIa, IV, Vb, VI, VII, VIII, IXa			
Spawning component	Western	Southern	North Sea
Spawning areas	VI, VII, VIIIa, b, d, e	VIIIc, IXa	IV, IIIa

The western component is defined as mackerel spawning in the western area (ICES Divisions and Subareas VI, VII, VIIIa, b, d, and e). This component currently comprises 81% of the entire Northeast Atlantic stock. Similarly, the southern component is defined as mackerel spawning in the southern area (ICES Divisions VIIIc and IXa). Although the North Sea component has been at an extremely low level since the early 1970s, ICES regards the North Sea component as still existing. This component spawns in the North Sea and Skagerrak (ICES Subarea IV and Division IIIa). Current knowledge of the state of the spawning components is summarized in ICES (2007c).

Mackerel mature at around the end of age 3 and at a length of ca. 30 cm. Spawning occurs from March to July. In the Mediterranean, mackerel spawn in March–April, west of Ireland they spawn in May–June, and in the North Sea they spawn in June–July. Peak spawning has been reported to occur in May off southwest Ireland. The spawning migration path follows the shelf edge for most of its route, with the fish being found generally between the 100- and 250-m contours (Walsh *et al.*, 1995). Mackerel are batch spawners. Close to the surface, females lay ca. 200 000–450 000 eggs, and larvae are 3–4 mm long at ca. 6 d post-hatch. Eggs and larvae are pelagic.

After spawning, the adults forage very actively in small shoals. Adults exhibit diurnal feeding activity, and diets consist of zooplankton and small fish, such as young cod (*Gadus morhua*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), and sandeel (*Ammodytes marinus*). The most important feeding areas are located around the Shetland Islands and in the northern North Sea. The diet of the juveniles in spring consists of euphausiids, crustacean larvae, and other zooplankton. Euphausiids were reported to form 90% of the spring diet in adults. In autumn, juveniles were reported to eat hyperiids and gelatinous zooplankton, whereas adults targeted blue whiting (*Micromesistius poutassou*; Olaso *et al.*, 2005). During the long-distance feeding migration, mackerel can form schools that are 200 m wide and extend to a depth of 100 m. School density can be ca. 9 fish m^{-3} (Walsh *et al.*, 1995; Muus *et al.*, 1997; Muus and Nielsen, 1999).

Mackerel are preyed upon by the porbeagle shark (*Lamna nasus*), spiny dogfish (*Squalus acanthias*), cod, bluefin tuna (*Thunnus thynnus*), swordfish (*Xiphias gladius*), harbour porpoise (*Phocoena phocoena*), and harbour seal (*Phoca vitulina*). Parasites of the species include the monogenean *Kuhnia scombri* on the gills, trematodes (*Podocotyle atomon* and *P. simplex*), and nematodes (*Anisakis simplex* and *Haematractidium scombri*; Scott and Scott, 1988).

Mackerel can attain a maximum size of 60 cm (Muus and Nielsen, 1999). The maximum published weight of a mackerel is 3.4 kg (Frimodt, 1995), and the maximum reported age is 17 years. Mackerel do not have a swimbladder and can therefore quickly change depth without suffering from pressure differences.

14.3 Fisheries

The Northeast Atlantic mackerel stock currently supports one of the most valuable European fisheries, with annual landings around 500 000 t. The internationally agreed TACs have covered the total distribution area of the stock since 2001. They are split into two groups: northern (ICES Subareas or Divisions IIa, IIIa, b, and d, IV, Vb, VI, VII, VIIIa, b, d, and e, XII, XIV) and southern (VIIIc, IXa). The western spawning component contributes the vast majority of biomass and catch to the stock (Figure 14.1). Norway and the UK have taken the largest amount of the total international catch for the past three decades, followed by Denmark and the Faroe Islands. The North Sea mackerel component is considered to have been overfished since the late 1970s.

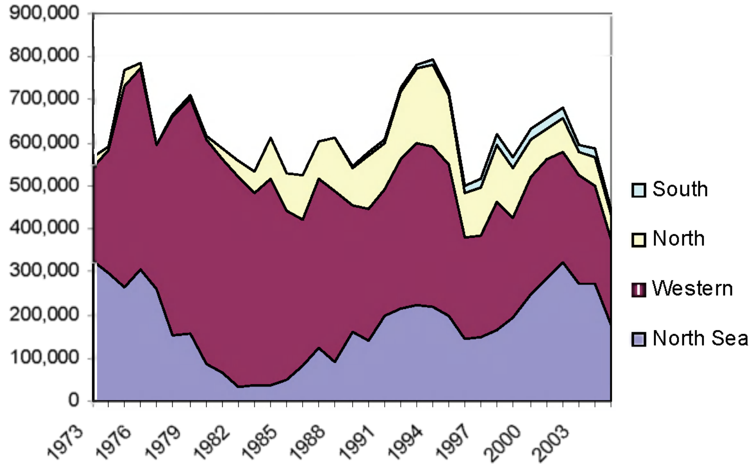


Figure 14.1. Northeast Atlantic mackerel: trends in total landings (in t) by ICES fishing region, 1973–2005. North Sea = ICES Areas IV and IIIa; Western = Areas VI, VII, and VIIIa, b, d, and e; North = Areas I, II, and Vb; and South = Areas VIIIc and IXa. (Data from ICES Fisheries Statistics.)

Based on the most recent estimates of fishing mortality (F), which have been above F_{pa} since the mid-1970s and above F_{lim} for the past decade (cf. Figure 14.2), ICES classifies the stock as being harvested unsustainably (ICES, 2007c, 2007i). Apart from TACs, existing management measures include a minimum landing size of 30 cm in Subarea IV, a closure for mackerel fishing in Divisions IIIa and IVb and c, and a temporary closure in Division IVa during the period 15 February–31 July.

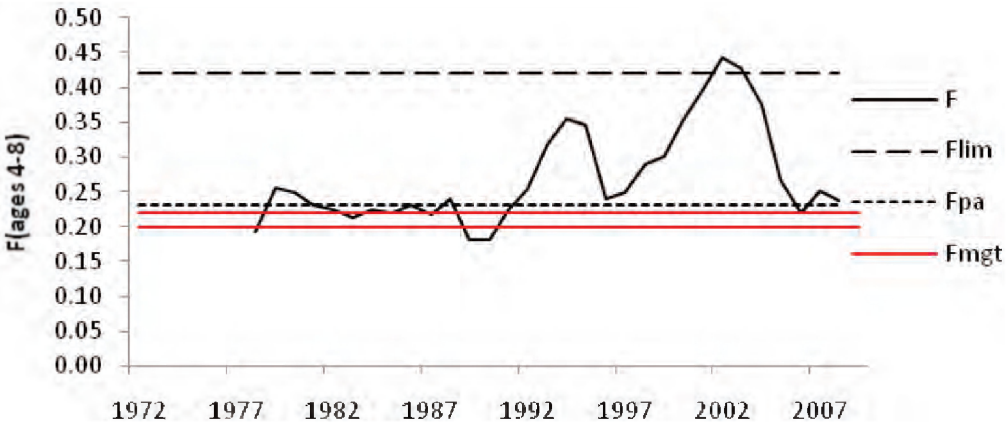


Figure 14.2. Northeast Atlantic mackerel: time-series of ICES working group estimates of fishing mortality of mature Northeast Atlantic mackerel (averaged over ages 4–8). (Source: ICES, 2007i.) Showing precautionary and limit reference points (F_{pa} and F_{lim}) and the spread of the target F for the management plan.

Northeast Atlantic mackerel is mainly exploited in a fishery directed at human consumption, and is fished by a variety of fleets, ranging from open boats using handlines along the Iberian coasts to large freezer-trawlers and refrigerated seawater (RSW) vessels in the northern area. The fishery on spawning mackerel in the eastern and central Cantabrian Sea in the first half of every year targets mackerel from the northwestern area that are extending their southward spawning migration through ICES Division VIIIc before returning north. The strong seasonality of the southern fishery on adult mackerel is the result of the migration pattern of mackerel (Uriarte and Lucio, 2001). During the second half of the year, those adults disappear from that area. Mackerel is traded fresh, frozen, smoked, and canned.

In the southern part of the distribution area, Atlantic mackerel can be caught together with the related Spanish mackerel (*Scomber japonicus*). In recent years, catches of Spanish mackerel have increased. The catch in 2005 was the highest since 1982. Catches of both species are landed separately. ICES advice applies only to Atlantic mackerel (ICES, 2007c).

14.4 Observed changes in production

Owing to unknown levels of underreporting of the catch, spawning-stock biomass (SSB) in recent years, relative to B_{pa} (the precautionary limit reference for biomass) cannot be accurately estimated, but indications are that SSB has increased since 2003 and has been stable for the last three years at approximately B_{pa} (ICES, 2007c; Figure 14.3).

The stock has demonstrated much more variable recruitment in the years 2000–2003 than in the past. The 2000 and 2003 year classes are estimated to be poor, whereas both the 2001 and the 2002 year classes are above average. The 2002 year class is estimated to be the highest in the time-series. There is insufficient information to confirm the size of the 2004, 2005, and 2006 year classes (Figure 14.4).

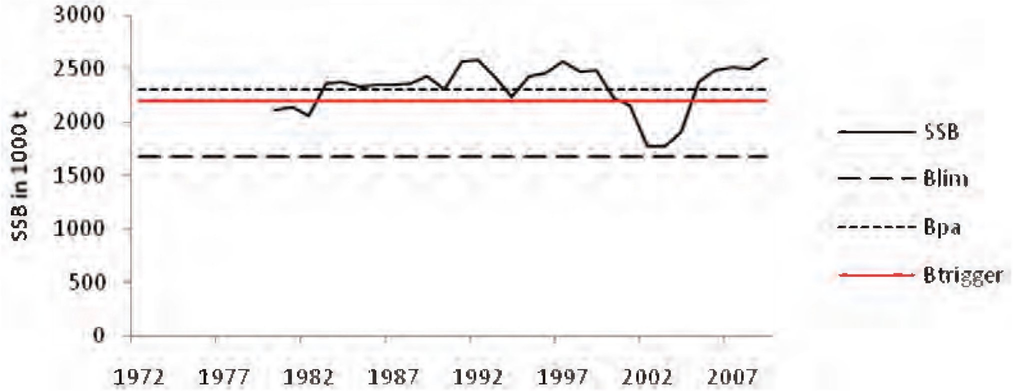


Figure 14.3. Northeast Atlantic mackerel: time-series of ICES working group estimates of the spawning-stock biomass, in 1000 t. (Source: ICES, 2007c.) Showing precautionary and limit reference points (B_{pa} and B_{lim}) and the trigger biomass for the management plan.

Figure 14.4. Northeast Atlantic mackerel: time-series of ICES working group estimates of recruitment, in billions of recruits at age 0. (Source: ICES, 2007c.)

Variability in annual growth rates of Northeast Atlantic mackerel may be influenced by environmental factors as well as by population and life-history factors. During their migrations, adult mackerel are subject to highly variable environmental conditions (e.g. upwelling), which influence their growth and reproductive potential and may have a major effect on juvenile growth. Dawson (1986), Eltink (1987), and

Villamor *et al.* (2004) hypothesized that growth differences between mackerel in different areas are caused by gradual spatial and temporal changes in length-at-age during migration. The largest fish of a certain age can migrate greater distances, reach spawning areas earlier, and leave for feeding areas earlier than smaller ones. This would lead to successive changes in length- and weight-at-age and, thus, a variable growth pattern along the geographic distribution range of the species.

Another cause of variability in mackerel growth rate may be the effect of population density, which particularly affects growth of the youngest ages. Agnalt (1989) estimated a negative correlation between the mean length at ages 1 and 2 and the North Sea mackerel stock biomass in the 1970s. Similar findings were reported for the Northwest Atlantic (Mackay, 1973; Overholtz, 1989; Neja, 1995). Moreover, Agnalt (1989) reported that mean length- and weight-at-age of Atlantic mackerel in the North Sea increased significantly between 1960 and 1979, but decreased markedly during the 1980s. In contrast, median age-at-maturity decreased from 1960. Median length-at-maturity remained stable until the 1980s, when it declined sharply. Changes during the 1980s may have resulted from immigration of the western mackerel stock.

One should be cautious when interpreting data on growth studies, as input data in growth studies is often biased, especially for migratory species like mackerel. Samples might be unrepresentative owing to missing elements, as the whole cohort may not be present in the area where the samples are taken. Moreover, the interpretation of growth depends on the season when samples are obtained (Castelló and Hamre, 1969).

14.5 Observed changes in distribution

Some surveys and fisheries for other species found changes in the distribution of mackerel, with a decrease in abundance in the south and an increase in the north and west, and in the Skagerrak and Kattegat (ICES, 2007c). A shift in spawning area and period has also been indicated. French acoustic surveys in Divisions VIIIa and VIIIb in May demonstrated a reduction in adult Northeast Atlantic mackerel within the survey area in both 2006 and 2007 when compared with previous studies. This suggests a northward shift in mackerel distribution in recent years (ICES, 2007i). Furthermore, analysis of egg survey data suggests that mackerel appeared to be spawning slightly earlier farther north and farther west of the shelf break over the past 20 years (Bez *et al.*, 1995; Reid, 2001). These changes may have implications for the growth, pattern of transport, and survival of larvae and, thus, may affect both stock dynamics and fisheries.

Changes in the Spanish fishery as well as survey results hint at changes in mackerel distribution. The Spanish fishery in Divisions VIIIb and VIIIc has, since 2005, started and ended earlier than in previous years. Surveys confirmed the indication of a temporal shift of approximately one month in the migration pattern of mackerel in the southern area, which might be linked to a more northerly distribution pattern (ICES, 2007i).

Regarding the distribution and dispersal of the early life-history stages, we quote results from the European Union project SEFOS (Shelf Edge Fisheries and Oceanography Studies), in which mackerel was the most intensively examined species (Reid, 2001). Mackerel eggs were found over a wide range of water temperatures (8 –±18 °C), but the majority were encountered in the range 10–15 °C. This corresponded well with the optimum temperature range for survival (>84%, 9.4–15.1 °C). The northward shift in the distribution of spawning closely followed the northward shift of the area encompassed by the 11–14 °C isotherms. A parallel seasonal shift also took place in the vertical distribution of eggs as the vertical temperature structure changed. Thus, at the beginning of the spawning season, when the water column was mixed, eggs were found over a wide depth range (Coombs *et al*., 2001). As stratification developed, the depth range of the eggs decreased. Once a thermocline was present, the majority of eggs were confined to the layer in and above the thermocline.

Mackerel eggs were most common in mixed Atlantic shelf water between salinities of 35.20 and 35.70 psu. Local spawning hot spots were not associated with local variations in salinity, nor was the northward seasonal shift in spawning marked by a similar shift in salinity. Salinity may therefore be considered less influential than temperature on the distribution of spawning (Reid, 2001).

Extensive data on both egg and subsequent larval distributions were available from the analysis of the triennial egg surveys (Fives *et al*., 1996). The value of these surveys is that they are synoptic and cover the whole spawning season. Thus, the egg distributions in one month can be related through the application of the individual-based statistics to the movements of the larvae after spawning. One surprising outcome of this study was that larvae appeared to become more aggregated as they developed. This may have been the result of differential growth rates and survival, with larvae in some areas failing to survive, whereas larvae in other more suitable areas may have flourished. These analyses also indicated that the centre of gravity of spawning demonstrated relatively little change during the season, and that the transport of the larvae was generally, although not exclusively, polewards along the shelf break. These analyses were somewhat compromised by the fact that the surveys were designed to study only eggs, not larvae, and so survey coverage was not always adequate to determine changes in distribution between developmental stages (Reid, 2001).

14.6 Processes underlying observed changes

It has been hypothesized that changes in Northeast Atlantic mackerel production are related to stock size as well as to environmental conditions, the former possibly affecting growth of the youngest fish and the latter possibly affecting the growth and spawning potential of adults, as well as juvenile and larval growth. The shift in distribution may be explained by a combination of variability in hydrographic factors and indirect effects (such as plankton abundance), as well as life-history aspects. The following factors have been explicitly suggested in the literature to interact with, and to affect, changes in mackerel production and distribution:

- zooplankton
    - abundance in spawning area
    - abundance, availability, and suitability as larval food source
- ocean circulation patterns
- temperature

Direct links between climate change and changes in distribution and production specifically of Northeast Atlantic mackerel have yet to be studied. However, some indirect links with climate change, via one of the above-listed factors, have been studied and, where available, the conclusions of those studies are presented below.

14.6.1 Zooplankton

Distribution of plankton is driven by hydroclimatic, hydrological, and biophysical factors. In the past decade, global air and sea temperatures have increased as a consequence of global warming (Levitus *et al.*, 2000). Analyses of Continuous Plankton Recorder data as well as of surface ichthyoplankton samples have demonstrated that variations in plankton abundance can be linked to changes in oceano-climatic conditions (Beaugrand *et al.*, 2002; Edwards and Richardson, 2004; Hays *et al.*, 2005; d'Elbée *et al.*, 2009). Beaugrand *et al.* (2002) demonstrated that mass biogeographic movements in all copepod assemblages – the food of larval mackerel – occurred over previous decades. These biogeographic shifts have been related to both the increasing trend in northern hemisphere temperature and the North Atlantic Oscillation (Beaugrand *et al.*, 2002; Edwards *et al.*, 2008). Moreover, it has also been demonstrated that the marine pelagic community responds to climate change, and that the level of response differs throughout the community and the seasonal cycle, leading to a mismatch between trophic levels and functional groups (Edwards and Richardson, 2004).

Zooplankton abundance in the spawning area

In his synthesis of SEFOS, Reid (2001) concludes with this quotation from Conway *et al.*, (1996): "most authors link fish distribution to hydrography via food (zooplankton) availability in different waters". The project revealed that mackerel peak spawning (late May/early June) appeared to coincide closely with peak zooplankton abundance in the spawning area (phytoplankton peaked generally in mid-May, ±2 weeks). There was also evidence of a strip of enhanced plankton abundance at the shelf edge in the main spawning area in both May and June. Egg patches beyond the shelf break (in northern Biscay) as well as egg numbers far west of the shelf edge (in the Porcupine area) were matched by high plankton abundance. In most months and most areas sampled, mackerel eggs were absent from areas of low plankton abundance. However, there were also observations of egg production areas that did not coincide with areas of high plankton concentrations and vice versa. Overall, the studies indicate that there was a reasonably good association between spawning location and plankton distribution, but suggest that this was not the only determinant of spawning area (Bez *et al.*, 1995).

Zooplankton suitability as larval food source

Updating an earlier study by Runge *et al.* (1999) in the southern Gulf of St Lawrence, Castonguay *et al.* (2008) provided the first field-based evidence linking availability of actual plankton prey in the sea to early growth of larval mackerel and ultimately to year-class strength. This demonstrates that Atlantic mackerel recruitment is strongly dependent on production of the copepod nauplii species that contribute to the diet of mackerel larvae. Castonguay *et al.* (2008) also emphasize the importance of focusing on the actual zooplankton prey of larvae when trying to link recruitment variability to fluctuations in ecosystem productivity and, thus, potentially to climate change. The availability of nauplii of the copepods *Calanus finmarchicus*, *Pseudocalanus* spp., and *Temora longicornis* was approximated by the number of eggs spawned by females (Ringuette *et al.*, 2002; Castonguay *et al.*, 2008).

The two theories above need further validation in other mackerel spawning regions in order to test the generality of relationships between copepod production and pelagic fish recruitment.

14.6.2 Ocean circulation patterns

During SEFOS (Reid *et al.*, 2001a), substantial changes in mackerel recruitment success and juvenile distribution were analysed by comparing transport model runs with real spawning distributions. The circulation patterns north and south of Porcupine Bank, an area west of Ireland and in the centre of the mackerel spawning area, were markedly different, particularly during the spawning season (Reid *et al.*, 2001a). The progressively more northern spawning of the mackerel, combined with changes in circulation pattern, might have resulted in increasing numbers of larvae being retained west of Ireland or being transported onto the shelf north of Ireland. Additionally, eggs that had been spawned west of the shelf break in recent years might, therefore, have failed to reach the shelf (Reid *et al.*, 2001a). Both observations might have caused lower recruitment of mackerel in recent years (Walsh *et al.*, 1995; Skogen *et al.*, 1996). However, the 2002 year class, which has now entered the fishery, is the biggest one in the 36-year record, thus contradicting this hypothesis. There is no evidence that particular scenarios of water temperature and salinity distribution have a significant impact on mackerel recruitment success, but it is clear from the modelling work that circulation patterns, in combination with variation in spawning location, may have a significant impact on mackerel recruitment (Reid *et al.*, 2001a). Currently, it remains unknown how circulation patterns in the North Atlantic and the North Sea will be affected by climate change.

14.6.3 Temperature

Clear links were reported between oceanographic parameters, in particular temperature, and the prespawning migration of mackerel (Reid, 2001). Under normal circumstances, mackerel began their migration toward their spawning grounds southwest of Ireland when water temperature fell below ca. 9°C. Prior to migration, the schools were relatively immobile, in contact with the seabed, and remaining concentrated in the Viking Bank area. Once migration commenced, schools that encountered areas of markedly warmer waters along the shelf edge west of Shetland appeared to stop migrating and began to disperse (Walsh *et al.*, 1995; Reid *et al.*, 1997, 2001a).

This temperature preference would tend to result in the mackerel being associated with a particular type of water. In this context, it was notable that the fish appeared to be associated with the water of the slope/shelf edge current at all stages of their annual migration. This might result in mackerel being found in a fairly restricted range of salinities as well. Evidence for such a salinity preference was more equivocal than that for temperature, and it seems likely that temperature is the main controlling parameter (Reid, 2001). How specifically climate change will affect the temperature of these water masses has yet to be studied.

The variation in abundance of mackerel in the North Sea has been related to temperature and salinity anomalies and, in turn, to winds (Corten and van de Kamp, 1996). These authors argue that positive anomalies of winter temperature and salinity in the North Sea are correlated with southerly winds over the Netherlands. They suggest that increased southerly winds cause an increased inflow of Atlantic Water through the Strait of Dover into the North Sea, increasing the transport of southern fish species, such as mackerel, into the North Sea. The results of this study, however, have not been statistically tested, but are based on visual comparisons of two periods of positive anomalies (1974–1977 and 1988–1990).

In contrast to this study, Beare *et al.* (2004) found that mackerel, together with several other species classified as having southern biogeographic affinities, has demonstrated sudden, almost exponential, increases in abundance since the mid-1990s. They argue that the changes appear to be part of a systematic, long-term trend, contradicting the conclusions of Corten and van de Kamp (1996). Beare *et al.* (2004) argue that the increase in mackerel prevalence observed in the North Sea is the result not of an overall expansion in stock size, but rather of changing patterns of migration caused perhaps by environmental stimuli. Postuma (1972) was already suggesting a link between environmental stimuli and mackerel abundance in the North Sea. He demonstrates that mackerel recruitment to the North Sea started to decrease after 1958 (i.e. before the period of most intensive fishing) and thus was potentially triggered by environmental change.

Hannesson (2007) carried out statistical analyses to detect potential correlations between changes in catches of key fish species and changes in water temperature. He found some indication that catches of mackerel in the Norwegian Sea increased with rising temperature in that area, but the correlation was not statistically significant. The sharp peak in the mackerel fishery in the North Sea in the late 1960s was brought about by improved technology. There was, however, a significant and positive correlation between temperature and catches of mackerel in the North Sea after the stock recovered in the 1970s.

14.7 Conclusion

The mackerel is a species with a high level of natural variability in abundance. In addition to this natural variability, changes in production and distribution have been observed over the past four decades. As itemized in Section 14.6, three main intermediate factors are proposed in the literature as potentially affecting mackerel population dynamics: zooplankton abundance, ocean circulation patterns, and temperature.

It is well known that global climate change affects zooplankton abundance and distribution as well as ocean temperature and ocean circulation patterns. However, how climate change will affect the Northeast Atlantic mackerel stock, specifically via these intermediate factors, requires further study.

15 Horse mackerel

Christine Röckmann and Mark Dickey-Collas

15.1 Introduction

This section reviews knowledge of the horse mackerel (*Trachurus trachurus*; order Perciformes, family Carangidae) in relation to the effects of climate change on the distribution and production of the stocks, focusing on observed changes as well as the underlying mechanisms.

15.2 General biology

The horse mackerel is a species of commercial importance and also a game fish. It is a pelagic, ocean-dwelling, marine species, occupying a broad range of depth (0–1050 m). Occurring between 19°S–67°N and 26°W–41°E, the horse mackerel is considered to be a subtropical fish species that inhabits the eastern Atlantic from Iceland to Senegal, including the Mediterranean, Marmara, and Black seas (Smith-Vaniz, 1986). Horse mackerel also inhabit the western Atlantic, Indian Ocean, and western Pacific (Ly *et al.*, 1996). Adults form large schools, mostly in coastal areas with sandy substrata. They feed on fish, crustaceans, and cephalopods.

Horse mackerel can attain a maximum size of 70 cm (Smith-Vaniz, 1986) and a maximum weight of ca. 2–3 kg (Ly *et al.*, 1996). They mature at age 3–4, at a length of ca. 25 cm. Until the year 2000, the horse mackerel was assumed to be a determinate spawner, but new fecundity studies in 2000 indicated that it might be an indeterminate spawner (HOMSIR, 2001; ICES, 2001). Females are batch spawners and lay around 140 000 eggs, which hatch into larvae 5 mm long (Muus and Nielsen, 1999). Larvae eat plankton and often dwell directly beneath jellyfish.

According to results from egg surveys and the temporal and spatial distribution of the fishery, ICES considers horse mackerel in the Northeast Atlantic area to be separated into three stocks (management units) with distinct spawning locations (ICES, 1990b; HOMSIR, 2001; Table 15.1): western, southern, and North Sea.

Table 15.1. Horse mackerel in the Northeast Atlantic: ICES stock divisions. (Source: ICES, 2007c.)

HORSE MACKEREL	WESTERN	SOUTHERN	NORTH SEA
Management areas	IIa, IVa, Vb, VIa, VIIa–c, e–k, VIIIa-e	IXa	IIIa, IVb,c, VIId

Shelf attachment is a predominant distributional pattern of horse mackerel. The western and southern stock components are closely connected to the shelf contour, as demonstrated on a number of occasions (HOMSIR, 2001, and references therein).

Migration may be driven mainly by water temperature. In autumn, when the temperature falls below ca. 10 °C, horse mackerel retreat from the feeding areas in the southern Norwegian Sea and the North Sea and migrate to overwintering areas farther south. The main spawning period of horse mackerel is the second quarter of the year (ICES, 2007i). The Western stock spawns in a belt from the Bay of Biscay to Ireland in early spring and, after spawning, migrates north and east to south Norway and the northern North Sea. The North Sea stock spawns in the southern North Sea in summer and migrates to the central North Sea, Skagerrak, and Kattegat thereafter. Little information exists on the southern stock. It may be linked to a larger stock in the south.

15.3 Fisheries

The commercial importance of horse mackerel has grown during the past decades. During the 1990s, annual landings were ca. 500 000 t, the majority of which originated from the Western stock (Figure 15.1). The total international catch of horse mackerel in 2006 from all areas in the Northeast Atlantic was 215 277 t, which is 19 600 t less than in 2005. The three management areas do not properly reflect stock distribution, which causes distortions in the exploitation rates.

Landings from the Netherlands, Ireland, Norway, Denmark, Portugal, Russia, UK, France, and Germany usually make up more than 95% of the international landings. Spanish and Portuguese vessels mainly target the southern horse mackerel stock (ICES, 2006h).

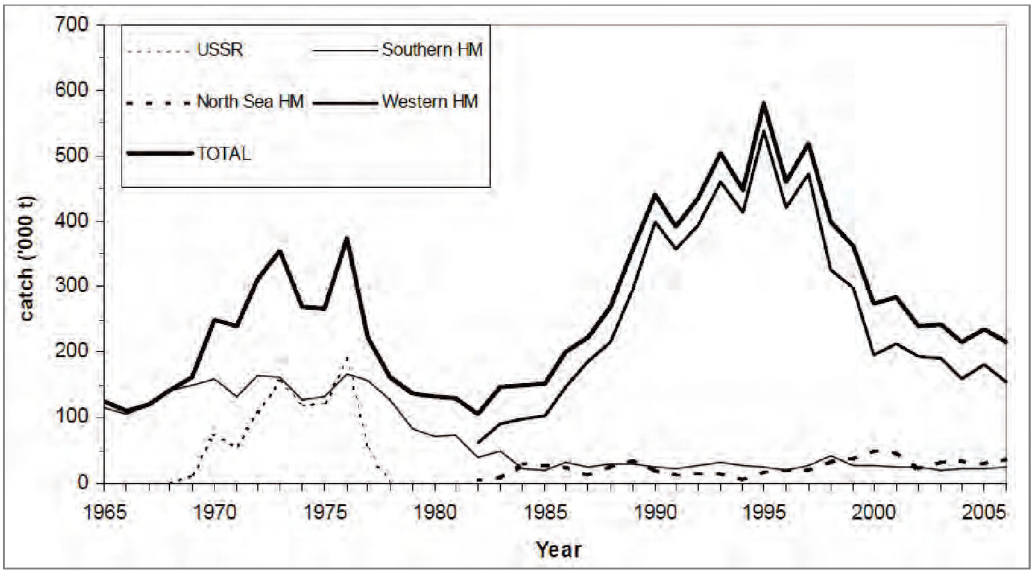


Figure 15.1. Total catches of horse mackerel (in 1000 t) in the Northeast Atlantic during the period 1965–2006. The catches taken by the USSR (later the Russian Federation) and catches taken from the southern, western, and North Sea horse mackerel stocks are shown in relation to the total catches in the Northeast Atlantic. (Source: ICES, 2007c, 2007i.)

Western horse mackerel are taken in a variety of fisheries that exploit juvenile fish for human consumption, mid-aged fish mostly for the Japanese market, and older fish, either for human consumption (mostly for the African market) or for industrial purposes (ICES, 2007c). In earlier years, most of the catches were used for meal and oil, whereas in later years, most of the catches have been used for human consumption (ICES, 2007i). Ireland, Denmark, the UK, France, Germany, and the Netherlands have directed trawl fisheries and Norway has a directed purse-seine fishery for horse mackerel. Spain and Portugal have both directed and mixed trawl and purse-seine fisheries (ICES, 2007i). Horse mackerel are marketed and utilized fresh, smoked, canned, and frozen; they can be fried, broiled, or baked (Frimodt, 1995).

15.4 Observed changes in production

The horse mackerel stock has increased substantially because of an extraordinary year class in 1982 (Figure 15.2). Since the late 1980s, the stock has declined because landings continued to increase, although no new strong year classes were observed to recruit to the stock. The 1982 year class has dominated the catches of western horse mackerel in most western fishing areas since 1984, and in the North Sea since 1987 (Iversen *et al.*, 2002; ICES, 2007i).

Owing to the lack of defined reference points and a full analytical assessment, the state of the stock is unknown (ICES, 2007a, 2007b, 2007c). For the Western stock (i.e. the largest stock component), a relative assessment is carried out. The fishery-independent data for this stock are extremely limited, with only one data point for egg production every three years (ICES, 2007l). Hence, the assessment, which is described as "relative", does not reflect the absolute state of this stock component.

Relatively high catch rates of the 2001 year class in 2002–2006 and an increase in egg production in 2007 suggest that the spawning-stock biomass (SSB) has increased in recent years. The 2001 year class is stronger than those observed in recent years, but not at the same magnitude as the 1982 year class (Figure 15.2).

The time-series of mean weight-at-age for western horse mackerel illustrates that the weights of older fish have decreased over time. The weight for the older ages is based on fish sampled from Dutch freezer-trawlers in the first and second quarters in ICES Division VIIj. Mean weight-at-age groups in the stock and in the catches were lower than usual in 2001, but returned to normal in 2002–2006.

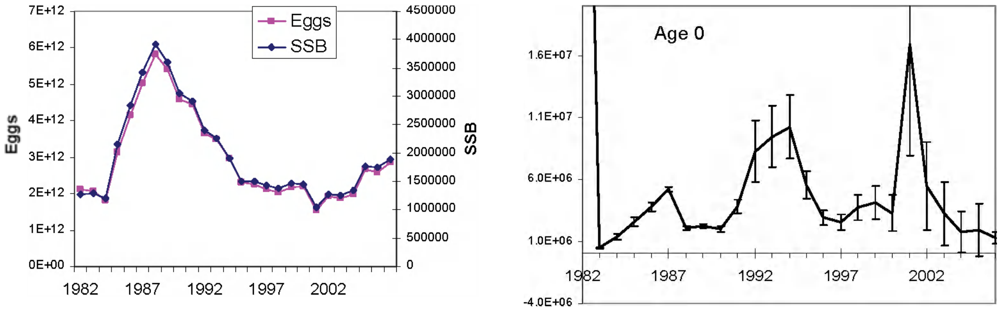


Figure 15.2. Western horse mackerel: SADVF model. Left: modelled SSB and modelled egg production. Right: recruits at age 0 (including error bars (2 x s.d.)), scaled to capture more model detail. (Source: ICES, 2007i.)

15.5 Observed changes in distribution

The spatial distributions of mackerel (*Scomber scombrus*) and horse mackerel have always been considered to have substantial overlap. At least since the late 1980s, western horse mackerel appear to have adopted similar migration patterns as western and southern mackerel (ICES, 1990b, 1991, 1996; SEFOS, 1997). A large-scale shift in the spatial distribution of Northeast Atlantic mackerel is assumed to have taken place in 2005–2007, and this may have consequences for future abundance, spawning, growth, and recruitment of western horse mackerel (ICES, 2007i).

After spawning, the fish migrate northwards in late July to the Norwegian and North seas for feeding. It seems that horse mackerel have to be 5 years or older before they migrate to the North Sea. Surveys in the Norwegian Sea have demonstrated that the largest horse mackerel migrate the longest distance (Iversen *et al.*, 2002).

The European project SEFOS (Shelf Edge Fisheries and Oceanography Studies) put particular emphasis on recent strong migrations of horse mackerel into the North Sea (Reid, 2001). The main finding of these studies was the predominance of the exceptionally strong 1982 year class. As this year class became more important, the fish appeared to start undertaking much longer migrations into the North Sea, whereas migrations were previously thought to have gone only as far as the north of

Scotland. From 1986 onwards, the extent of the fishery in the northern North Sea has also grown.

As no good recruitment has occurred since 1982, this has major implications for the future of the North Sea fishery.

15.6 Processes underlying observed changes

Research over the last decade has demonstrated strong links between horse mackerel migration into northern areas and water-mass transport patterns in the Northeast Atlantic (ICES, 2007h). The following interacting processes have been proposed as triggers of changes in production and distribution of horse mackerel in the Northeast Atlantic:

i) stock size (density-dependent processes) and migration;

ii) stock age structure and migration;

iii) climate and ocean processes (wind, Atlantic inflows, temperature) indirectly affecting migration, distribution, and production via plankton abundance.

15.6.1 Stock size, stock structure, and migration

The predominance of the exceptionally strong 1982 year class in the stock has probably triggered an expansion of the feeding migration; it was postulated that this had been a result of density-dependent effects (Reid, 2001; Reid *et al*., 2001b). This expansion is also believed to have led to the growth of the fishery targeting horse mackerel in the northern North Sea (Reid, 2001). The extent of migration might also be related to fish age, as the SEFOS data appeared to indicate that older fish migrated farther north than young fish.

15.6.2 Climate and ocean variables affecting biology

Studies within SEFOS investigated interactions between climate, ocean, and biological variables. One of the clearest results was the relationship between the transport of Atlantic Water into the North Sea in winter and catches of horse mackerel in the northern North Sea six months later (Iversen *et al*., 2002). Modelled Atlantic inflow during the winters from 1976 to 2000 was strongly correlated with the Norwegian fleet's catch of horse mackerel ($r^2 = 0.70$) the following autumn. Iversen *et al*. (2002) hypothesized that a large influx of this relatively warm and nutrient rich Atlantic Water during winter may support early spawning of zooplankton and high biological production during spring and summer. This might be the biological reason for a large fraction of the horse mackerel stock migrating into the North Sea during strong inflows. Furthermore, Borges *et al*. (1996) demonstrated that the more northerly migration of the western horse mackerel (much farther north along the shelf edge to the west of the British Isles and into the Norwegian Trench than observed previously) coincided with the change in planktonic environment in the North Sea after 1987 (Borges *et al*., 1996; Reid *et al*., 2003; Beaugrand, 2004).

Reid *et al*. (2001b) argued that the substantial increase in oceanic inflow in winter and the concomitantly higher sea surface temperatures in spring and summer may have been a response to observed changes in pressure distribution over the North Atlantic. From 1988 onwards, the North Atlantic Oscillation (NAO) index increased to the highest positive level observed this century. Positive NAO anomalies are associated with stronger and more southerly tracks of the westerly winds and higher temperatures in western Europe. These changing wind distributions may have led to an increase in the northward advection of water along the western edge of the European shelf. Whether these increased currents can assist the migration of horse mackerel remains questionable, although it has been put forward as a hypothesis (Reid *et al.*, 2001b). Nonetheless, there is a clear link between increased Atlantic inflow, increased food availability, and the recent migration of horse mackerel into this area. Iversen *et al.* (2002) suggest that food production and temperature may be the variables affecting the migration and, thereby, the catches.

The low catches prior to 1987 might be explained by low stock sizes rather than low influx of Atlantic Water, as similar influxes in later years have given higher catches. Also, prior to 1987, the stock size of fish older than 4 years (i.e. 5+) was probably at such a low level that no extensive migration to increase the feeding area was required (Iversen *et al.*, 2002).

It remains to be seen whether or not the changes will continue once the very strong 1982 year class has disappeared from the population. Migration into the North Sea coincided with both the advent of this age group and the increase in plankton abundance. It has not yet been possible to determine whether one or both of these factors was most important (Borges *et al.*, 1996; Murta and Borges, 1996; Reid, 2001; Reid *et al.*, 2001b).

15.7 Conclusion

Horse mackerel dynamics and, in particular, migration appear to be driven by climatic, oceanographic, and biological processes. Specifically, temperature, food production (zooplankton), density-dependence (stock size), and stock age structure have been proposed as possible prominent variables affecting the migration of horse mackerel and, thereby, the catches.

Under climate change, the pressure distribution patterns over the North Atlantic (as measured by the NAO index) may change, probably affecting oceanic transport and circulation patterns. In turn, sea surface temperatures (SSTs) will change, which could lead to changes in primary production patterns. An hypothesized increase in biological productivity in the North Sea might be stimulated by higher SSTs as a result of stronger Atlantic inflows into the North Sea.

Apart from climatic triggers, density effects seem to influence the extent of horse mackerel migration and distribution. A large horse mackerel stock seems to migrate farther than a smaller stock. Additionally, it has been observed that older fish migrate farther than younger ones. There has been a pronounced decrease in the weight of older horse mackerel over the past three decades. Future studies could investigate if this change in weight-at-age is related to climate change and if it will affect horse mackerel population dynamics.

16 Sandeels

Henrik Jensen and Asbjørn Christensen

16.1 Introduction

This section reviews knowledge of sandeels (*Ammodytes* spp.; family Ammodytidae, order Perciformes), with particular reference to the effects of climate change. It begins with an overview of the general biology and ecology, which are relevant to understanding the possible impact of climate change, and then reviews evidence for changes in distribution and production in relation to climate.

16.2 General biology

16.2.1 Overall geographic distribution and abundance

Sandeels are small, semi-pelagic fish that have a worldwide distribution (Anon., 1960; Smith and Heemstra, 1986) in both temperate and tropical waters (Jordan, 1907; Scott and Scott, 1988), as well as in Arctic waters (see Jákupsstovu and Røttingen, 1975; Petersen, 1977; Simonsen *et al.*, 2006).

The family Ammodytidae contains five genera of which three, *Ammodytes, Gymnammodytes,* and *Hyperoplus,* are represented in the Northeast Atlantic (Jordan, 1907; Macer, 1966; Robins and Bohlke, 1970; Masuda *et al.*, 1984).

Species of *Ammodytes* occur in three geographic areas: *A. marinus* and *A. tobianus* in the eastern Atlantic and European waters, *A. americanus,* and *A. dubius* in the Northwest Atlantic, and *A. hexapterus* and *A. personatus* in the North Pacific. Detailed accounts of the distribution of the Atlantic species have been written by Corbin and Vati (1949) and Reay (1970).

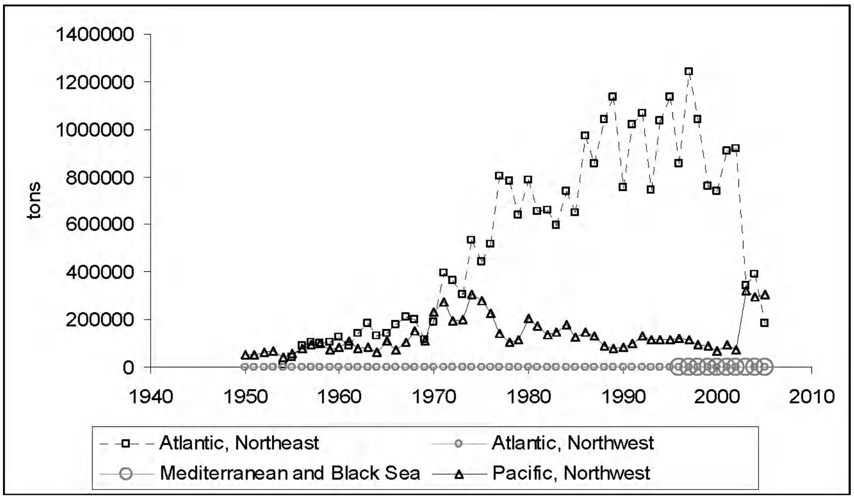


Figure 16.1. Total international landings of sandeels by region. (Data from FAO, http://www.fao.com.)

Sandeels usually constitute a large proportion of the fish biomass in the regions where they occur (e.g. Reay, 1970). However, knowledge of their population dynamics exists for only a few areas, which represent a small part of the total distribution range. Total international landings may give some indication of where the highest production of sandeels occurs. There are two major sandeel fisheries: one in the Northeast Atlantic and one in the Northwest Pacific (Figures 16.1 and 16.2).

These two fisheries were at approximately the same level from 1955 to 1975. The fishery in the Northeast Atlantic increased to a much higher level from 1975 to 2003, when it collapsed. From 2003, when the fishery in the Northwest Pacific increased markedly, the fisheries in the Northeast Atlantic and in the Northwest Pacific have been at about the same level.

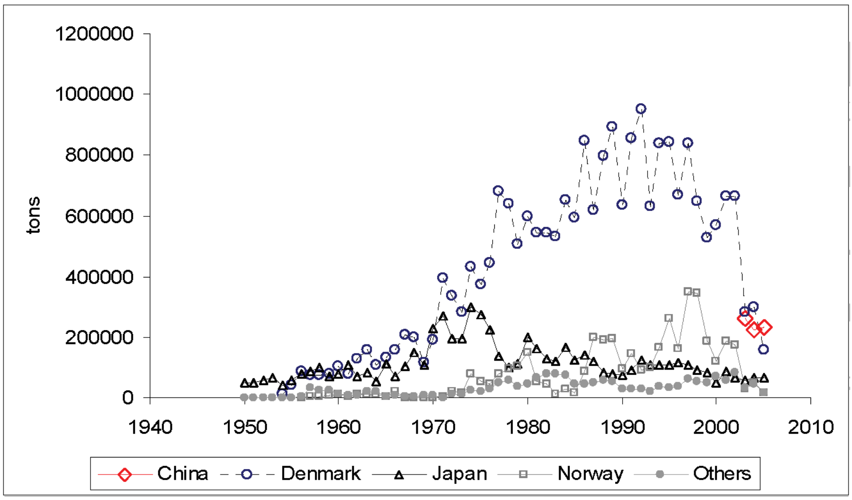


Figure 16.2. Total international landings of sandeels by country. (Data from FAO, http://www.fao.com.)

The sandeel fishery in the Northwest Pacific is synonymous with the fishery in Japanese waters (Inoue *et al.*, 1967; http://www.fao.com). The catches consist primarily of *A. personatus*, with a smaller component of *A. hexapterus* (Hashimoto, 1984). Although the catches are primarily taken by Japan, the increase in landings from 2003 is the result of Chinese landings (Figure 16.2), which are taken in other waters.

The sandeel fishery in the Northeast Atlantic takes place almost exclusively in the North Sea, in Division IIIa (Kattegat/Skagerrak, Figure 16.3). Denmark and Norway take by far the largest proportion of the landings (Figure 16.2).

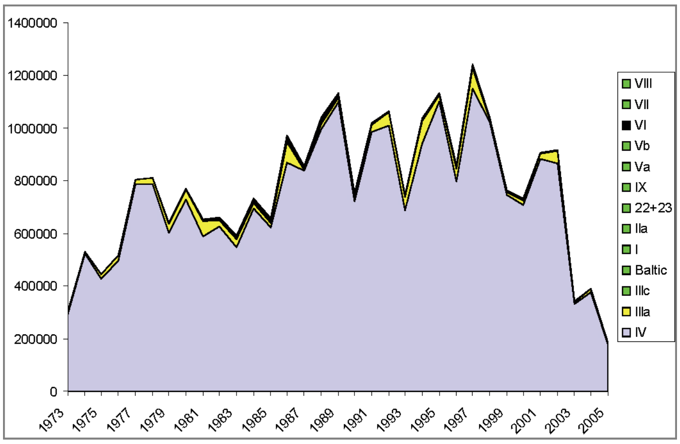


Figure 16.3. Total international landings of sandeels in the Northeast Atlantic (FAO Area 27) by ICES area. (Data from ICES, http://www.ICES.dk.)

There are five species of sandeel in the North Sea, of which *A. marinus* is by far the most abundant (Macer, 1966; Popp-Madsen, 1994; ICES, 2004a). In the North Sea, sandeels constituted an average 15% of the total biomass of fish in the period

1977–1986, when only common dab (*Limanda limanda*) were more abundant (Sparholt, 1990). This review focuses on the lesser sandeel (*A. marinus*) in the North Sea (referred to as "sandeels" below).

16.2.2 Spawning

Spawning occurs in the North Sea between December and January (Macer, 1966; Gauld and Hutcheon, 1990; Bergstad *et al.*, 2001). Eggs are demersal and are spawned at the demersal habitat of post-settled sandeels, where they remain until hatching (Reay, 1970; Winslade, 1971).

16.2.3 The larval phase

Hatching occurs from February to May (Macer, 1965; Langham, 1971; Wright and Bailey, 1996; Jensen, 2001; Stenevik and Osland, 2001). The hatching season is relatively long compared with that of other fish species in the same region, a strategy that is probably suitable for dealing with the high variability in environmental conditions.

The duration of the larval phase (32–90 d; Jensen, 2001; Wright and Bailey, 1996), and the locations of the spawning grounds (Proctor *et al.*, 1998) lead to the rapid and variable transport of newly hatched larvae away from the spawning grounds (Berntsen *et al.*, 1994; Proctor *et al.*, 1998). This is confirmed by the size-stratified distributions of early sandeel larvae (Henderson, 1954; Macer, 1965; Jensen, 2001; Munk *et al.*, 2001).

Observations on recently hatched *A. marinus* larvae (length 6–15 mm in February–March) in the central and southern North Sea suggest that most of these small larvae are advected to and retained in shallow areas of frontal zones between freshwater-influenced water masses and the shelf water of the central North Sea (Munk *et al.*, 2001).

When the larvae reach a length of 20–30 mm, they become good swimmers and congregate in the feeding areas of adult sandeels. These areas coincide with frontal areas (Jensen, 2001).

Vertical distribution of *A. marinus* larvae depends on both length and environmental factors, with larger larvae demonstrating more extensive vertical migrations than smaller larvae (Jensen *et al.*, 2003). Larvae congregate in the water layers containing the highest zooplankton abundance during the day. In areas without marked vertical hydrographic gradients, larvae are relatively more abundant in surface waters during the day. Larvae of all sizes are generally distributed more homogeneously in the water column during the night than during the day.

Larvae of *A. marinus* metamorphose 32–90 d after hatching at a length of ca. 40 mm (Wright and Bailey, 1996; Jensen, 2001). After metamorphosis in May/June, juvenile fish exhibit the burying behaviour of adult sandeels. Juvenile *A. marinus* seem to recruit directly to the habitat of adult sandeels (Wright *et al.*, 2000; Jensen, 2001).

16.2.4 Sandeel burying behaviour

Post-settled sandeels bury into the sediment when they are not feeding in the water column, i.e. in winter, when feeding is energetically inefficient because sea temperatures are low (Winslade, 1974c), when prey abundance is low (Winslade 1974b), and at night when low light intensity limits prey visibility (sandeels are visual feeders; Winslade, 1974b).

The overwintering period for *A. marinus* starts in about September and ends around March or April (Macer, 1966; Winslade, 1974a, 1974b, 1974c). age-0 and age-1 fish usually have a longer feeding season than older sandeels (Reeves, 1994). Whereas age-1 sandeels emerge from the sediment to feed earlier in spring than older sandeels, the age-0 group may extend their feeding season until the end of November.

Sandeel burying behaviour has frequently been observed in response to predators foraging near the seabed (Girsa and Danilov, 1976; Pearson *et al.*, 1984; Pinto *et al.*, 1984) and can therefore be interpreted as anti-predator behaviour. Many predators are, however, capable of capturing buried sandeels (Hobson, 1986).

16.2.5 Habitat and distribution pattern

The distribution of post-settled sandeels is highly patchy and primarily limited by the availability of suitable substrata (Macer, 1966). Sandeels avoid sediments with a weight fraction of fine particles (<0.09 mm) of >10% (Wright *et al.*, 2000). A map of the sandeel fishing grounds (Jensen and Rolev, 2004) can be used as a proxy for the distribution of sandeel habitat (Figure 16.4). More than 200 individual sandeel fishing grounds have been identified. The estimated area of the smallest ground was 0.2 km^2, and that of the largest ground was 878 km^2. The estimated total area of the sandeel fishing grounds was 15 831 km^2, less than 3% of the North Sea area from 51°N to 62°N. Although the fishing grounds are believed to represent the major areas of sandeel distribution in the North Sea, small patches of additional suitable habitat exist (Bergstad *et al.*, 2001). Also, the sandeel habitats in the Orkney–Shetland area are not included in the map. Furthermore, a large but unknown number of non-fished grounds are situated close to the coast, where *A. tobianus* tend to be more abundant than *A. marinus* (Macer, 1966; Reay, 1970, 1972).

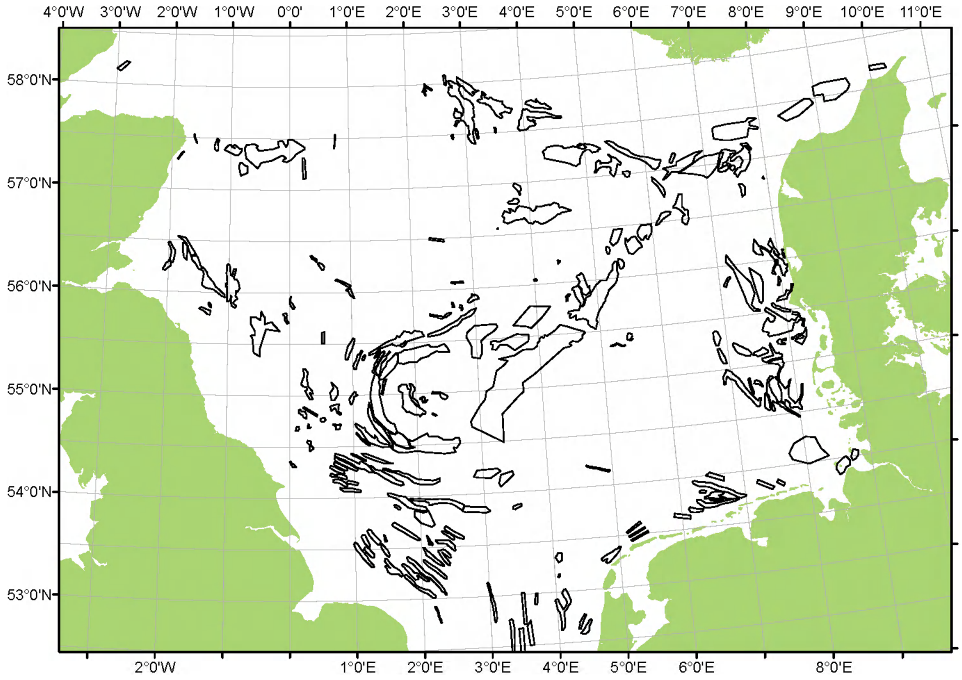


Figure 16.4. Sandeel fishing grounds in the North Sea. (From Jensen and Rolev, 2004.)

Sandeels appear to tolerate a wide range of salinities. For example, larvae have been found in salinities as low as 1.8–4.3 psu (Norcross *et al.*, 1961), and *A. dubius* has been found in a salinity as high as 36 psu (Richards *et al.*, 1963). Larvae also appear to be tolerant of a wide range of temperatures. Temperature is not an important factor in sandeel larval distribution (Norcross *et al.*, 1961). Monteleone and Peterson (1986) found the water temperature during the larval season to be in a range of 0–10°C, which is similar to the temperature range of 0–13°C recorded by Richards and Kendall (1973).

16.2.6 Population structure

There is only limited movement of post-settled sandeels between habitat areas (Kunzlik *et al.*, 1986; Gauld, 1990). The demersal habitat of sandeels therefore corresponds mainly to the spawning habitat. This stationary habit and the patchy distribution of habitat imply that interchange of sandeels between spawning grounds is restricted to the pelagic larval stage (Proctor *et al.*, 1998; Wright *et al.*, 2000).

Based on the distribution and simulated dispersal of larval stages, Wright *et al.* (1998) suggest that the North Sea stock could be split between six areas, including the Shetland population. Assessments made for some of these areas (Pedersen *et al.*, 1999; Lewy *et al.*, 2004) are less certain, but demonstrate approximately the same stock trends as the one-area assessment of ICES (2006l). The biological, more-realistic approach taken in the spatially disaggregated analyses did not improve the precision of the assessments, mainly because of a lack of spatially disaggregated biological data (age/length/weight keys).

Recent studies indicate a low interchange of pre-settled sandeels between the spawning grounds identified (Christensen *et al.*, 2007, 2008), suggesting that the population structure proposed by Wright *et al.* (1998) needs to be revised.

16.2.7 Feeding biology

The diet of sandeel larvae consists mainly of copepods. As the larvae increase in size, their preference switches from copepod eggs and nauplii (at 8–12 mm) to nauplii and copepodites (at 12–20 mm) and then to larger copepodites and adult copepods (larger larvae, post-larvae, and adult sandeel; Covill, 1959; Macer, 1966; Monteleone and Peterson, 1986).

Ryland (1964) demonstrated that *A. marinus* larvae <8 mm fed mainly on copepod nauplii, but that green material occurred in 40% of the guts analysed. In larvae >8 mm, green material was almost absent, whereas the proportion of nauplii fell substantially and that of appendicularians increased.

Macer (1966) investigated the dietary composition for juvenile and adult sandeels at the beginning of the 1960s in the southwestern North Sea. The diet consisted mainly of copepods, crustacean larvae, and annelids, with a tendency for larger fish to take larger food items. Although sandeels <10 cm fed mainly on copepods (mostly *Temora* followed by *Calanus*), for larger sandeels (>10 cm), newly metamorphosed polychaetes and copepods dominated by *Calanus* became more important. There is no information about regional differences in dietary composition for *A. marinus* within the North Sea, or about any potential changes in dietary composition that might result from changes in the abundance or distribution of the prey items.

16.2.8 Growth

Growth rate of post-settled sandeels is highest during the main feeding season between March and July (Winslade, 1974c; Bergstad *et al.*, 2001).

There is considerable variation in size- and age-at-maturity between regions in the North Sea (Boulcott *et al.*, 2007). Sandeels from regions of faster growth mature earlier and at a larger size. For example, sandeels off the Firth of Forth area have lower growth rates than those from offshore banks, and mature later.

Weight-at-age aggregated by half year is highly variable (Figure 16.5), owing to spatial variation in growth and the large variability in fishing pattern between years (ICES, 2006m). Weight-at-age is generally higher in the northern than in the southern North Sea, especially for age-2+ sandeels.

Density-dependent growth has been found for other species of sandeels (Nagoshi and Sano, 1979), but has not been documented for *A. marinus* in the North Sea. Bergstad *et al.* (2001) reported differences in size-at-age between unexploited sites and commercially fished areas, but these differences could not be related to population density.

Based on observations of the food items that Atlantic puffin (*Fratercula arctica*) fed to their chicks, Wanless *et al.* (2004) concluded that there was a decrease in size of sandeels in the Firth of Forth area off the Scottish east coast over a 30-year period. Changes in growth of sandeels in the rest of the North Sea have not been analysed over the same period.

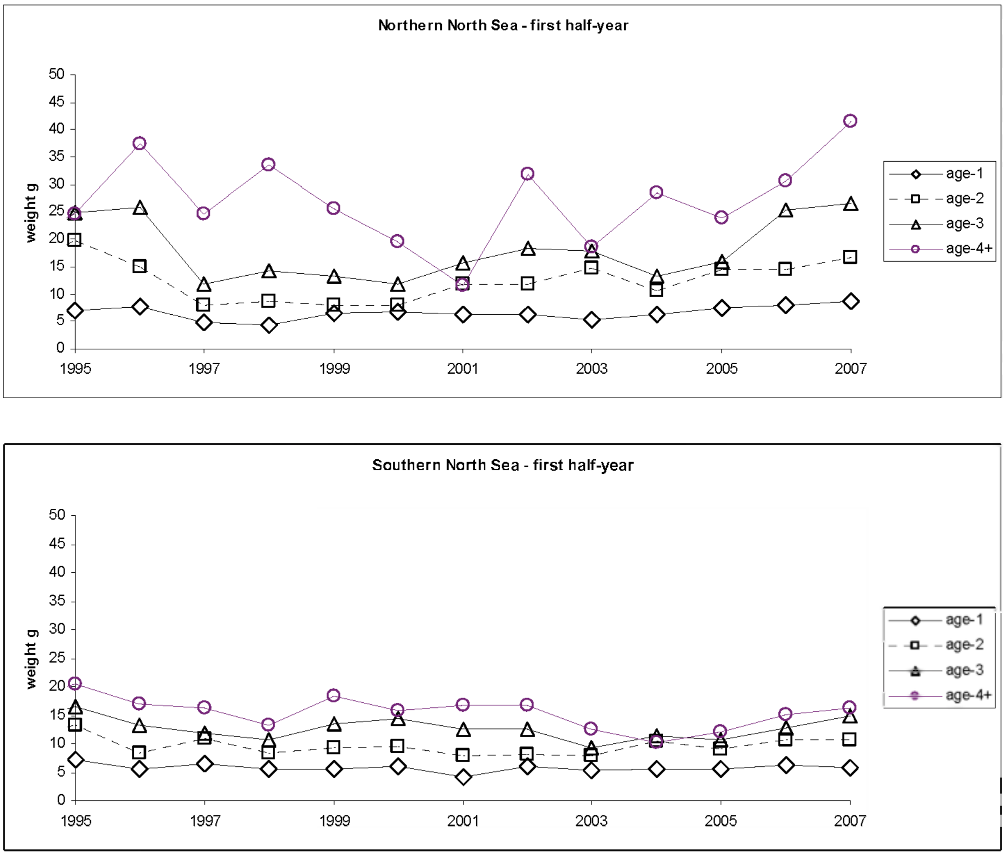


Figure 16.5. Variations in the mean weight-at-age of sandeels during the first half of the year in the northern North Sea (upper panel) and southern North Sea (lower panel).

16.2.9 Ecosystem role and trophic interactions

Sandeels are a valuable food source for many marine predators because of their high abundance and high caloric value (Hislop *et al.*, 1991). They are preyed upon by a range of fish species (ICES, 2005c), seabird species (Wright and Tasker, 1996; Furness and Tasker, 1997), and marine mammals (Harwood and Croxall, 1988), and their abundance may be highly influenced by the abundance of their predators (Sherman *et al.*, 1981).

A significant relationship between seabird breeding success and sandeel abundance has been demonstrated for the black-legged kittiwake (*Rissa tridactyla*; Daunt *et al.*, 2008; Frederiksen *et al.*, 2008). For the guillemot (*Uria aalge*), however, it appears to be the length of age-1 sandeels, and not abundance *per se*, that influences breeding success (Frederiksen *et al.*, 2006). MacLeod *et al.* (2007) relate the local decline in sandeel abundance to starvation in harbour porpoise (*Phocoena phocoena*) in the Scottish North Sea and speculate that the impact of climate change on sandeels may subsequently affect the survival of these porpoises.

16.2.10 Life-history strategy

Sandeels produce large, energy-rich demersal eggs. Demersal eggs are generally richer in energy than pelagic eggs of the same size (Lønning *et al.*, 1988) and usually larger than pelagic eggs. Larvae that hatch from demersal eggs are therefore better suited to withstand unfavourable nutritional conditions than those hatched from pelagic eggs (Einum and Fleming, 2000). Sandeel larvae have a long transition period from internal to external feeding, indicating that sandeels are less sensitive to environmental factors, such as temperature and prey densities, than species with other adaptive characteristics. This was confirmed by Malzahn *et al.* (2007), who found that sandeel larvae are fairly robust to variable external feeding conditions.

Like Wright and Bailey (1996), Malzahn *et al.* (2007) found a strong seasonality in larval condition, as favourable feeding conditions occur only during a short period of the year. However, contrary to the match–mismatch hypothesis (Cushing, 1990), the period of highest larval condition was not at the peak of food availability, but 2–3 wk earlier.

In conclusion, as a short-lived species living in a highly variable environment, sandeels seem to have adopted a conservative reproductive strategy involving the production of larger eggs and a longer transition phase from internal to external feeding in order to ensure that at least subsets of their offspring will survive.

16.2.11 Stock dynamics

The stock dynamics of sandeels is driven by highly variable recruitment, high natural mortality, and fishing.

Published information has generally demonstrated that the stock–recruitment relationship of sandeels is either weak or non-existent (Arnott and Ruxton, 2002; ICES, 2006l, 2007l). However, the biomass of age-1 sandeels (non-spawners) seems to be negatively correlated with recruitment (Arnott and Ruxton, 2002). This may be ascribable to intraspecific competition or cannibalism (Kishi *et al.*, 1991; Kimura *et al.*, 1992). Cannibalism may also explain why large year classes have never been observed in two succeeding years (Daan *et al.*, 1990) and the negative correlation between larval abundance and commercial landings, as found by Hart (1974).

It has also been claimed that herring (*Clupea harengus*) influence stock dynamics (Sherman *et al.*, 1981). Herring are known to prey on sandeel larvae and early juveniles (Savage, 1937; Hopkins, 1989; Pommerantz, 1981; Last, 1989); however, information about the effect of this predation on sandeel population dynamics is still lacking. On the other hand, for the Shetland stock, the negative covariation between sandeel total-stock biomass and herring spawning-stock biomass is striking (Frederiksen *et al.*, 2007). This may support a predation interaction, but other interpretations are also possible, such as an opposite dependence on a common external driving factor.

16.3 Fisheries

Sandeels in the North Sea are taken by trawlers using small-mesh trawls (<16 mm mesh). The fishery developed during the 1970s, and landings peaked in 1998 at more than 1 million t (Figure 16.3), when the stock was subject to the largest fishery in the North Sea.

The fishery is seasonal, owing to changes in the availability of sandeels in the water column (Figure 16.6). The sandeel fishing season usually starts in March and normally peaks in May/June. Landings tend to decrease in summer and increase again towards the end of the season, when age-0 fish are exploited, generally in the eastern North Sea (ICES, 2005a). Commercial fishing never takes place at night because sandeels are then buried in the seabed and inaccessible to trawl gear.

The fishery starts and ends each year in the southern part of the Norwegian zone. The majority of the landings takes place in the second quarter of the year in the central North Sea, with the largest landings from the Dogger Bank area and the southern part of the Norwegian zone. In the third quarter, the distribution of catches generally changes from a dominance of the west Dogger Bank area to fishing grounds located farther east. From 1991 onwards, grounds off the Scottish east coast have been targeted, particularly in June. However, since 2000, the banks in part of the Firth of Forth area have been closed to fishing (Greenstreet *et al.*, 2006; Daunt *et al.*, 2008).

The fishery targeted on age-0 sandeels was stopped in 2006, when a closed season was introduced and no fishing was allowed after 1 August.

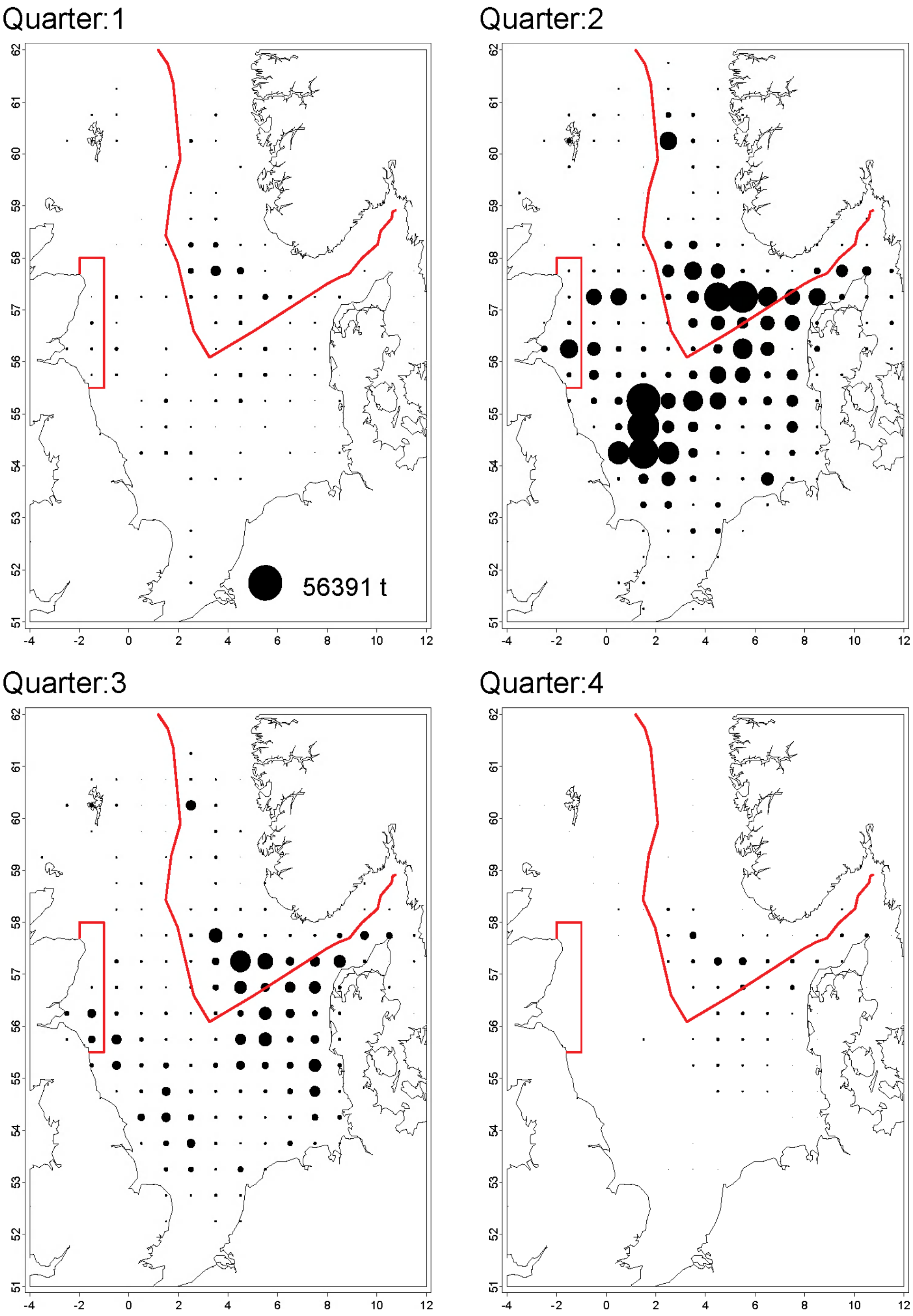


Figure 16.6. Landings of sandeels by quarter of the year and ICES rectangle, averaged over the period 1994–2003. Landings include: Danish and Norwegian landings for the whole period, Scottish landings from 1997 onwards, and Swedish landings from 1998. Landings for other countries are negligible. The sizes of the circles correspond to landings by ICES rectangle. All rectangle landings are scaled to the largest rectangle landings shown in the Quarter 1 map. The area off the east coast of Scotland has been closed to the sandeel fishery since 2000, and the boundary between the EU and the Norwegian EEZ is shown. (Source: STECF, 2005b.)

16.4 Changes in production

The sandeel stock in the North Sea has been at a low level since 2000, with an increase in stock size from 2005 to 2007 (ICES, 2007j). Since the strong 1996 year class, only the 2001 year class has been above average; since 2002, recruitment has been low (Figure 16.7). Since 2002, small year classes have been produced by small spawning populations. From 2002 to 2003, there was a large decrease in total landings owing to the decline in stock size (Figure 16.3).

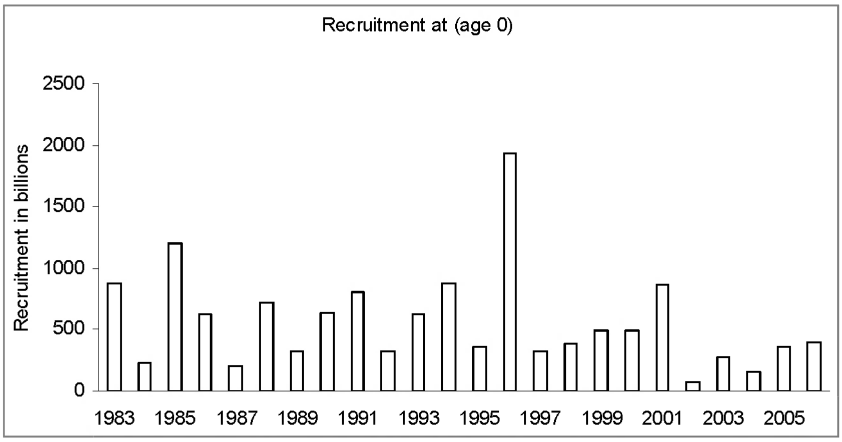


Figure 16.7. Time-series of recruitment of sandeels (age 0) in the North Sea. (Source: ICES, 2007b.)

Recent analyses of the variability in sandeel abundance in the Firth of Forth area, which was closed to fishing in 2000 (Greenstreet *et al.*, 2006), demonstrated that the biomass of age-1+ sandeels increased sharply during the first year of the closure (2006) and remained higher. In all four of the closure years analysed, it remained higher than in any of the preceding three years when the fishery was operating. The closure appears to have coincided with a period of enhanced recruitment.

16.5 Changes in distribution

The spatial distribution of landings is considered to be a good representation of stock distribution, except for areas where severe restrictions on fishing effort are applied. Yearly maps of landings by ICES rectangle (Figure 16.8) demonstrate a large reduction in landings and fishing patterns since 2003. The reduction in landings has been particularly marked in the northern part of the North Sea. In the Norwegian EEZ, landings fell by almost 90% in 2003 and 2004 when compared with 1994–2002. Survey data demonstrate that the reduction in landings in the northern North Sea was caused by local low abundance (ICES, 2006l). In 2006, concurrent with the overall increase in stock size, several areas in the northeastern North Sea, with previously low abundance, were recolonized by age-0 sandeels and subsequently fished in 2007.

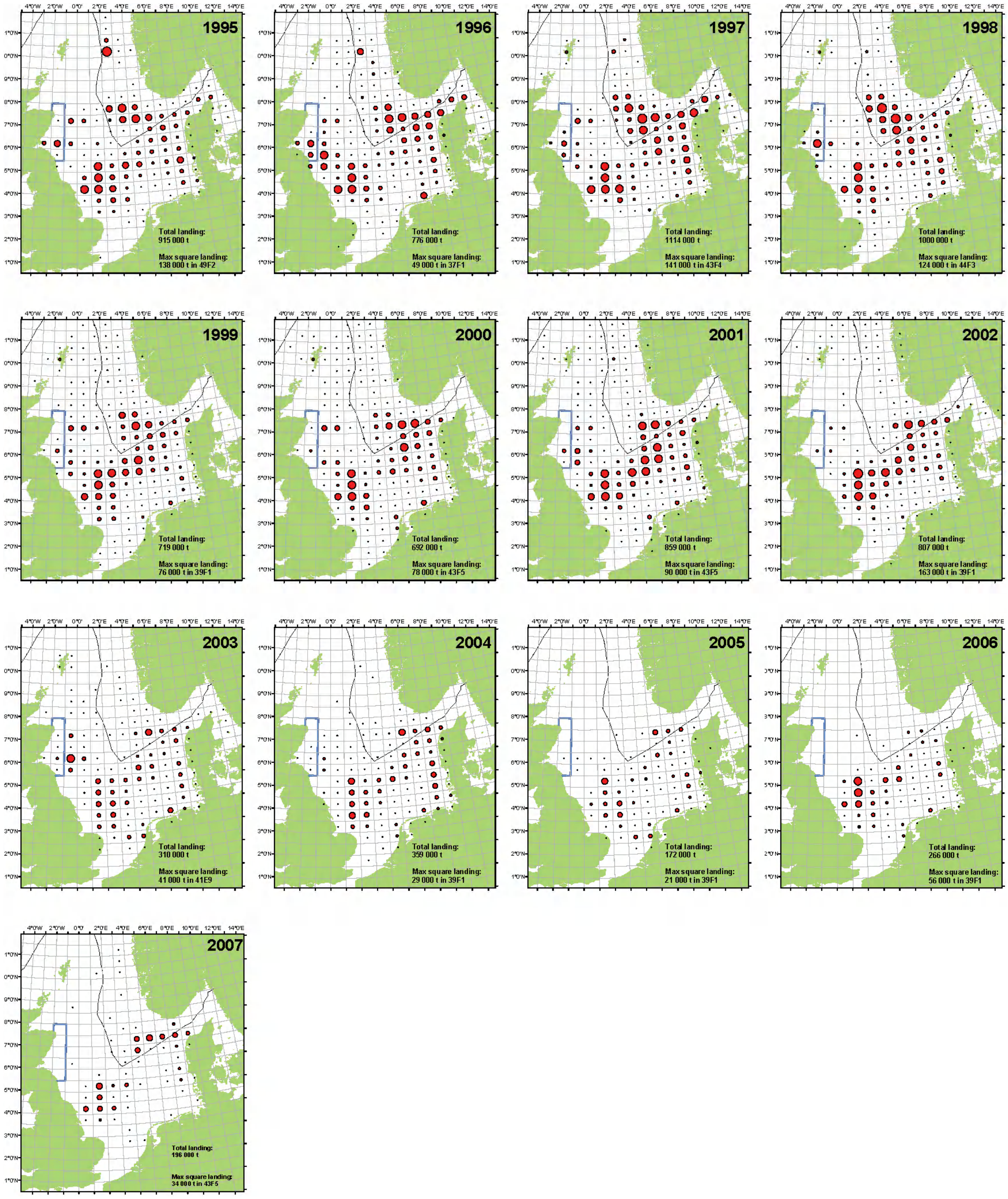


Figure 16.8. Landings of sandeels by year and ICES rectangle for the period 1995–2007. Landings include: Danish and Norwegian landings for the whole period, Scottish landings from 1997 onwards, and Swedish landings from 1998 onwards. Landings for other countries are negligible. The sizes of the circles correspond to landings by rectangle. All rectangle landings are scaled to the largest rectangle landings shown in the 1995 map. The boundary between the EU and the Norwegian EEZ is shown in the map. (Source: ICES, 2007j.)

16.6 Processes underlying observed changes

Wright and Bailey (1996) found that coupling between hatching and the onset of secondary production is important for growth and survival of larvae. Furthermore, Malzahn *et al.* (2007) found that low RNA:DNA in larvae was only linked to poor feeding conditions at times of an extreme decrease in food availability. Although smaller larvae demonstrated no significant decline in condition with decreasing prey abundance, larger larvae suffered from poor feeding conditions and only the fittest survived. In contrast, smaller larvae were not affected by low zooplankton prey densities, probably because of their ability to utilize two sources of energy: internal yolk reserves and external food. Changes in the timing of hatching and the temporal and spatial variation in abundance of zooplankton may therefore be one of the explanations for the observed changes in stock dynamics.

Analyses carried out by ICES (2006o) demonstrated that there was a significant change in recruitment in 2001 for herring, Norway pout (*Trisopterus esmarkii*), and sandeel, but that different mechanisms may have been responsible. Although the decline in sandeel recruitment could be linked to both the North Atlantic Oscillation (NAO) index and the annual average abundance of *Calanus finmarchicus* in the central North Sea, it was not possible to determine the mechanisms driving recruitment in sandeels or the link between changes in the environment and sandeel population dynamics.

ICES (2007l) reanalysed the stock–recruitment relationship of sandeels in the North Sea. The residuals in the stock–recruitment relationship were distributed evenly and randomly around the mean value and did not appear to reflect any obvious trends in stock dynamics. Productivity (recruits per spawner) was highly variable throughout the time-series modelled (1984–2005), with the highest productivity in 1997 and 2002, followed by a sharp decrease in the following year. An increasing trend in productivity was observed for the most recent years.

Recently, the abundance of jellyfish (e.g. *Aurelia aurita*) in the North Sea has been increasing (ICES, 2007l), and several projects are currently beginning to assess their impact on fish recruitment. Even though sandeel polytypes have a high invasive potential (being abundant in most northern shelf coastal areas), jellyfish species can prevent sandeels from realizing their full recruitment potential.

16.7 Conclusions on climate effects

Wright and Bailey (1996) and Malzahn *et al.* (2007) demonstrated that climatic variability affecting the dynamics of the zooplankton food of sandeels can affect the population dynamics of sandeels. This was also indicated by Arnott and Ruxton (2002) and ICES (2006o), who found year-class strength to be inversely related to the NAO index. High water temperatures during the egg stage lead to early hatching (Winslade, 1971), which, in turn, seems to lead to small year classes as a result of unfavourable feeding conditions and lower growth in early hatched larvae. This coupling between the appearance of first-feeding larvae and the onset of spring secondary production appears to be common among winter-hatching *Ammodytes* species; outside the North Sea, it has also been reported for sandeel larvae in the Northwest Atlantic (Sherman *et al.*, 1984; Monteleone and Peterson, 1986; Fortier *et al.*, 1995) and in Japanese waters (Inoue *et al.*, 1967).

As a large proportion of the total mortality of sandeels is the result of predation, any changes in predator distribution and abundance that result from climate change may have a strong impact on sandeel population dynamics.

Addressing the potential direct and indirect impacts of abiotic climate-related change requires a comprehensive description of both the physiological and habitat requirements of sandeel, most importantly *A. marinus*, which dominates the sandeel biomass in the North Sea. Unfortunately, many pieces of the puzzle are currently missing, but a few important results should be mentioned.

i) **Habitat quality and location**. The burrowing habit of the sandeels requires a sandy substratum, without too fine-grained fractions, to meet respiratory needs. The depth range does not appear to be sharply defined, but is normally less than 150 m (Reay, 1970). Other habitat attributes may also be required, but are not currently well described.

ii) **Local physical–biological environment**. Historically, the southern distribution limit of *A. marinus* has been the Channel areas at the southern boundary of the North Sea (Reay, 1970). Temperature may well determine this distribution limit, which life stage or physiological aspect is mainly affected is currently unknown. The temperature or salinity affinity of sandeels is not well described, although sandeels are found in both brackish water and salt water. Eggs are demersal, so transport mechanisms will not be affected by egg buoyancy properties. Stomach analysis of sandeel larvae has indicated that they digest a composite of zooplankton species (Ryland, 1964), but the relative nutritional value of the various dietary groups needs further investigation.

iii) **Non-local physical-biological conditions**. The above points concern local, observable attributes that quantify the suitability of a given area to support local sandeel subpopulations. However, sandeel larvae depend heavily on successful larval transport from hatching areas to settlement areas (which may be coincident); hence, interhabitat connectivity and relative regional retention of larval production are a major issue. With state-of-the-art, three-dimensional hydrodynamic models, this issue can be addressed from first principles, and, indeed, strong interannual and spatial variability in larval transport success has recently been demonstrated for North Sea sandeels (Christensen *et al.*, 2008).

17 Cod

Georg H. Engelhard, Michael R. Heath, and John K. Pinnegar

17.1 Introduction

This section reviews knowledge of the Atlantic cod (*Gadus morhua*; order Gadiformes, family Gadidae), with particular reference to the effects of climate change. It starts with an overview of the general biology and ecology, which is relevant to understanding the possible impact of climate change, and then reviews the evidence for changes in distribution and production in relation to climate.

17.2 General biology

The Atlantic cod, a species of prime commercial significance, is among the top predators inhabiting the northern temperate and cold waters of the Atlantic. A range of stocks is distributed from North Carolina on the east coast of the US up to Labrador, around Greenland and Iceland, and from Spitsbergen and the Barents Sea to the Bay of Biscay. Cod can attain a maximum size of >190 cm, although individuals >125 cm are uncommon nowadays, especially in areas more to the south.

Juvenile cod up to 6 months of age are pelagic and feed mainly on copepods. Upon reaching a length of ca. 7 cm, they adopt a demersal way of life and, as so-called "codling", become largely benthivorous, feeding especially on crustaceans. As they grow larger, however, the diet becomes increasingly dominated by fish, which may include young cod. Their depth range is 10–500 m (usually 20–150 m); feeding temperatures range from −1°C to 10°C. Growth rates vary markedly by stock, with southern stocks generally growing faster; for example, the average weight of age-4 cod ranges from ca. 0.6 kg off Labrador to 7.3 kg in the Celtic Sea (Brander, 1995). Accordingly, maturity differs between stocks, with males tending to mature earlier than females. In the North Sea, males and females start to mature at age 2 and age 3, respectively, and all fish have reached maturity by age 6. In Irish Sea cod, maturity is complete by age 3, whereas in slower-growing, northern stocks, maturation occurs at considerably greater ages; in the Barents Sea, some fish may not mature until age 11 (and historically, up to age 14; Jørgensen, 1990).

In February–April, cod migrate to the spawning grounds, which are often well defined and typically in areas with depths of 40–350 m. Dense aggregations may occur at the spawning sites, and these have traditionally been of great importance to the fisheries. Spawning temperatures range from −0.5°C to 6°C, and the spawning salinity is 33–35 psu (Svetovidov, 1948; Rose and Leggett, 1988; Heessen and Daan, 1994; Rose, 2005). Females have high fecundity (up to 9 million eggs fish^{-1}); this is especially the case for larger, older females, which have considerably higher fecundity per kilogramme body weight than smaller, first-time spawning females (Kjesbu *et al.*, 1991; Trippel, 1998).

17.3 Fisheries

Historically, cod has arguably been one of the most commercially important fish species, and its fisheries have played a prominent role in the economical and political development of Europe as well as North America over the past centuries (Solhaug, 1976; Kurlansky, 1997). More recently, disputes over cod fishing grounds have led to such well-known conflicts as the British–Icelandic "cod wars" of 1958–1961, 1972–1973, and 1975–1976 (Gilchrist, 1978; Jónsson, 1982), which ultimately contributed to the international establishment of 200-mile Exclusive Economic Zones. Currently, cod remains one of the world's most important fish species, and in 2004, ranked 12th among all fish species in terms of global landings (and even higher in terms of value of landings; FAO, 2007). This is despite significant declines in landings of most cod stocks, including the most productive ones, during recent decades (see Section 17.4).

Among the most important stocks in the Northwest Atlantic are northern (or Newfoundland) cod, Georges Bank cod, and Gulf of Maine cod, currently exploited by Canadian and US fisheries, but previously also by Basque, French, British, Soviet, and other European fisheries (e.g. Kurlansky, 1997). In the Northeast Atlantic, the largest stocks are those off Iceland and, historically even more productive (Godø, 2003), in the Northeast Arctic (or Arcto-Norwegian). The latter stock uses the Barents Sea as its main feeding and nursery areas and spawns off Norway's Lofoten Islands (Godø, 2003). It is this stock that, since medieval times, has supported the trade of "stockfish", or "bacalao", commenced by the Hanseatic League. Among Northeast Atlantic stocks, North Sea cod ranks third; together with Icelandic cod, this is the chief ingredient of England's popular "fish and chips" meal. Other cod stocks of great importance to the fisheries of various European countries are distributed over the Baltic, Irish and Celtic seas, and the English Channel.

In the context of the well-publicized, low levels of many cod stocks, it is of note that, traditionally, these often formed the "backbone" for local, demersal trawl fisheries. Until approximately two decades ago, cod often made up approximately one-sixth of the total demersal landings by British trawlers from the North Sea and as much as a third or a quarter of pre-1970s landings from Icelandic waters (Engelhard, 2005). Although the otter trawl is the most important gear, cod are also caught by beam trawl, and have been caught by longline since ancient times. They are, in addition, of some interest to marine recreational fisheries.

17.4 Observed changes in production

In recent decades, cod landings have declined almost throughout the species' range. In the Northwest Atlantic, the huge northern (Newfoundland) cod stock collapsed in the early 1990s and has, until now, failed to recover, despite stringent fishery restrictions (Hutchings and Myers, 1994a; Rose *et al.*, 2000; Fu *et al.*, 2001; Olsen *et al.*, 2004). In the Northeast Atlantic, cod landings in most European countries have generally declined. A fairly consistent, although less clear-cut, picture emerges if landings are visualized separately for each of the major fishing regions (Figure 17.1), and only in Icelandic and northeast Arctic cod has there been some reversal or attenuation of the declines.

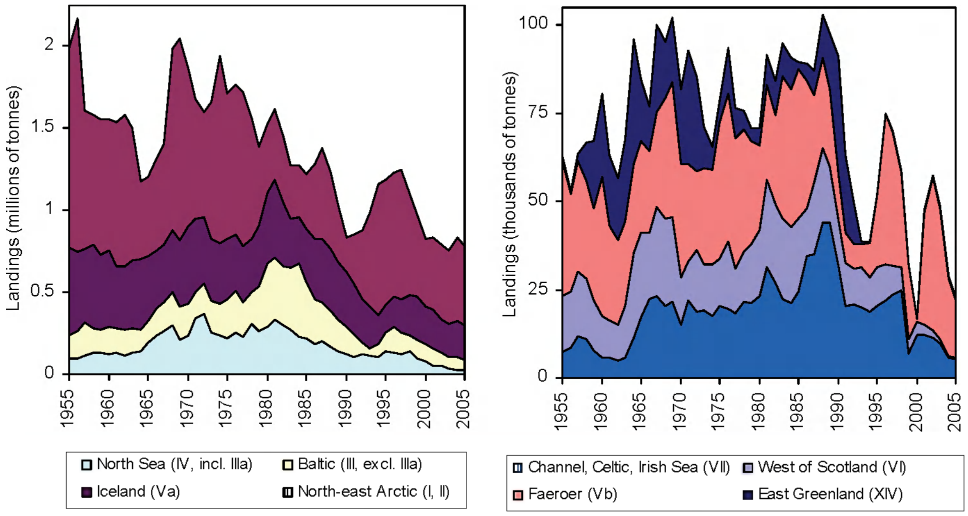


Figure 17.1. Northeast Atlantic cod: trends in total landings by fishing region. Left panel: the four most productive cod stocks (unit: millions of tonnes). Right panel: stocks or regions of secondary importance (unit: thousands of tonnes). (Data from ICES Fisheries Statistics.)

In the North Sea, the recent drop in landings is noteworthy because it followed two decades of particularly high productivity known as the "gadoid outburst" (late 1960s to mid-1980s; Daan, 1978; Hislop, 1996). During the "gadoid outburst", not only cod, but also haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), and Norway pout (*Trisopterus esmarki*) produced some of the largest year classes on record (Holden, 1978; Jones and Hislop, 1978). Whereas landings of various gadoid species had remained fairly stable throughout the period 1900–1950, they rose enormously during the 1960s and remained very high until the mid-1980s, after which they tended to decline again. Survey indices have indicated that this resulted not only from substantially increased fishing effort, but also, to a considerable extent, from high stock levels generally. Climatic influences have been widely indicated to account for these changes, but there are alternative hypotheses, e.g. a lack of herring (*Clupea harengus*) predation on juvenile gadoids through overfishing of herring. During the "gadoid outburst", each of the above gadoid species had generally high recruitment, but there was no particular year when all of the species had outstanding year classes (Jones, 1977).

Cod stocks have been subjected to excessive fishing pressure for many years, and 14 out of 15 Northeast and Northwest Atlantic stocks analysed by Brander (2007) have declined since 1970. Remarkably, in 10 of these 15 stocks, the periods of population decline were preceded by, or coincided with, declines in mean weight-at-age. Therefore, reductions in stock biomass were the result not only of a decrease in number, but also of a decrease in size of individual fish. Ten of the stocks have also experienced temporary increases in biomass, which were accompanied by increasing weight-at-age (Brander, 2007). Whereas this does not challenge fishing as a major cause of population declines, it does suggest that environmental factors are also important contributors to the fluctuations by affecting not only recruitment but also growth rates of cod (Brander, 2007).

17.5 Observed changes in distribution

At the scale of the Northeast Atlantic, Heath (2007b) reported an indication of changes in regional productivity of cod stocks over time, but no evidence from landings data that a wholesale northward shift in distribution might have occurred.

Recent warming has, however, probably resulted in enhanced productivity at the northern edge of the range and reduced productivity at the southern edge (Planque and Frédou, 1999; Heath, 2007b).

Within the North Sea, a northward shift in the mean latitudinal distribution of cod has occurred over the past three decades. This was demonstrated by several studies on cod distribution based on the North Sea International Bottom Trawl Survey or subsets thereof (Hedger *et al.*, 2004; Perry *et al.*, 2005; Rindorf and Lewy, 2006), although the evidence of northward distribution shifts is less clear-cut if based on commercial trawler catch per unit of effort (cpue) data (Engelhard *et al.*, 2008). Perry *et al.* (2005) estimated that the centre of population shifted 117 km towards the Arctic between 1977 and 2001. However, it is unclear to what extent the observed changes relate to climate warming, or might be caused by higher fishing pressure in the south central North Sea compared with northern North Sea, or to other factors.

In agreement with the "climate hypothesis", Hedger *et al.* (2004) found that cod were caught in deeper water during 1990–1999 than during 1980–1989, but their distribution with respect to temperature was unchanged. Although this suggests that cod responded to changing sea temperatures by actively seeking out a temperature niche, such an explanation of "cod swimming north" is probably too simplified (Hedger *et al.*, 2004; Heath, 2007b). The following also needs to be considered: (i) although the southern North Sea is typically warmer than the northern North Sea in summer, the opposite is true during winter; (ii) within North Sea cod, there are distinct subpopulations that appear to be reproductively isolated, implying little interbreeding and mixing (Hutchinson *et al.*, 2001; Wright *et al.*, 2006); (iii) information from data-storage tags, recovered from 129 individual cod throughout the North Sea, revealed that the fraction of the sea experienced by these fish was actually warmer than that potentially available to them (Neat and Righton, 2007). This was especially the case in the southern North Sea, where, during summer, most of the individuals experienced temperatures considered superoptimal for growth, well in excess of 14°C. In the northern North Sea, temperatures experienced rarely exceeded 14°C, but were, nevertheless, generally close to the upper seasonal trend in local bottom temperature; a few cod were exceptions, actively seeking out colder temperatures, confirming that cooler waters were within reach of the fish (Neat and Righton, 2007). Most did not, however, leading the authors to conclude that the changing thermal regime of the North Sea is not yet causing adult cod to move to cooler waters. Further evidence of active, small-scale, thermoregulatory movements is provided by Jones and Campana (2009).

As a possible climate-driven mechanism for distribution shifts, Rindorf and Lewy (2006) suggested that, during a recent series of winters characterized by high temperatures and southerly winds, increased northward transport of eggs and larvae may have occurred, leading to a northward shift in the distribution of juveniles the following year. Once settled at a location more to the north, cod may "home" to the same spawning sites year after year, resulting in genetically distinct spawning aggregations (Ruzzante *et al.*, 2001, for northern cod). This may make it difficult for the southernmost spawning sites, after they have become depleted, to become visited again once a more northward distribution shift of adolescent cod has occurred (Rindorf and Lewy, 2006).

Meanwhile, within the North Sea, there are considerable spatial differences in trawling effort distribution, which is generally higher in the southern and central North Sea than in the northern North Sea (Jennings *et al.*, 1999b; Callaway *et al.*, 2007).

Hence, it is likely that unbalanced depletions of local cod concentrations (Hutchinson *et al.*, 2001) have taken place, so that greater depletion in the south may well have caused the overall distribution shifts (Heath, 2007b). There is also some evidence that the general decline in North Sea cod recruitment took effect earlier in the reproductively segregated substock in the southern North Sea than in the northern North Sea, contributing to the more serious decline in the south (Holmes and Wright, 2005; Heath, 2007b). Finally, the northward distribution shift could be explained by the strong population decline *per se*. As populations decrease, they have a tendency to contract into areas of highest habitat suitability (in line with predictions from ideal free-distribution theory). Blanchard *et al.* (2005) demonstrated that the locations of such "basins" of good habitat are fairly persistent and are in the northeastern North Sea for age-1 cod and in the northwestern North Sea for age-2 cod, with the diminished stock having become increasingly confined to these sites.

17.6 Processes underlying observed changes

17.6.1 Growth

There is evidence that temperature is linked to growth and development of cod throughout life, from the egg and larval phases through to the adult stage. The developmental rates of the eggs in a wide range of cod stocks have been demonstrated experimentally to increase significantly with temperature, at least within a temperature range of ca. 0–12 °C (see references in Geffen *et al.*, 2006). At the same time, egg survival was negatively related to temperature, albeit to a much lesser extent than the positive effect on growth (Geffen *et al.*, 2006). As a result, optimal temperatures for egg development appear to lie between 2°C and 7°C, with less optimal but potentially viable temperatures outside this range, but within 0–10 °C (Geffen *et al.*, 2006). Van der Meeren and Ivannikov (2006) confirmed that temperatures above 9.6 °C resulted in significant reductions in fertilization and normal egg development and that, concurrently, fractions of dead and unfertilized eggs increased with elevated temperature.

Larval and juvenile growth is also temperature dependent. For example, Otterlei *et al.* (1999) demonstrated that reared larvae and juveniles, followed over the first two months after hatching, grew faster as temperatures increased from 4°C to 14°C; this corresponded to a considerably reduced larval stage at higher temperatures (Otterlei *et al.*, 1999). The optimum temperature of larval cod fed to excess was estimated at between 14°C and 16 °C, and temperature and condition were, moreover, positively correlated (Otterlei *et al.*, 1999). In the field, a positive link between temperature and larval growth has also been found, although there appears to be a stronger positive link with photoperiod (Buckley *et al.*, 2006). However, it is important to note that, when food is scarce, higher temperatures can lead to decreased growth through higher metabolic costs, as demonstrated experimentally (Buckley *et al.*, 2006).

Experiments have demonstrated that temperature is still related to the (food-unlimited) growth rate of larger cod up to several years old, although the effects are not as pronounced as in small juvenile cod (Björnsson and Steinarsson, 2002). Moreover, the optimal temperature for growth of cod decreases with increasing size of fish, from 14.3 °C for 50 g fish to 5.9 °C for 5000 g fish (Björnsson and Steinarsson, 2002), so that weight at age 3 would be maximal at an ambient temperature of ca. 8 °C. If field observations of length-at-age are compared between cod stocks, it is evident that warm-water stocks generally grow faster than cold-water stocks (Brander, 2007). The effect of temperature change is progressively greater at low temperatures (Björnsson and Steinarsson, 2002; Brander, 2003; Folkvord, 2005 for the larval stage). This may explain why the warm-water stocks (Georges Bank and the North, Irish, and Celtic seas) demonstrate less variability in weight-at-age than cold-water stocks (Brander, 2007).

Brander (2007) emphasized that decreases in mean weight-at-age have preceded or coincided with biomass declines in a range of cod stocks. Reductions in growth rates may well have been a contributory factor in population declines, given that body size, survival, and reproductive potential are well known to be tightly interlinked (Roff, 2002). Clearly, temperature effects have played a role in the changes in growth rates, but there is also evidence for effects of prey availability (Krohn *et al.*, 1997), density-dependence, and possibly size-selective effects of fishing, whereby larger, heavier individuals are more at risk from mortality through fishing than smaller ones (Heino and Godø, 2002; Swain *et al.*, 2003).

17.6.2 Recruitment

Planque and Frédou (1999) demonstrated that, at a global scale, there are differences between cod stocks in how recruitment is related to sea temperatures. Generally, stocks demonstrate high variability in recruitment (Figure 17.2). If analysed separately by stock, only four of nine stocks demonstrated statistically significant relationships of sea surface temperature (SST) with recruitment anomalies (i.e. the residuals of $\log_2$ recruitment, after fitting the stock–recruitment relationship). However, in a meta-analysis of the combined stocks, they found that the sign of the relationships was generally positive for cold-water stocks (inhabiting bottom temperatures <6 °C), negative in warm-water stocks (inhabiting bottom temperatures >9 °C), and very close to zero in stocks inhabiting intermediate bottom temperatures (7–8 °C). Thus, towards the northern end of the species' distribution range, recruitment appears to benefit from higher than average ambient temperatures; the opposite is true towards the southern end of the distribution range.

On top of direct temperature effects on development, growth, and survival, climate is probably also indirectly linked to cod recruitment by affecting the abundance and availability of prey. Differences in temperature–recruitment relationships between cod stocks are probably largely attributable to different climatic impacts on zooplankton composition and biomass. Calanoid copepods, in particular, provide the main prey for larvae in many cod stocks, as well as for several other fish species that, in turn, are eaten by larger cod. In the Barents Sea, where northeast Arctic cod demonstrate a significant, positive temperature–recruitment relationship (Ottersen and Sundby, 1995; Planque and Frédou, 1999), abundance of *Calanus finmarchicus* is thought to be positively related to sea temperature, because warmer temperatures are associated with an increased influx of copepod-rich waters from the Atlantic (Aksnes and Blindheim, 1996; Helle and Pennington, 1999).

The opposite appears to be true in the North Sea, where temperature and cod recruitment have a significant negative relationship (Planque and Frédou, 1999; O'Brien *et al.*, 2000; Beaugrand *et al.*, 2003; Clarke *et al.*, 2003). Cold conditions during the 1960s and early 1970s were correlated with a sequence of positive recruitment deviations (O'Brien *et al.*, 2000; Brander and Mohn, 2004), and so contributed to the "gadoid outburst" of the late 1960s to mid-1980s, when productivity of cod and other roundfish stocks was very high. The end of the gadoid outburst has often been related to significant warming of the North Sea, especially since 1988, in addition to overexploitation of the spawning stock (O'Brien *et al.*, 2000).

Beaugrand *et al.* (2003) proposed a mechanism that acted through zooplankton, demonstrating that survival of larval cod was primarily related to the abundance of *C. finmarchicus* and euphausiids, and the mean size of calanoid copepods; there was a negative link to *Calanus helgolandicus* and weaker, but again positive, links to total calanoid biomass and the genus *Pseudocalanus*. Each of these have generally been high from the colder mid-1960s to mid-1980s and low from the mid-1980s to the present, with the exception of *C. helgolandicus*, which demonstrates opposite trends (Beaugrand *et al.*, 2003). By including temperature–zooplankton–cod recruitment links, Planque *et al.* (2003b) were able to make short-term recruitment forecasts where, based on late January SST, cod recruitment could be projected with 42% accuracy (as opposed to 17% if SST was not included).

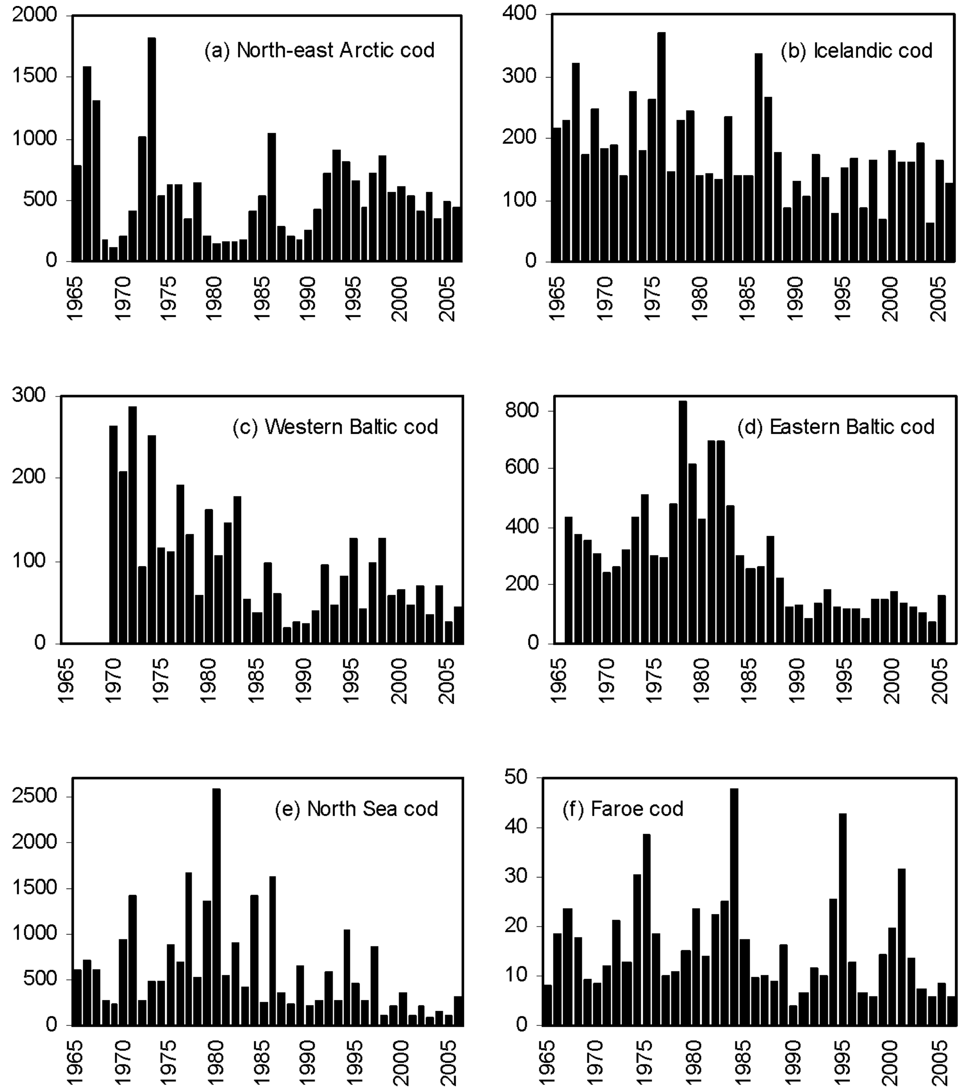


Figure 17.2. Northeast Atlantic cod: time-series of recruitment (in millions) for (a) northeast Arctic cod at age 3, (b) Icelandic cod at age 4, (c) western Baltic cod at age 1, (d) eastern Baltic cod at age 2, (e) North Sea cod at age 1, and (f) Faroe cod at age 2. (Data from ICES, 2006a, 2006b, 2006c, 2006d, 2006g.)

Nevertheless, although *C. finmarchicus* abundance and North Sea cod recruitment were found to have a significant positive relationship (Beaugrand *et al.*, 2003), some controversy remains about whether the two are mechanistically linked or subject to common, underlying causes (C. J. Fox, pers. comm.). Notably, the majority of cod larval production within the North Sea, both historically and recently, has occurred in the mid- to southern regions (Fox *et al.*, 2005). Here, *C. finmarchicus* are considerably less abundant than in more northern latitudes, comprising only a small fraction of the total copepod abundance (Pitois and Fox, 2008), and diet studies have demonstrated that *Pseudocalanus* copepods make up the bulk of the food for cod larvae in these regions.

In the Baltic Sea, cod recruitment and development appear to be related to an interplay between salinity, oxygen concentration, temperature, and eutrophication (MacKenzie *et al.*, 2002). Unlike elsewhere, cod eggs in the Baltic are neutrally buoyant in deep water below the permanent halocline. Salinity and oxygen concentrations below the halocline vary relative to major, climate-driven inflows from the North Sea. They have a direct impact on the development of the eggs, which require a salinity of at least 11 psu and an oxygen concentration of at least 2 ml l^{-1} to develop (Nissling *et al.*, 1994; Wieland *et al.*, 1994). Within the Baltic, the volume of water with these characteristics has been termed the "reproductive volume" for Baltic cod (Plikshs *et al.*, 1993; MacKenzie *et al.*, 2000), and modelled variability in the reproductive volume has been applied in the development of Baltic cod stock–recruitment models (Köster *et al.*, 2001a, 2001b; Röckmann *et al.*, 2007a, 2007b). Climatic variables directly and indirectly influence the Baltic Sea hydrography and, therefore, the reproductive volume for the cod stock. Moreover, climate effects on the zooplankton prey for cod juveniles (specifically the copepods *P. acuspes* and *Acartia* spp.) have also been demonstrated to be important in influencing cod population dynamics in the Baltic Sea (Möllmann *et al.*, 2008).

17.6.3 Mortality

For the early life stages, experimental work suggested that positive effects of temperature on growth (within a range of ca. 0–12°C) were partly offset by apparently weaker, negative effects on survival (Otterlei *et al.*, 1999; Geffen *et al.*, 2006), resulting in optimal temperatures for early growth and survival combined of ca. 2–7°C (Geffen *et al.*, 2006). When cod grow large enough to be caught by commercial fisheries (from ca. age 1–2 onwards), fishing mortality (F) is generally thought to become the dominant source of mortality in many cod stocks, often far exceeding natural mortality (M; e.g. for age-3+ North Sea cod: M assumed to be 0.2 year^{-1}, F estimated at ca. 0.4–0.6 year^{-1}; ICES, 2006l). Thus, temperature effects on mortality are likely to be most prominent during the early life stages and, in later life stages, are likely to become overshadowed by the effects of exploitation. However, this does need to be examined further, particularly because there is evidence that decades of sustained high fishing mortality may have made cod stocks more sensitive to climate change by altering such aspects as stock structure, age composition of the spawning stock, and ages and sizes at maturation.

Marked changes in maturity have taken place in a variety of cod stocks. At the present time, cod are maturing at earlier ages and smaller sizes than they did some decades ago (northeast Arctic cod: Jørgensen, 1990; Heino *et al.*, 2002a, 2004; Georges Bank and Gulf of Maine cod: O'Brien, 1999; Barot *et al.*, 2004; northern cod: Olsen *et al.*, 2004). In northeast Arctic cod, for example, age at first spawning is now typically 5–8 years compared with ca. 10–11 years in the 1930s, and average length at maturation has decreased in parallel, from ca. 85–90 to 70–75 cm (Jørgensen, 1990; Heino *et al.*, 2002a, 2004). These changes have been attributed to (i) fishery-induced genetic selection for earlier maturation (evolutionary change), where, under high fishing pressure, very few late-maturing individuals survive until first spawning, and, hence, despite larger size, on average produce fewer offspring than early-maturing, small individuals (Borisov, 1978; Heino and Godø, 2002); and (ii) to faster growth leading to earlier maturation. The latter can be a compensatory response to a reduction in stock size caused by fishing, thus relaxing intraspecific competition for food (Jørgensen, 1990). However, faster growth can also result from changing climatic conditions directly influencing food abundance. Of course, this is not a straightforward relationship because there is a balance between increased temperature, food availability, higher metabolic cost, and reduced oxygen loading, which can lead to the onset of metabolic stresses that may reduce growth rates (Pilling *et al.*, 2007). Both fishery-induced selection pressures and environment-driven changes in growth rates have contributed to maturity changes in cod stocks (Heino *et al.*, 2002a; Barot *et al.*, 2004; Olsen *et al.*, 2004). An important implication is that, as a result of changes in age and size at maturation caused by high fishing mortality, the mean age and size of spawning cod have dropped substantially. However, larger, older cod have disproportionally higher fecundity and also produce individual eggs of higher quality (Kjesbu *et al.*, 1991; Trippel, 1998). As a result, the observed changes towards earlier maturity at smaller sizes are negatively affecting the reproductive potential of cod stocks (Heino and Godø, 2002; Marshall *et al.*, 2003) and are therefore making cod stocks more sensitive to climate change.

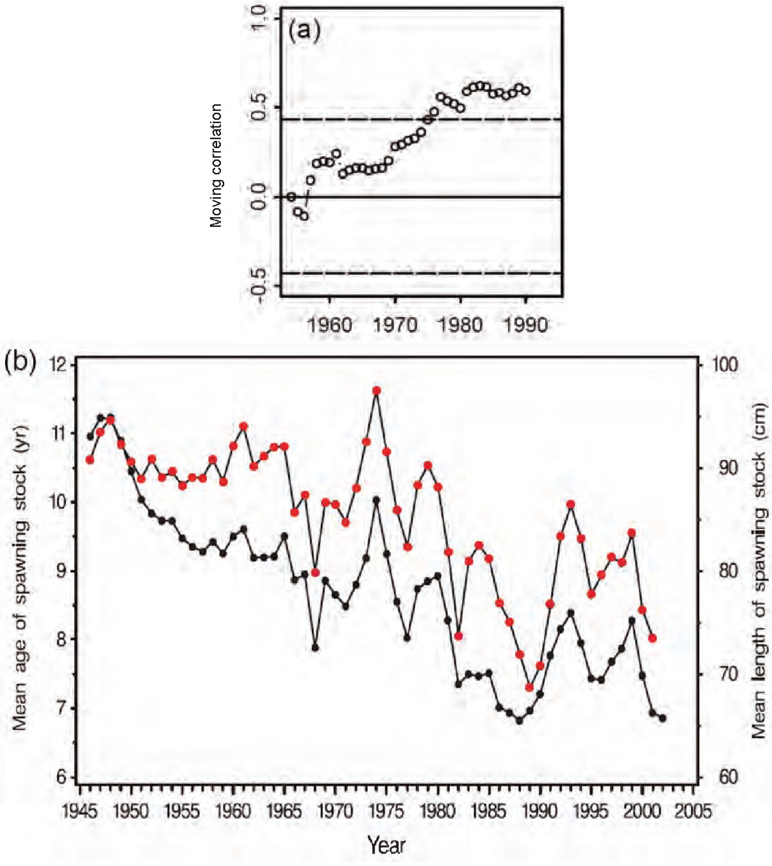


Figure 17.3. **(a) Increasingly strong moving correlation (21-year time window) between year-class strength at age 3 of northeast Arctic cod and sea temperatures in the Kola section of the Barents Sea (0–200 m depth, 1943–1999). A 21-year correlation outside the stippled bands is statistically significant (p <0.05). (b) Long-term decreases in the mean age (black circles) and mean length (red circles) of spawning cod. (Reproduced with permission from Ottersen *et al.*, 2006.)**

There is evidence that, apart from reductions in age and size of first-time spawners, truncations in the age structure of spawners in general are also making cod more responsive to climate change. For northeast Arctic cod, links between climate and recruitment have already been suggested in Hjort's (1914) classical paper, and Sætersdal and Loeng (1987) demonstrated that cold years never provide strong year classes. This stock has the Barents Sea as a nursery area, and explanatory mechanisms include more inflow of warmer, prey-rich Atlantic water from the southwest in warmer years (Helle and Pennington, 1999). During recent decades, there has been a clear positive temperature–recruitment correlation; remarkably, this link was weak or non-existent in earlier decades (Figure 17.3a; Ottersen and Stenseth, 2001). As pointed out by Ottersen *et al.* (2006), the current higher dependence of recruitment on climate is probably related to changes in stock structure (Figure 17.3b), notably, a change in the average age and length of spawners from 10–11 years and >90 cm to 7–8 years and 80 cm, and a decrease in the number of age classes. This has been attributed to high fishing mortality, especially from the 1960s onwards (Godø, 2003; Ottersen *et al.*, 2006), and to decreased age and size at maturation (Heino *et al.*, 2002a). A major implication is that fishery-induced impoverishment of stock structure (reduced and fewer ages, smaller sizes) can increase the sensitivity of a previously robust stock to climate change. Worryingly, truncations in the age distributions of spawners have occurred in most cod stocks.

17.6.4 Consequences for future management

Future, CO_2-induced, climate-change scenarios from global circulation models (GCMs) indicate increasing air temperatures, especially in the Arctic and Subarctic where cod are distributed (IPCC, 2001, 2007). Several studies have recently addressed how, against this background, future management of cod may have to be adapted to account for climate-change impacts. Drinkwater (2005) modelled how the major cod stocks might respond to climate change in future under different global-warming scenarios predicted by the IPCC. He built further upon the stock-specific, temperature–recruitment relationships described by Planque and Frédou (1999), with some modifications, and extrapolated these to four global warming scenarios, with average temperature increases of 1°C, 2°C, 3°C, and 4°C (Figure 17.4). Predictions were that

> …stocks in the Celtic and Irish seas are expected to disappear under predicted temperature changes by the year 2100, whereas those in the southern North Sea and Georges Bank will decline. Cod will likely spread northwards along the coasts of Greenland and Labrador, occupy larger areas of the Barents Sea, and may even extend onto some of the continental shelves of the Arctic Ocean. In addition, spawning sites will be established farther north than currently. It is likely that spring migrations will occur earlier, and fall returns will be later. There is the distinct possibility that, where seasonal sea ice disappears altogether, cod will cease their migration. Individual growth rates for many of the cod stocks will increase, leading to an overall increase in the total production of Atlantic cod in the North Atlantic.

At the same time, Drinkwater (2005) noted that predicted responses remain highly uncertain because, apart from temperature, they will also depend on changes to climate and oceanographic variables, such as plankton production, abundance of predators and prey, as well as the development of the fisheries.

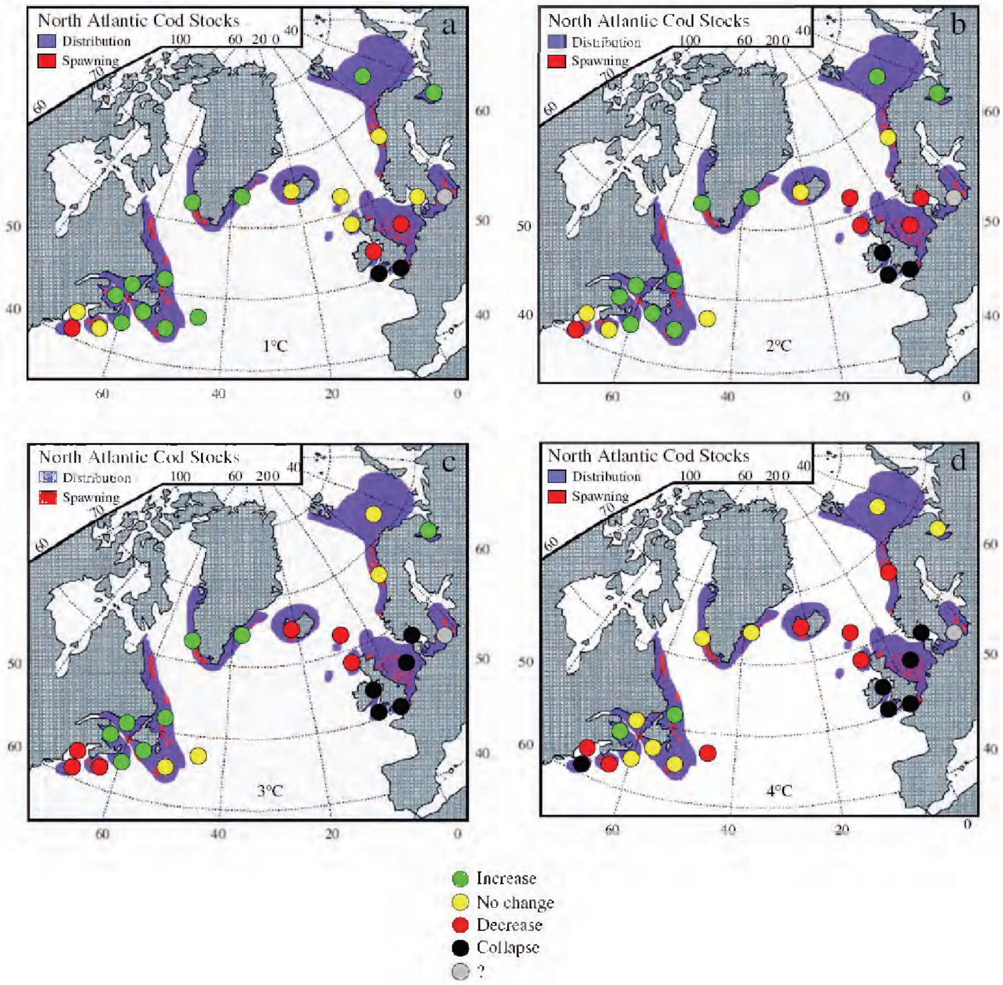


Figure 17.4. Expected changes in the abundance of cod stocks, assuming future climate-change scenarios where the temperature increases by (a) 1°C, (b) 2°C, (c) 3°C, and (d) 4°C above current levels. (Reproduced with permission from Drinkwater, 2005.)

Fishery management will have to adapt to account for climate-driven changes in stock productivity (Cook and Heath, 2005; Kell *et al.*, 2005; Röckmann *et al.*, 2007a, 2007b). This will include adjustment of biological reference points (BRPs) that form the benchmarks for managing fish stocks. For six North Sea stocks, including cod, Cook and Heath (2005) investigated how a warmer temperature regime might alter BRPS, including maximum sustainable yield (MSY), F_{msy}, B_{pa}, and F_{pa} by fitting historical Ricker stock–recruitment relationships with a temperature effect incorporated (as in Planque and Frédou, 1999). This revealed that, in a warmer temperature scenario, recruitment would be expected to decrease in three of the six stocks (cod, plaice (*Pleuronectes platessa*), and sole (*Solea solea*)) and to increase in one stock (saithe); there was no significant temperature effect in the other two stocks (haddock, whiting). In the case of cod, this implies that management would have to be based on adjusted BRPs, with lower MSY, F_{msy}, and F_{pa} and higher B_{pa} than would be the case at a lower temperature regime. Later, Heath (2007a) also incorporated the positive effect of temperature on growth in the above simulations, as there are some indications that growth in North Sea cod has increased since 1985 by ca. 0.4% per decade. However, this effect is so small that, by and large, it would not make up for the reduced recruitment under the warmer temperature regime. One positive finding in these simulations was that, with proper management, the MSY is potentially larger during a warm period than the mean catch in recent years (Cook and Heath, 2005).

This is because the stock has now been fished well beyond F_{msy} for many years, contributing to its current depleted state. Provided the stock can recover, there is the potential for a much larger fishery.

Simulation studies on the future management of cod have also been carried out for the eastern Baltic stock, under projected scenarios of low, medium, or high climate change (Röckmann *et al.*, 2007a, 2007b). These studies suggest that productivity is likely to decrease and that strict management regulations will be required to avoid stock collapse. This is perhaps best achieved through marine protected areas coinciding with the "core" cod spawning habitat (Röckmann *et al.*, 2007a) or through drastic reductions in fishing mortality, although a potential collapse of Baltic cod may be unavoidable under projected environmental change scenarios (Röckmann *et al.*, 2007b).

The importance of adjusting BRPs was confirmed by Kell *et al.* (2005), who examined implications of climate change for the management of North Sea cod and, in particular, the robustness of BRPs to climate change. They demonstrated that climate-change effects are likely to affect management in the longer term. The implications of climate change for BRPs depended upon the mechanism through which temperature acted on recruitment (i.e. on juvenile survival or carrying capacity). Although biological studies were recommended to identify the likely mechanism through which climate change affected stock processes, in the absence of this knowledge, simpler management procedures that are robust to uncertainty about the true dynamics are needed. They found that BRPs based on stock biomass, such as B_{pa} and B_{lim}, are particularly sensitive to climate change and, given high uncertainty, may be unsuitable as a basis for stock management decisions. In contrast, BRPs based on fishing mortality (F_{pa}, F_{lim}) were found to be relatively robust to climate change and, hence, may be more suitable for managing a cod stock where the biomass response to climate change is not fully understood.

17.7 Conclusion on climate effects

The response to climate change of cod, perhaps the most extensively studied among fish, remains enigmatic but crucially important, given the species' huge commercial importance. Landings throughout nearly the entire range of the species have recently demonstrated marked, and sometimes catastrophic, declines at a time when temperatures have generally warmed. Within the North Sea, a northward shift in the mean latitudinal distribution of cod has occurred, but there is much controversy about the causes: active migrations (now considered unlikely), higher fishing mortality in the south, local differences in recruitment, or a mixture of these and other factors.

Experiments have demonstrated that eggs and larvae develop best at specific temperatures, although this also depends on other factors, such as prey. Recruitment is related negatively to temperature in populations located more to the south, but positively in the northern ones, with no significant relationships recorded for some stocks at intermediate latitudes. Within the North Sea and the Barents and Baltic seas, recruitment has also been demonstrably linked to copepod zooplankton (in turn, affected by climate) and, in the Baltic, there are clear links with salinity. Marked maturity changes have taken place in several cod stocks in recent decades; these have been attributed partly to climate, partly to selective effects of fishing, and partly to density-dependent effects through stock depletion. A warmer climate may have had a subtle, positive effect on growth rates.

One forecasting study has modelled the possible responses of different cod populations to future climate-change scenarios projected by the IPCC. For Baltic and North Sea cod, several authors have studied the implications of projected climate change for future fishery management. An important point of agreement was that, in general, fishing mortality needs to be reduced in the short to medium term, while the potential effects of climate change should be considered in the longer term.

18 Red mullet

Georg H. Engelhard, Jim R. Ellis, Doug J. Beare, and John K. Pinnegar

18.1 Introduction

This section gives an overview of the general biology and ecology of the striped red mullet (*Mullus surmuletus*; order Perciformes, family Mullidae) and reviews the evidence for changes in distribution and production, and their relationship with climate change.

18.2 General biology

The striped red mullet has a moderately elongated body, steep snout, and two long, mobile barbels; adult body length is typically 33–37 cm (maximum 40 cm; Miller and Loates, 1997). There is some taxonomic confusion between this species and the common red mullet (*Mullus barbatus*; note that both species may be referred to as red mullet), and it is unclear whether or not the latter species occurs in northern European waters.

It is found along the European coasts from Norway, north Scotland, and the Faroes, south to the Strait of Gibraltar, into the Mediterranean and Black seas, and along the coast of northwest Africa to Senegal and the Canary Islands (see references in ICES, 2007d). It is infrequent off Norway, around Ireland, the northeast coast of England, and western Scotland (ICES, 2007d). It is a so-called Lusitanian species, with southern biogeographic affinities within the Northeast Atlantic (Knijn *et al.*, 1993; see Section 19, this volume).

The striped red mullet is a benthic, schooling species. It feeds primarily on benthic invertebrates (crustaceans and molluscs; ICES, 2007d) and small fish, using its sensory barbels to locate prey (Miller and Loates, 1997). It is recorded from depths ranging from 5 to 409 m (Ben-Tuvia, 1990) and seems to prefer elevated temperatures. It tolerates both low and high salinities (corresponding, respectively, to the habitats of juveniles and adults) and is rarely found in transition zones of intermediate salinity. This species prefers sandy sediments (Carpentier *et al.*, 2005). Its growth rate is relatively rapid and, during the first two years of life, similar for both sexes; thereafter, females grow faster than males and at 5 years they are on average ca. 6 cm longer than males (Mahé *et al.*, 2005). In the Northeast Atlantic, males and females have been estimated to commence reproduction upon reaching a body length of 16.5 and 18 cm, respectively (Desbrosses, 1935).

18.3 Fisheries

The striped red mullet is a non-quota species of moderate, but increasing, importance to the fisheries, especially given its high market value. According to ICES statistics, the main country catching red mullet in the Northeast Atlantic is France (Figure 18.1). It is a target species for this country and is mainly caught (>90%) by bottom trawlers using a 70–99 mm mesh (ICES, 2007d).

Exploitation occurs mainly in ICES Subareas and/or Divisions IV, VIId, and e, and VIIIa and b, mostly in inshore waters (Figure 18.1b). Over the entire zone, French catches are the most important (although Spanish catches predominated before ca. 1975). The Netherlands and the UK are also currently important with regard to the English Channel (Divisions VIId and e) and the North Sea (Division IV), where catches are concentrated in the south (Division IVb and c). The northern part of the

Bay of Biscay (Divisions VIIIa and b) is exploited by France and Spain, whereas the southern part (Division VIIIc) is exploited only by Spain. Other countries with small catches include Germany, Scotland, Denmark, and Ireland. For this species, therefore, three Subareas/Divisions should be considered: IV, VIId and e, and VIIIa and b.

The species is not discarded by French vessels in the eastern English Channel (Division VIId) or in the southern North Sea (Division IVc). However, more investigations on discards by other countries should be carried out in these and the other areas (ICES, 2007d). This is a relatively high-value species, with a minimum landing size of 15 cm (Dunn, 1999).

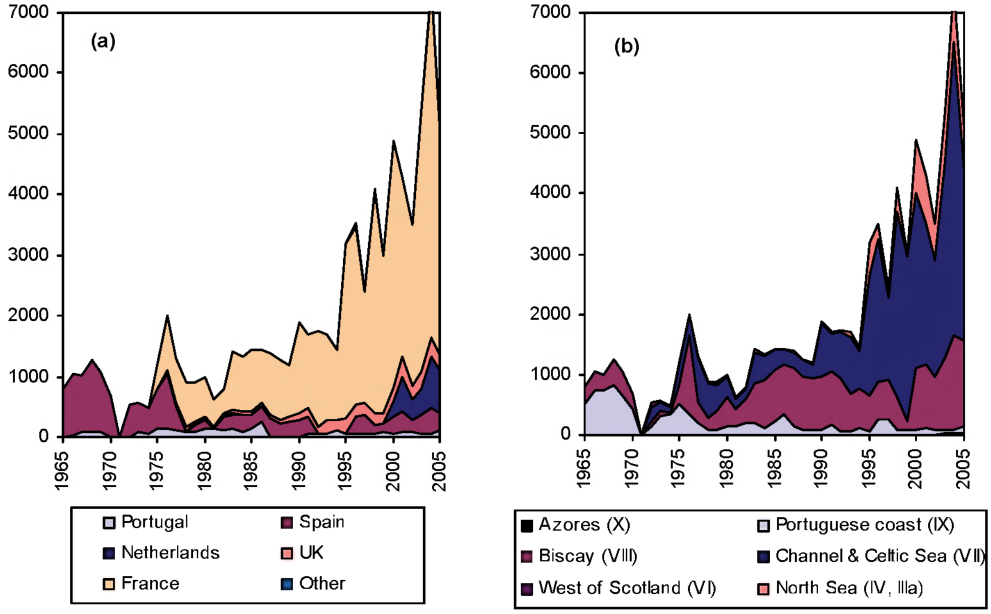


Figure 18.1. Northeast Atlantic red mullet: trends in total landings (a) by country of landing, and (b) by fishing region (in t). (Data from ICES Fisheries Statistics. French data before 1975, and Spanish data for 1971 and 1992–1994 possibly incomplete. In (a), "other" includes Belgium, Ireland, and Denmark.)

18.4 Observed changes in production

The majority of global (striped) red mullet landings are taken from the Mediterranean and Black seas, while a comparatively smaller number are taken from the Atlantic Ocean. In both regions, international landings have increased substantially from 1950 to 2004 (from 800 to 14 500 t for both regions combined). Since 1991, global production has stabilized between 13 000 and 15 000 t (ICES, 2006k).

Within the Atlantic Ocean, red mullet was, until 1975, only exploited significantly by the Spanish fleets, along the Spanish coast and in the Bay of Biscay. French landings commenced in 1975; initially they were mainly in the Bay of Biscay and less so in the English Channel. However, since approximately 1990, French landings from the English Channel have increased markedly, making up the majority of all French landings; French landings from the North Sea have also increased. French landings from Subarea VIII have generally remained stable or high, especially in 2004 and 2005.

Similarly, UK landings have increased in recent decades; these are mainly taken in the English Channel, with smaller quantities from the North Sea. The increase, which has occurred in both regions, has been especially marked from the early or mid-1990s onwards. Dutch landings of red mullet from the same fishing regions have demonstrated a large increase, from (near) zero levels in the 1990s to several hundred tonnes since 2000 (ICES, 2007d).

These recent landings should also be viewed historically. For example, reported landings of red mullet in the North Sea between 1905 and 1907 were, on average, 20 t year^{-1}, and there have been other intervening periods when red mullet have been landed in relatively large quantities.

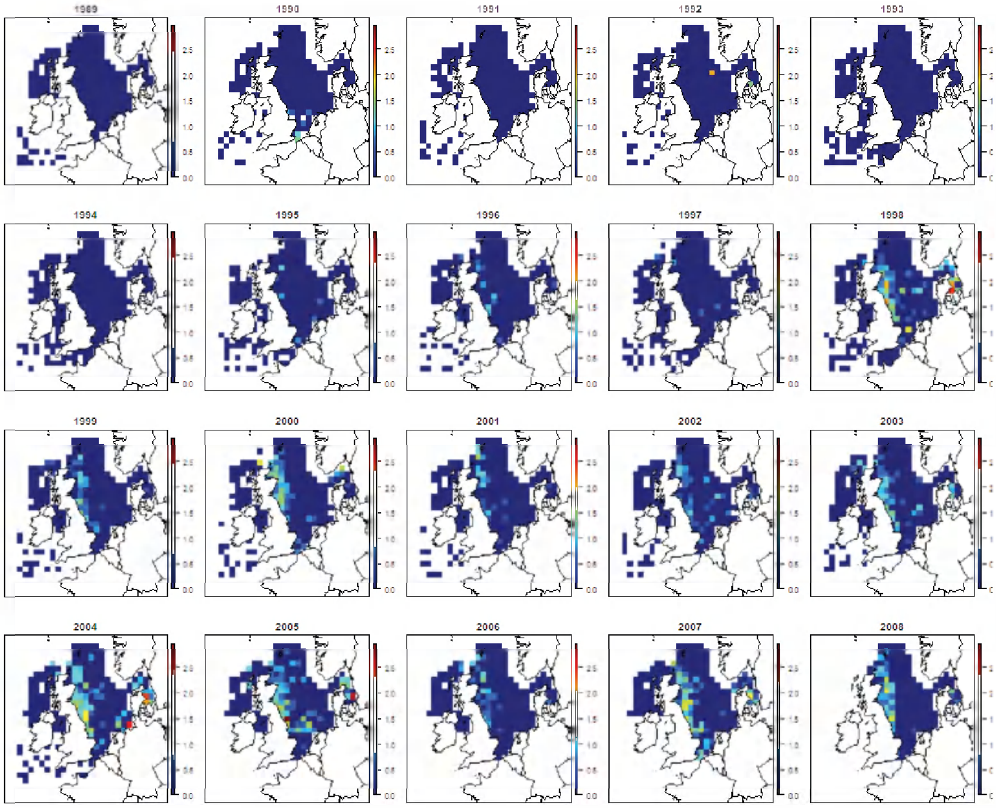


Figure 18.2. Long-term changes in red mullet distribution during winter (Quarter 1) between 1989 and 2008. Colours indicate log (numbers caught h^{-1}) by rectangle, as observed in the North Sea International Bottom Trawl Survey (1989–2008), in surveys west of Scotland by Fisheries Research Services, Aberdeen (1989–2007), and south and west of England and Wales by Cefas, Lowestoft (1989–2004).

18.5 Observed changes in distribution

There are indications that red mullet have undergone a northward distribution shift in recent years. The species was not included in the study by Perry *et al.* (2005) on distribution shifts of North Sea fish. However, Beare *et al.* (2004) demonstrated that red mullet is one of several species with southern biogeographic affinities that have recently become significantly more prevalent in North Sea International Bottom Trawl Surveys (combined FRS and IBTS databases). For example, within Division IVb, it has increased from near absence during surveys between 1925 and 1990 to ca. 0.1–4 fish h^{-1} between 1994 and 2004 (Figure 4c in Beare *et al.*, 2004, 2005).

Within the North Sea, seasonal differences in distribution have been noted in red mullet, as well as in several other "southern" species that have recently become more apparent (Figures 18.2 and 18.3). During summer (Quarter 3) surveys, red mullet have been mainly observed in the warmer, shallower waters of the southeastern North Sea, from Belgium to the German Bight (Beare *et al.*, 2004; Figure 18.3). In contrast, during winter (Quarter 1) surveys, they have been mainly observed to the northeast of the British Isles (Figure 18.2); in fact, all red mullet caught during FRS surveys off Scotland have been taken in Quarter 1, despite extensive sampling in Quarter 3 (Beare *et al.*, 2005). It has been postulated that the red mullet observed in the northern North Sea are part of an increasing southern North Sea population that migrates northwards in winter, when water temperatures in the south are higher (Beare *et al.*, 2005). Moreover, the southern North Sea may well have been colonized from the eastern English Channel during the first and second quarters of the year, with nursery areas being established by autumn (Mahé *et al.*, 2005).

Archaeological excavations have revealed that increased presence of red mullet in the North Sea is not an entirely new phenomenon. Bones of this and some other warm-water species, recovered from excavations in Denmark and England, date from Roman and medieval times (Enghoff, 2000; Barrett *et al.*, 2004), indicating that, during previous, historical, warm climatic periods, the species has been more widespread in northern Europe.

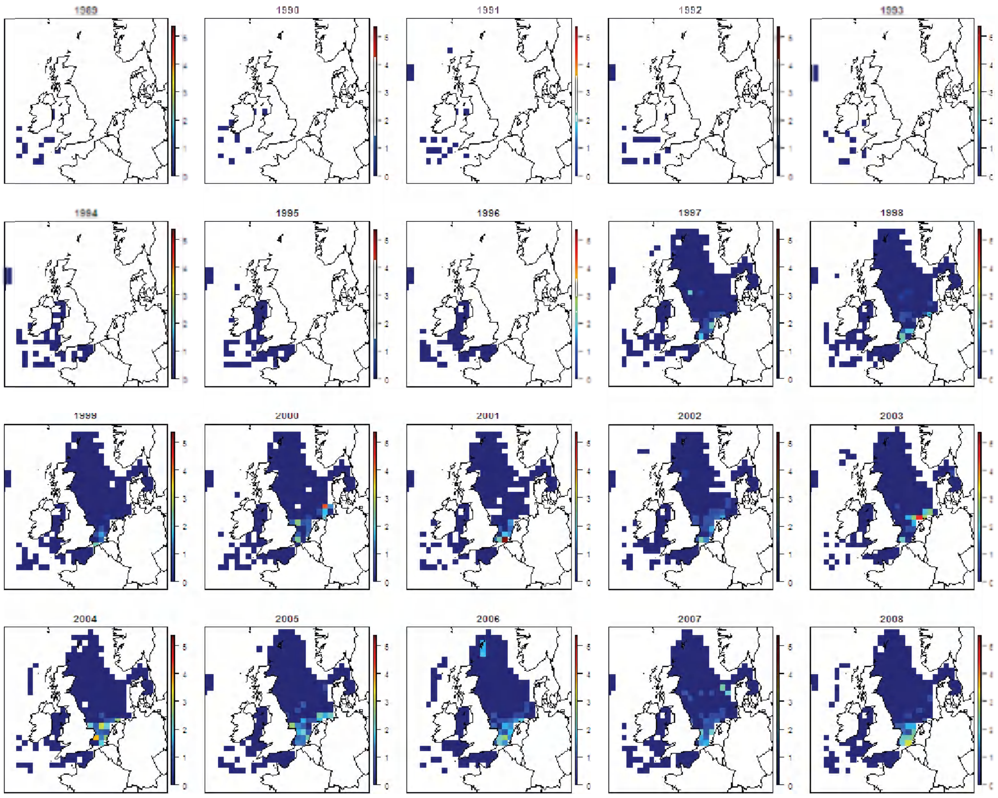


Figure 18.3. Long-term changes in red mullet distribution during summer (Quarter 3) between 1989 and 2008. Colours indicate log (numbers caught h^{-}) by rectangle, as observed in the North Sea International Bottom Trawl Survey (1997–2008), in surveys west of Scotland by Fisheries Research Services, Aberdeen (1991–2008), and south and west of England and Wales by Cefas, Lowestoft (1989–2008).

18.6 Processes underlying observed changes

Given the warm-water affinities of the red mullet, the very marked increase in landings of this species in recent years might be partly explained by a northward distribution shift or increased abundance in northern parts of the distribution range. For the North Sea, this possibility appears to be confirmed by the long-term study of Beare *et al.* (2004, see Section 18.5). For the eastern English Channel, survey catch per unit of effort (cpue) from 1988 to 2006 demonstrated large fluctuations and, although indicative that the year 2003 constituted the best recruitment, did not show a clearly increasing trend (ICES, 2007d).

In the English Channel, the red mullet has been an important bycatch species for many years. From 1980 to 1985, the UK price at first sale was ca. £2.40 kg^{-1}, but since 1986, red mullet has fetched in excess of £4 kg^{-1} (Dunn, 1999). Hence, more-targeted fishing in recent years may have contributed significantly to the increased landings. Also, red mullet are probably no longer being discarded by either the English (Dunn, 1999) or the French (ICES, 2007d) trawl fleets. Furthermore, restrictions in the quotas of other species might have redirected fishing effort towards this species (Dunn, 1999). In many aspects, these changes are similar to those in John dory (*Zeus faber*), where significantly increased landings and (to a lesser extent) redirected fishing effort have also occurred in response to northward distribution shifts (see Section 19).

18.7 Conclusion on climate effects

The red mullet is a highly relevant case study in the context of climate change and fishery management because of: (i) the high market value of this non-quota species and its potentially increasing presence in northern parts of its distribution range in response to warming climate; and (ii) the likelihood of a more targeted fishery for the species in future. It is noteworthy that this species has a relatively high growth rate and a planktonic egg life-phase, which may make it more capable of rapidly responding to climate warming by colonizing new habitats. The availability of historical data for the species will allow analyses of longer-term datasets to be undertaken, which could shed light on the extent to which northward range expansions of red mullet are a phenomenon common to warmer periods or specific to the significant warming that is currently taking place.

19 John dory

Georg H. Engelhard, Jim R. Ellis, Doug J. Beare, and John K. Pinnegar

19.1 Introduction

This section gives an overview of the general biology and ecology of the John dory (*Zeus faber*; order Zeiformes, family Zeidae) and reviews the evidence for changes in distribution and production, and their relationship with climate change.

19.2 General biology

The John dory is a distinctive fish with a very deep, laterally compressed body, a large head, and highly protrusible jaws. It has 9–11 long dorsal spines, which, in older fish, may have very long filaments attached (Miller and Loates, 1997). On each side of the body, which is yellow-brown to grey, a large black spot is visible, which has led to its vernacular name "St Peter's fish".

In the eastern Atlantic, the John dory is distributed from Norway to South Africa and also in the Mediterranean and Black seas (Karrer and Post, 1990). The species is also widely distributed in the western Pacific (from Japan and Korea to Australia and New Zealand) and is known from the Indian Ocean, although populations outside the Atlantic have previously been regarded as separate species. Within the Northeast Atlantic, the John dory is regarded as a Lusitanian species, i.e. of a southern biogeographic affinity (Ellis *et al.*, this volume), and even within the eastern Mediterranean, the species is associated with warmer water temperatures (Maravelias *et al.*, 2007).

John dory are found close to the seabed at depths of 5–400 m and are generally solitary. They feed mainly on schooling bony fish, cephalopods, and crustaceans (Bianchi *et al.*, 1993). Ontogenetic shifts in their diets have been reported off Portugal and northwest Spain, where younger John dory preyed primarily on invertebrates, with larger individuals consuming more fish, including pelagic teleosts (Velasco and Olaso, 1998; Silva, 1999). As a slow-swimming fish, John dory usually stalk their prey and suck it in by the sudden protrusion of the mouth (Miller and Loates, 1997).

Reproduction takes place at the end of winter and at the start of spring in the Northeast Atlantic, but earlier in the Mediterranean. The eggs are pelagic, and maturity is reached ca. age 4 (FishBase, 2007). The fish are sexually dimorphic; in the English Channel, mean length-at-maturity was estimated at 26 cm for males and 34.5 cm for females (Dunn, 2001).

19.3 Fisheries

John dory is highly regarded as a food fish and is of commercial importance because of its high price in fish markets. Although traditionally not targeted in fisheries, this species is an important bycatch in various trawl fisheries of the Northeast Atlantic. In recent years, motivated partly by increased abundance of this high-value, non-quota species, some fishing vessels in the southwest UK have modified nets (e.g. increased headline height) to maximize catches of John dory. Despite its high price, very little research on the fishery has been done, although Dunn (2001) described the exploitation of John dory around England and Wales.

In terms of John dory landings from the Northeast Atlantic, France and Spain are the most important countries, landing on average 43% and 29%, respectively, of the total nominal catch between 2000 and 2005. The remaining nominal catches were landed by Portugal (11%), the UK (9%), and Ireland (8%).

Within the Northeast Atlantic, by far the most important fishing region is Subarea VII, where approximately 68% of the catch is taken (mainly in Divisions VIIe and VIIh). Relatively large fractions of the total catch of dory are also taken from the Bay of Biscay (Subarea VIII: 10%) and the Spanish and Portuguese coasts (Subarea IX: 20%). Few dories are landed from northern subareas, including the North Sea (Subarea IV: 0.2%), west of Scotland (Subarea VI: 1.4%), and off the Azores (Subarea X: 0.4%).

19.4 Observed changes in production

Between 1978 and 2005, international landings of Northeast Atlantic John dory have quadrupled: from <1000 t in 1978 to ca. 4000 t in 2005 (Figure 19.1a; ICES Fisheries Statistics). This increase in landings appears to have occurred in at least four of the five countries that regularly land John dory (with the possible exception of Portugal; see Figure 19.1). In relative terms, the increases in landings appear more marked for the "northern" countries (fivefold for the UK and 300-fold for Ireland between the early 1980s and 2000s) than for the "southern" countries (e.g. 2.7-fold for France and 1.3-fold for Portugal). Earlier (pre-1983) data were lacking for Spain, and pre-1978 data were lacking for France.

Furthermore, increases in landings have occurred in each of the major subareas where John dory are caught (Figure 19.1b). Throughout the period, Subarea VII has maintained the highest catches of John dory.

For the UK, Dunn (2001) examined trends in both quantities and values of the landings in more detail. Since 1980, the importance of exploitation of John dory within the UK has risen sharply. Not only have total landings increased from 46 t in 1980 to 148 t in 1997, after a peak of 287 t in 1995 (Dunn, 2001), but the price has increased sharply, from £1.59 kg^{-1} in 1980 to £4.68 kg^{-1} in 1997 (Dunn, 2001), and to £4.96 kg^{-1} in 2001 (Parker-Humphreys, 2004). Hence, the total value of annual landings rose approximately tenfold from approximately £70 000 in 1980 to more than £1 million in 1995, and to ca. £690 000 in 1997 (Dunn, 2001). The relative importance of John dory compared with other species has also increased (Dunn, 2001); from the mid-1980s to the mid-1990s, the value of total demersal fish landed in England and Wales increased 1.5-fold, while that of John dory increased more than sixfold. After Dunn's (2001) study, UK landings of John dory have somewhat stabilized and remained at high levels (>270 t year^{-1}; Figure 19.1a). To some extent, this has been the result of small, but increasing, quantities being landed in Scotland (e.g. 66 t in 2005).

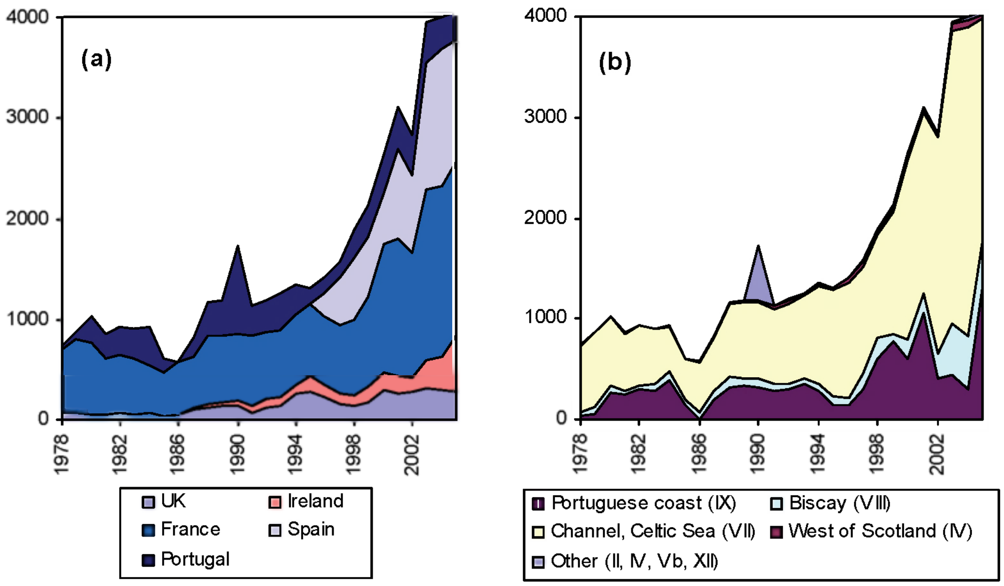


Figure 19.1. Northeast Atlantic John dory: trends in total landings (a) by country of landing, and (b) by fishing region (in t). Early French (pre-1978) and Spanish (pre-1984) landings data possibly incomplete. (Data from ICES Fisheries Statistics.)

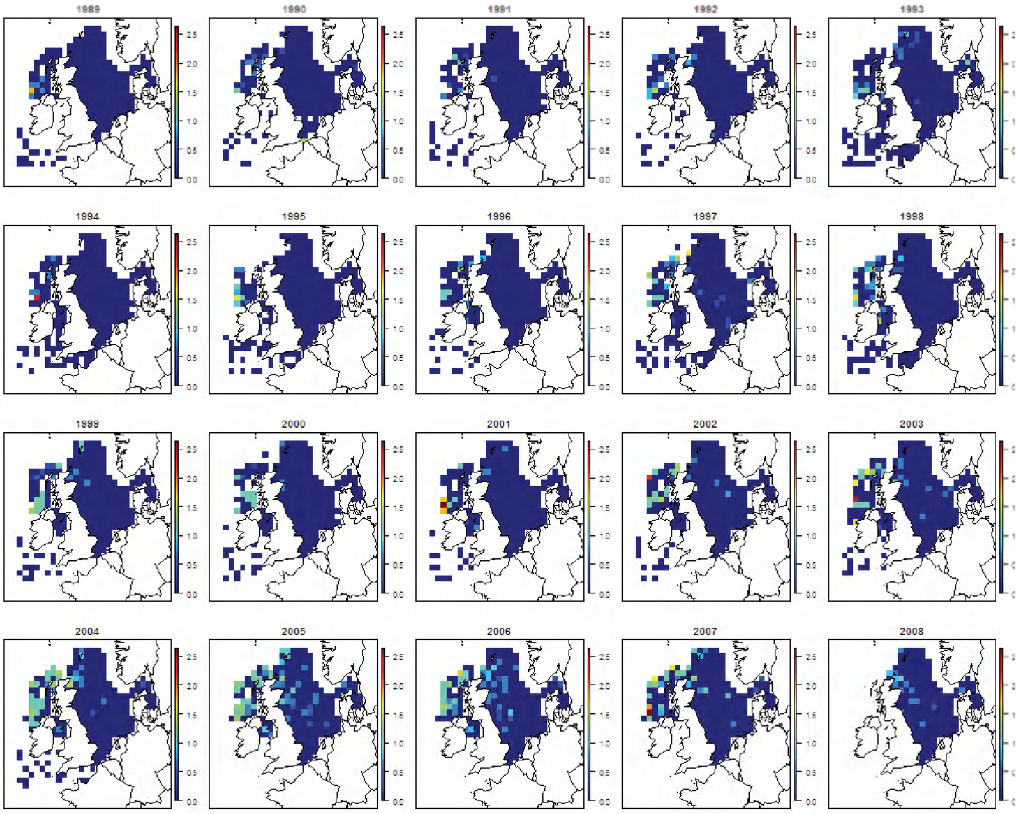


Figure 19.2. Long-term changes in John dory distribution during winter (Quarter 1) between 1989 and 2008. Colours indicate log (numbers caught h^{-1}) by rectangle, as observed in the North Sea International Bottom Trawl Survey (1989–2008), in surveys west of Scotland by Fisheries Research Services, Aberdeen (1989–2007), and south and west of England and Wales by Cefas, Lowestoft (1989–2004).

19.5 Observed changes in distribution

Heessen (1996) analysed time-series data from North Sea International Bottom Trawl Surveys (IBTS) for the period 1970–1993 and reported that John dory was among four "southern" species that demonstrated a remarkable increase in the southern North Sea from the late 1980s until the end of the period examined (1993). In a more recent study, Beare *et al.* (2004) analysed a longer time-series (1925–2004; combined IBTS and Scottish FRS survey data) and confirmed that the John dory is among a number of "southern" species whose abundance in the North Sea increased markedly from the 1990s to the early 2000s. (In addition, John dory demonstrated a smaller peak in the mid-1950s.)

Although Beare *et al.* (2004) reported that John dory were only observed in the far northern parts of the North Sea in both winter and summer, increased abundance in the southern North Sea, coinciding with its northern prevalence, was described by Heessen (1996). We have extended the time-series of Beare *et al.* (2004) on John dory distribution (Figures 19.2 and 19.3), confirming significantly increased abundance from the 1990s to 2000s, but also revealing wide seasonal distribution differences, akin to those observed in red mullet (Beare *et al.*, 2005; Engelhard *et al.*, this volume). In winter (Quarter 1; Figure 19.2), John dory were far more widespread than during summer (Quarter 3; Figure 19.3), both in the North Sea and west of Scotland. It appears that the species enters the North Sea through both the northwestern influx of Atlantic Water and (possibly to a lesser extent) the influx of warmer waters from the English Channel.

ICES (2006n) examined the temporal changes in the spatial distribution of John dory in international groundfish surveys (Figure 19.4), which suggested that catches of John dory in fishery-independent surveys had increased, especially along the southwest and west coasts of the British Isles and along the west coast of France.

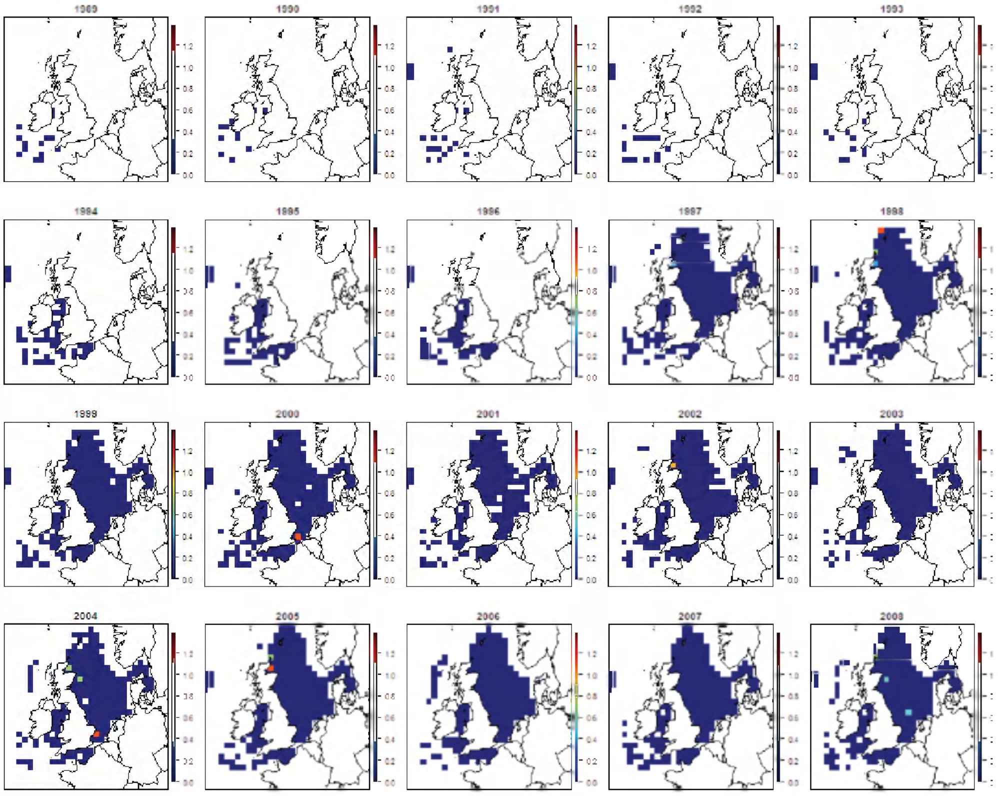


Figure 19.3. Long-term changes in John dory distribution during summer (Quarter 3) between 1989 and 2008. Colours indicate log (numbers caught h^{-1}) by rectangle, as observed in the North Sea International Bottom Trawl Survey (1997–2008), in surveys west of Scotland by Fisheries Research Services, Aberdeen (1991–2008), and south and west of England and Wales by Cefas, Lowestoft (1989–2008).

19.6 Processes underlying observed changes

The major increases in John dory landings in western Europe may well be explained by a combination of climatic warming and factors directly related to the fisheries. To our knowledge, there are no time-series on growth, recruitment, or mortality changes for the species. Given that this is a "southern" species, with warm-water affinities, a northward distribution shift or increased abundance in northern parts of the distribution range is to be expected in response to climate change. Indeed, the dramatic increase in John dory landings in the 1990s started when the NAO index began its increase and sea temperatures underwent a general rise (Ottersen *et al.*, 2001; Hughes *et al.*, 2009). Similar patterns have also been suggested for related species in the Bay of Biscay and Celtic Sea regions, including sailfin dory (*Zenopsis conchifer*; Quigley and Flannery, 1995; Quéro, 1998) and boarfish (*Capros aper*; Blanchard and Vandermeirsch, 2005).

As was the case for red mullet (*Mullus surmuletus*; Engelhard *et al.*, this volume), this possibility appears to be confirmed for the North Sea by analyses of long-term survey data (Heessen, 1996; Beare *et al.*, 2004); no such analyses could be identified for other fishing regions. John dory is likely to have become increasingly prevalent in the North Sea as a result of increased influx of warm Atlantic Water via both the northwest (north of Scotland; Beare *et al.*, 2004) and the southwest (English Channel; Corten and van de Kamp, 1996; Heessen, 1996). According to Corten and van de Kamp (1996), their increase, at least in the southern North Sea, does not reflect a long-term trend, but may be explained by temporary increases in southerly winds, resulting in increased transport of southern fish species into the North Sea, and favourable temperature conditions during winter.

At the same time, changes within the demersal fisheries may have contributed to sharply increased landings. The strong increase in market price and its status as a non-quota species may have made the John dory increasingly attractive and, to some extent, may have led to more targeted fishing. Furthermore, recent declines in various "traditional" fish stocks, such as cod (*Gadus morhua*), sole (*Solea solea*), and plaice (*Pleuronectes platessa*), have led to very restrictive catch limits (total allowable catches, or TACs) for these species. As a result, fishing effort is likely to have been increasingly redirected towards species with no such restrictions, such as John dory (Dunn, 2001).

19.7 Conclusion on climate effects

The John dory presents a highly relevant case study in the context of climate change for reasons comparable with the red mullet: the likelihood of increasing northern presence in response to climatic warming, high market value, and, especially given less fishing opportunities for other species, probably more targeted fisheries and increasing potential importance to the economy in the near future.

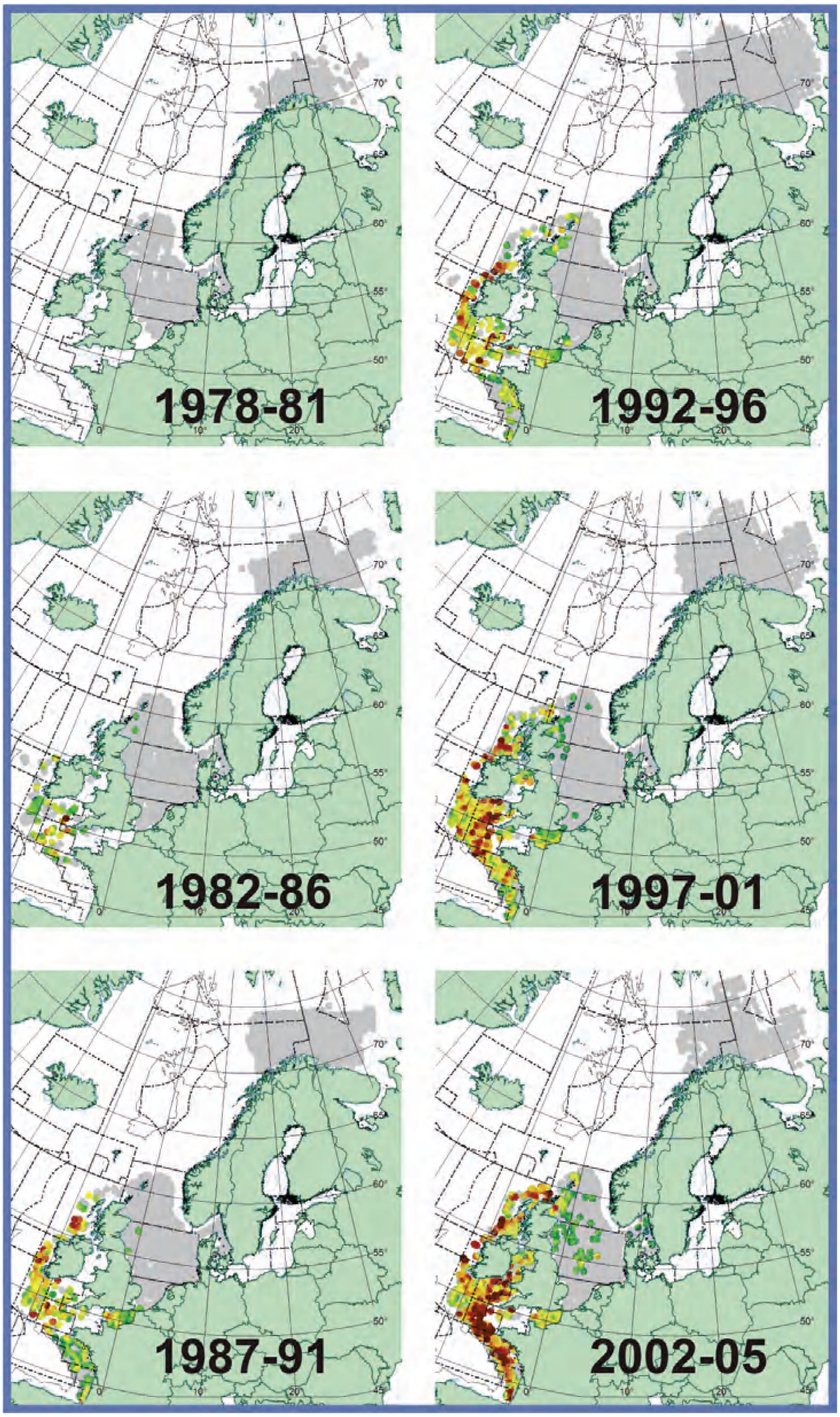


Figure 19.4. Distribution of John dory during six periods using combined international demersal surveys. Surveyed area (shaded grey) and increasing catch rates (colour-coded from green to yellow to red). (From ICES, 2006n.)

20 Plaice

Adriaan D. Rijnsdorp and Henk W. van der Veer

20.1 Introduction

This section reviews knowledge of the plaice (*Pleuronectes platessa*; order Pleuronectiformes, family Pleuronectidae), with particular reference to the effects of climate change. It starts with an overview of the general biology and ecology, which are relevant to understanding the possible impact of climate change, and then reviews the evidence for changes in distribution and production in relation to climate.

20.2 General biology

The plaice is a Boreal species that is distributed in the temperate waters of the eastern Atlantic between the Bay of Biscay in the south and the Barents Sea in the north and between the western Baltic in the east and Iceland in the west (Wimpenny, 1953).

The life cycle of the plaice begins with the developing pelagic eggs and larvae, which drift passively until they arrive in the coastal zone, where the larvae metamorphose, aggregate, and settle in so-called "nursery" grounds. These consist of shallow sandy bays, larger sandy beaches, and estuarine areas. After a juvenile stage of a few years, they migrate to deeper waters, where they join the adult stock and start to reproduce.

The spawning grounds of plaice reflect the distribution of the shallow nursery grounds in the sandy bays, larger sandy beaches, and estuarine areas. In areas with isolated nursery grounds, spawning may take place in coastal waters and bays, where circular current systems (eddies) entrain the pelagic eggs and larvae. In the English Channel and southern North Sea, spawning occurs over a large offshore area, from whence the eggs and larvae drift on currents towards the extensive nursery grounds along the continental coasts of Belgium, the Netherlands, Germany, and Denmark.

Size classes demonstrate distinct distributions. Small juveniles occur in shallow coastal waters and estuaries, but, as they grow, the fish gradually move offshore. Adult fish are restricted to deeper water. In the North Sea, spawning/feeding migrations occur along a north–south axis. The distances travelled increase with fish size (Rijnsdorp and Pastoors, 1995; Hunter *et al.*, 2003, 2004). Tagging experiments have distinguished several spawning populations that mix during the summer feeding season and separate during spawning (de Veen, 1978a). Despite the occurrence of separate subpopulations of plaice within the geographic distribution area, analysis of microsatellite data revealed no significant distinction among populations along the continental coast between the Bay of Biscay in the south and the Lofoten area in the north. Only plaice from the Faroes and Iceland demonstrated a small but significantly different pattern (Hoarau *et al.*, 2002, 2004).

Spawning occurs from December to March in the English Channel and southern North Sea (Houghton and Harding, 1976; Harding *et al.*, 1978) and around March in the Irish Sea and Iceland (Simpson, 1959; Fox *et al.*, 2000a; Solmundsson *et al.*, 2003). Eggs occur in water with a temperature between 4°C and 11°C (Harding *et al.*, 1978; Heessen and Rijnsdorp, 1989; Fox *et al.*, 2000a). In the North Sea, larval plaice may immigrate to coastal waters and settle on tidal flats as early as late February, when water temperatures are close to the seasonal minimum of 2–4°C.

The temperature tolerance range of eggs is 0–14 °C, with a mean temperature of 7 °C (Johansen and Krogh, 1914). The temperature tolerance range of age-0 plaice is 2–20 °C. Egg development to the end of stage V is inversely related to prevailing water temperature and ranges from ca. 1 d at 3 °C to ca. 9 d at 12 °C (Ryland *et al*., 1975; Fox *et al*., 2003). Larval development from hatching until settlement varies from ca. 168 d at 2°C to 36 d at 10 °C (Talbot, 1977). No information is available on the impact of salinity and low oxygen conditions on larval development. Growth rate of age-0 plaice increases from a minimum of 0.01 mm d^{-1} at 2 °C to a maximum of 0.8 mm d^{-1} at ca. 18–20 °C, but growth rate decreases at higher temperatures (Fonds *et al*., 1992). Upper lethal temperature is in the order of 26–27 °C (Waede, 1954). The optimum temperature for growth decreases with body size, which may explain the ontogenetic shift in distribution.

Successful fertilization is variable and low at salinities <12 psu, increasing to almost 100% at 15 psu (Nissling *et al*., 2002). A minimum salinity of ca. 15 psu is required for eggs to remain neutrally buoyant in the plankton. Juvenile plaice can be found over a salinity range of 15–35 psu (Riley *et al*., 1981; Jager *et al*., 1993). Oxygen conditions are critical below a level of 1.69 mg l^{-1} (LD_{50}) for newly metamorphosed plaice (de Silva and Tytler, 1973).

20.3 Fisheries

Most of the plaice landings occur in the North Sea and adjacent eastern English Channel and Skagerrak (Figure 20.1), where they are taken as a bycatch in the mixed demersal trawl fisheries. Major plaice landing countries are the Netherlands, UK, and Denmark.

In the North Sea, plaice has been exploited heavily since the late 19th century (Bannister, 1978; Rijnsdorp and Millner, 1996). Since the 1960s, plaice has been mainly landed by the beam-trawl fishery targeting sole (*Solea solea*) with small-mesh (80 mm) codends. As a result, large numbers of undersized plaice are caught and discarded (Pastoors *et al*., 2000). The survival chances of the discards are very low (van Beek *et al*., 1990). Large numbers of small plaice are also killed in coastal fisheries for brown shrimp (*Crangon crangon*; Rauck and Zijlstra, 1978; Berghahn *et al*., 1992). Although the introduction of separating panels and sorting equipment will certainly have reduced the negative impact on the recruitment of plaice (Boddeke, 1980), no quantitative information is available.

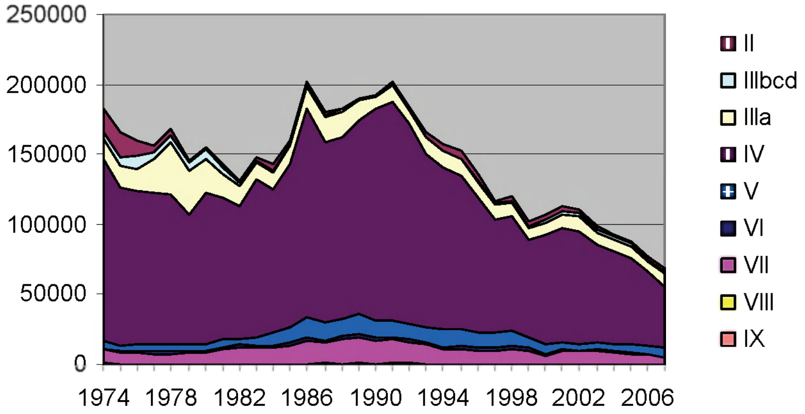


Figure 20.1. Trends in plaice landings (in t) by management area (ICES areas). II = Barents Sea; IIIb, c, and d = Baltic; IIIa = Skagerrak; IV = North Sea; V = Iceland; VI = northwest of Scotland; VII = Celtic Sea and English Channel; VIII = Bay of Biscay; and IX = Portugal.

20.4 Observed changes in production

Landings in the North Sea (Subarea IV) and adjacent areas were relatively high in the 1980s, but have since decreased (Figure 20.1). Landings in the southern part of the distribution area have decreased since the late 1980s (Figure 20.2, left panel). Landings around Iceland (Subarea V) demonstrated a similar pattern, with a rich period in the 1980s, as in the North Sea, whereas landings in the Barents Sea varied without a trend (Figure 20.2, right panel).

For the North Sea, trends in landings can be analysed over a longer time-scale (Figure 20.3). Until the 1950s, annual landings varied around 50 000 t, with the exception of the war years (late 1930s to mid-1940s). In the 1950s, landings steadily increased to a level of ca. 150 000 t, three times higher than the average level in the first half of the 20th century. Since 1990, landings have decreased to the level of the pre-war years.

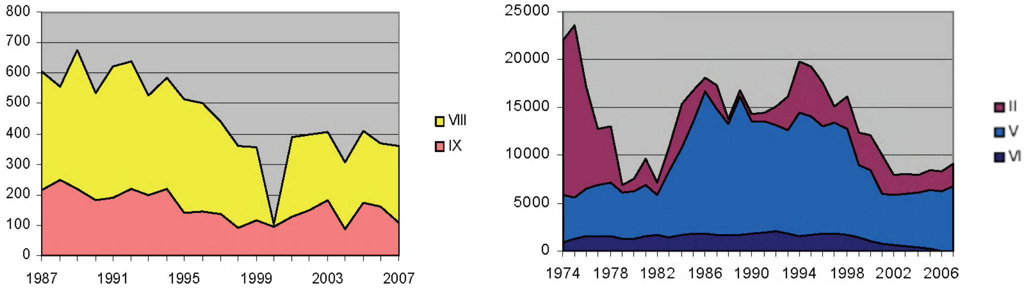


Figure 20.2. Trends in landings of plaice in ICES Subareas. Left panel: southern areas (VIII = Bay of Biscay; IX = off Portugal. Right panel: northern areas (II = Barents Sea; V = Iceland and Faroe; VI = West of Scotland).

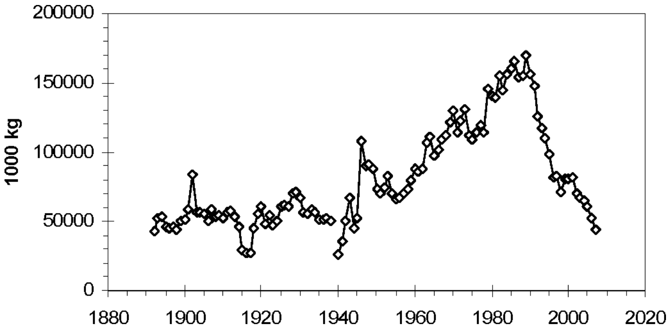


Figure 20.3. Trends in plaice landings from the North Sea. (From Rijnsdorp and Millner, 1996; ICES, 2006l.)

20.5 Observed changes in distribution

Although spawning locations in the eastern English Channel and southern North Sea demonstrate a remarkable stability over several decades, the number of eggs produced has varied among spawning locations (Harding *et al.*, 1978). Since the mid-1950s, egg production has been higher in the German Bight (Bückmann, 1961; Heessen and Rijnsdorp, 1989) and the western English Channel (Harding *et al.*, 1978), reflecting a relative increase in the local spawning population.

Beam-trawl survey data indicate that the catch rate has declined in the 1990s in the southern North Sea, but not in the central North Sea. Anecdotal information suggests an increase in the catch rate of the substock in the Moray Firth. No change in mean latitude was observed in the English groundfish survey data between 1977 and 2001, although an increase in mean depth was observed (Perry *et al.*, 2005). However, the abundance of prerecruits has declined with increasing temperatures in the Bay of

Biscay nurseries (Désaunay *et al.*, 2006). A shift in the depth distribution of young plaice was reported for the 1990s, whereas a shift to deeper waters of larger plaice (20–39 cm) was already apparent before the 1980s (van Keeken *et al.*, 2007). The change in distribution is illustrated in Figure 20.4, which compares the typical age-1 distribution patterns of the period before 1990 (left panel) and in the early 2000s (right panel).

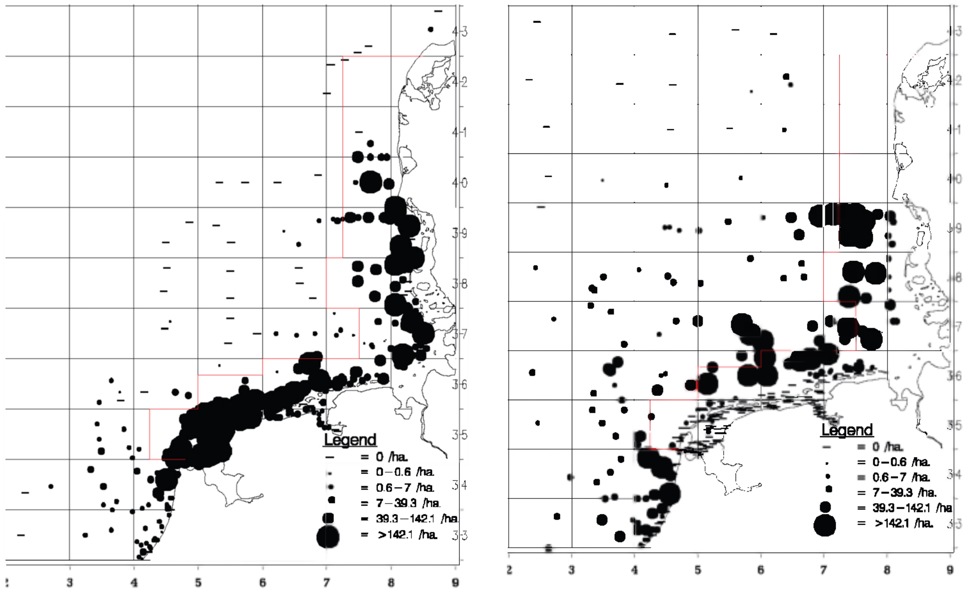


Figure 20.4. Changes in the September distribution of age-1 plaice in the prerecruit surveys of IMARES between 1990 (left panel) and 2002 (right panel). Note that all age-1 plaice have left the Wadden Sea. (From Grift *et al.*, 2004.)

20.6 Processes underlying changes

20.6.1 Productivity

Changes in productivity may be the result of changes in recruitment and/or growth. The threefold increase in landings in the North Sea was governed by an increase in both recruitment and growth rate (Rijnsdorp and Millner, 1996). Rijnsdorp and van Leeuwen (1996) suggested that the increase in growth rate of size classes up to 35 cm during the 1960s and 1970s was probably the result of the increase in productivity of the benthic system in response to increased nutrient loading (Rachor, 1990; Beukema *et al.*, 2002) and seabed disturbance (Rijnsdorp and van Beek, 1991). However, the effect of trawling on benthic productivity remains controversial (Jennings *et al.*, 2001a, 2002b; Hiddink *et al.*, 2006b, 2008b). On top of the general increase, a temporary density-dependent reduction in growth rate was observed in year classes that were exceptionally strong (Rijnsdorp and van Leeuwen, 1996).

Since the late 1980s, growth rate has declined in several plaice and sole stocks (Millner *et al.*, 1996), and may be related to a decline in productivity of the benthic system (Rijnsdorp *et al.*, 2004). No study has yet attempted to analyse the observed changes in relation to variations in ocean climate, river discharges, and food requirements of the benthivorous fish. A decrease in benthic productivity of coastal waters may be expected in response to the decrease in nutrient discharges (dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP): Boddeke and Hagel, 1995; Philippart *et al.*, 2007b). Growth of age-0 plaice is affected by temperature during the growing season. The effect is positive in the first few months after settlement but may become negative during warm summers, when temperature may increase above the optimum level (Teal *et al.*, 2008; van Keeken *et al.*, 2007). No relationship between temperature and the growth rate of larger size classes could be found, although this may be attributed to the lack of any accurate estimate of ambient temperature (Rijnsdorp and van Leeuwen, 1996). The onset of sexual maturity is affected positively by both growth rate and temperature (Rijnsdorp, 1993a).

20.6.2 Recruitment

Recruitment variations are mainly driven by variations in mortality during the pelagic egg and larval stage, as age-0 numbers in autumn are already significantly related to the strength of the year class recruiting to the fishery (van der Veer *et al.*, 2000). In the North Sea, egg mortality increases with temperature (van der Land, 1991) and year-class strength is negatively related to water temperature during the spawning period (van der Veer and Witte, 1999; van der Veer *et al.*, 2000). The number of settling plaice larvae at the Balgzand intertidal was negatively related to median temperature during larval drift, both within and across years (van der Veer *et al.*, 2009).

The higher survival during colder winters is probably related to the temperature sensitivity of predators, which respond more strongly to a decrease in temperature than developing eggs and larvae (van der Veer *et al.*, 2009). This may apply to predation during the pelagic phase as well as predation during the early demersal stage. During the first weeks after settlement, post-larval plaice suffer high predation mortality from shrimp (van der Veer *et al.*, 1990). After a cold winter, the shrimp delay their return to the tidal flats (Boddeke, 1976; Beukema and Dekker, 2005), enhancing the survival probability of age-0 plaice. Temperature may also affect the transport of the pelagic egg and larval stages and, hence, influence larval supply to the coastal nursery grounds (van der Veer *et al.*, 1998; Bolle *et al.*, 2009).

Recruitment of plaice is positively correlated among different stocks and negatively correlated with sea surface temperature, which is consistent with the hypothesis that the temperature effect is caused by changes in predation on planktonic stages (Fox *et al.*, 2000b). There is no evidence that the recruitment–temperature relationship differs between stocks in the southern and northern parts of the distribution area, although data for the most northern (Barents Sea) and southern stocks (Bay of Biscay) are lacking. Recruitment time-series demonstrate a favourable period in the mid-1980s and a less favourable period in the 1990s (Figure 20.5). No trends in recruitment are evident, except perhaps for a decreasing trend in the Irish Sea (Division VIIa). It should be noted that analyses of recruitment time-series estimated from commercial landings may underestimate true recruitment because discards are not included in the analysis. Only in North Sea plaice did the analysis include discards.

The timing of spawning is slightly advanced in warm winters (Rijnsdorp and Witthames, 2005; Teal *et al.*, 2008). Differences in transport have been observed between cold years, when atmospheric conditions were characterized by predominantly easterly winds, and normal years, when westerly winds were dominant (Talbot, 1978). Hydrodynamic models suggest that there may be large variations in the transport of pelagic stages from offshore spawning grounds to inshore nursery grounds (van der Veer *et al.*, 1998; Bolle *et al.*, 2009). Survival of age-0 plaice may be affected by UV-B radiation during the period when they inhabit tidal pools (Berghahn *et al.*, 1993).

20.6.3 Distribution

The change in depth distribution of plaice, as reported by Perry *et al.* (2005) and van Keeken *et al.* (2007), is probably related to the observed increase in water temperature. Experimental work demonstrated that, at temperatures above 20 °C, growth rate declines abruptly, possibly as a result of thermally limited oxygen delivery, as demonstrated in eelpout (*Zoarces viviparus*; Pörtner and Knust, 2007). The exodus of age-0 plaice from the tidal flats on days when temperature increases above 27 °C (Berghahn, 1984) is consistent with an avoidance response when temperature exceeds the thermal maximum (Waede, 1954). There is evidence that plaice suffer from a greater mortality rate in cold winters, when seabed water temperatures decrease to values around 1–3 °C (Woodhead, 1964b, 1964c).

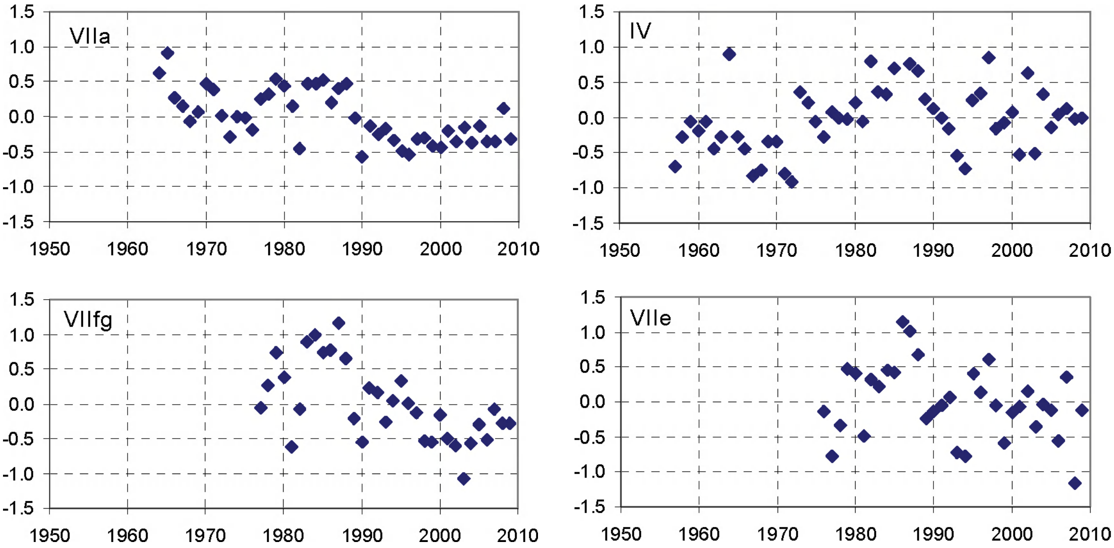


Figure 20.5. Normalized time-trends in age-1 recruitment in different plaice stocks (ICES areas): VIIa = Irish Sea; VIIf and g = Celtic Sea; IV = North Sea; and VIIe = western English Channel.

20.7 Conclusions

Climate change is expected to have negative effects on the quality of the shallow nursery grounds in the southern parts of the distribution range of plaice, where summer water temperatures may exceed temperature tolerance limits. Although plaice may respond by moving into deeper and cooler waters, this may negatively affect their survival, as they are likely to be exposed to higher levels of predation and fishing mortality. As nursery grounds appear to be of crucial importance in plaice production, a further decrease in productivity of the southern populations may be expected. How climate change may affect survival of the pelagic stages and transport between spawning areas and nursery grounds remains to be studied. The response of plaice will further depend on the impact of climate change on the productivity of benthic food.

21 Sole

Adriaan D. Rijnsdorp

21.1 Introduction

This section reviews knowledge of the common sole (*Solea solea*; order Pleuronectiformes, family Soleidae), with particular reference to the effects of climate change. It starts with an overview of the general biology and ecology, which are relevant to understanding the possible impact of climate change, and then reviews the evidence for changes in distribution and production in relation to climate.

21.2 General biology

The sole is a Lusitanian species (Ellis *et al.*, this volume, Section 2) with a distribution area that extends from the northwest African coast and the Mediterranean in the south to the Irish Sea, southern and south-central North Sea, Skagerrak, and Kattegat in the north. Sole occur in small numbers around Scotland and Ireland and occasionally along the south coast of Norway (Wheeler, 1969; Whitehead *et al.*, 1984–1986).

The temperature tolerance of sole was found to increase during the embryonic and larval stages (Irvin, 1974; Fonds, 1979). Embryonic stages were notably stenothermal in relation to the generally eurythermal larval stages, although tolerance continued to increase during larval development up to the period of metamorphosis. Successful full-term incubation of Stage 1A eggs was predictable between 7°C and 16°C, but successful first feeding of larvae hatched from these eggs was only obtained over a narrower range of 12–16°C. For Stage 5 larvae, the absolute tolerance range was 20–23°C (Irvin, 1974; Fonds, 1979). For age-0 juveniles, growth rate was almost zero at 6°C and increased to a maximum at ca. 25°C (Fonds and Saksena, 1977). For adult sole, the minimum temperature was ca. 3°C. When sole were exposed to temperatures below 3°C for a prolonged period, physiological functions, such as osmoregulation, were impaired and mortality increased (Woodhead, 1964b, 1964c). The salinity tolerance range of eggs was 20–40 psu (Fonds, 1979).

Sole spawn in late winter and spring. The peak in the spawning period shifts from late February or early March in the Bay of Biscay (Arbault *et al.*, 1986) to late May in the southeastern North Sea (Rijnsdorp *et al.*, 1992) and mid-May in the Irish Sea (Fox *et al.*, 2000a). In the North Sea, spawning is triggered by seawater temperature (ICES, 1965b) and the peak in egg production is advanced in a warm spring (van der Land, 1991; Greve *et al.*, 2004; Rijnsdorp and Witthames, 2005). In the Bay of Biscay and Bristol Channel, seawater temperature does not seem to affect the timing of spawning (Koutsikopoulos and Lacroix, 1992; Horwood, 1993). In most areas, spawning takes place in coastal waters, except in the western English Channel, Bristol Channel, and Bay of Biscay (ICES, 1986; Riley, 1986; van der Land, 1991; Horwood, 1993), where the main spawning activity occurs offshore (Koutsikopoulos and Lacroix, 1992). In all of the areas studied, the ambient temperature was between 9°C and 11°C for the egg phase, 10°C and 15°C for larvae (Koutsikopoulos and Lacroix, 1992; van der Land, 1991; Rijnsdorp and Vingerhoed, 1994). At these temperatures, larvae hatch after ca. 7–8 d (Riley, 1974; Fonds, 1979). Salinity of spawning areas is ca. 34.5–35.5 psu in the Bristol Channel (Horwood, 1993) and >32 psu in the Bay of Biscay (Koutsikopoulos and Lacroix, 1992). Larvae settle at the bottom during metamorphosis at a length of 7–10 mm and ca. 3 wk after hatching (Fonds, 1979). The duration of the planktonic phase is determined by the ambient temperature, but is normally ca. 4 wk. During the planktonic phase, the eggs and larvae are exposed to residual currents. As the duration of the planktonic phase is relatively short, the surviving post-larval sole usually settle close to the spawning area.

Nursery areas are confined to shallow sandy or muddy coasts, with a substratum characterized by a particle size of 400–500 µm and a depth of <20 m, although juveniles are most abundant at depths of <10 m (Deniel, 1981; Riley *et al.*, 1981; Koutsikopoulos *et al.*, 1989; van Beek *et al.*, 1989; Rogers, 1989, 1992; Marchand, 1991).

The mechanism by which the metamorphosing larvae reach their nursery areas is not well established. Marchand and Masson (1989) speculated that they carry out passive but selective movements using bottom currents to reach the coastal nursery grounds, as described for other flatfish species (Creutzberg *et al.*, 1978; Rijnsdorp *et al.*, 1985; Boehlert and Mundy, 1988). This hypothesis is supported by the observation of Berghahn (1984) that post-larval sole were heading to the ebb current in drainage gulleys of the tidal flats of the German Wadden Sea (positive rheotaxis). However, Koutsikopoulos *et al.* (1991) could find no evidence of selective tidal-stream transport in larval sole in the Bay of Biscay and suggested that they reached the coastal nursery grounds by diffusion.

Nursery grounds are believed to play a crucial role in the population dynamics of sole (Rijnsdorp *et al.*, 1992), a phenomenon that may apply to other flatfish species (Gibson, 1994; van der Veer *et al.*, 2000). The quality of the coastal nurseries may vary according to the availability of benthic food, density of predators, and negative anthropogenic impacts, such as pollution (Amara *et al.*, 2007). Sole populations may occur in areas where pelagic habitat, suitable for the survival of eggs and larvae, co-occurs with suitable nursery areas and where mechanisms are available for egg and larval transport from spawning grounds to nursery areas (Symonds and Rogers, 1995; van der Veer *et al.*, 2000).

During summer, adult sole are most abundant in waters down to a depth of ca. 40 m (North Sea) or 70 m (Bay of Biscay, Bristol Channel), with a seabed characterized by fine sediments. In the North Sea, sole are mainly found south of a line running southwest–northeast from Flamborough Head to the Danish coast. This line corresponds to a steep temperature gradient that divides the North Sea into a cold, stratified northern section in summer and autumn (with bottom temperatures of ca. 7°C) and a warm, mixed, southern section (with bottom temperatures as high as 17°C; ICES, 1965b; Rijnsdorp and van Beek, 1991). In autumn, when temperatures fall, sole leave the shallow coastal areas and migrate to the warmer offshore grounds (de Veen, 1978b).

In the North Sea, four main spawning grounds can be distinguished: those of the German Bight, Belgian–Dutch coast, Thames Estuary, and Norfolk Banks. In the English Channel, at least two separate spawning grounds occur along the UK coast, whereas along the French coast, separate spawning grounds occur in the Baie de Sommes, Baie de Seine, and Baie du Mont Saint Michel. Separate sole populations occur in the Irish Sea and Bristol Channel (Horwood, 1993; Fox *et al.*, 2000a).

Sole populations clearly differ in biological characteristics. Relative fecundity increases with latitude, whereas egg size decreases with latitude (Rijnsdorp and Vingerhoed, 1994; Witthames *et al.*, 1995). It is not known whether these differences are a reflection of local adaptations or a phenotypic plastic response to different environmental conditions. However, genetic information reveals a genetic differentiation among populations that increases with distance (Exadactylos and

Geffen, 1995; Kotoulas *et al.*, 1995). Tagging experiments of juveniles in a number of nursery areas in the English Channel and North Sea have demonstrated that each spawning population is supplied mainly by recruits from the nearby nursery ground (Rijnsdorp *et al.*, 1992). Tagging experiments in the Bay of Biscay did not show any particular link between spawning ground and nursery area (Koutsikopoulos *et al.*, 1989).

21.3 Fisheries

Sole is a valuable food fish, taken in both bottom trawls and fixed gear (gillnets, trammelnets). The species has a nocturnal activity pattern and lives close to the seabed. As its natural response to approaching gear is to dig into the seabed, the species is difficult to catch with bottom trawls. Therefore, the exploitation rate was rather low until the early 1960s, when heavy twin-beam trawling was developed in the Netherlands and Belgium, and then spread to neighbouring countries (de Veen, 1978b; Horwood, 1993; Daan, 1997). With the introduction of this gear, the exploitation rate has increased substantially. Main fishing areas for sole are in the North Sea, Celtic Sea–English Channel, and the Bay of Biscay (Figure 21.1). The main sole fishing countries are the Netherlands, Belgium, and France (Figure 21.2). Before the introduction of the beam trawl, sole was taken as bycatch in trawl fisheries and by static gear.

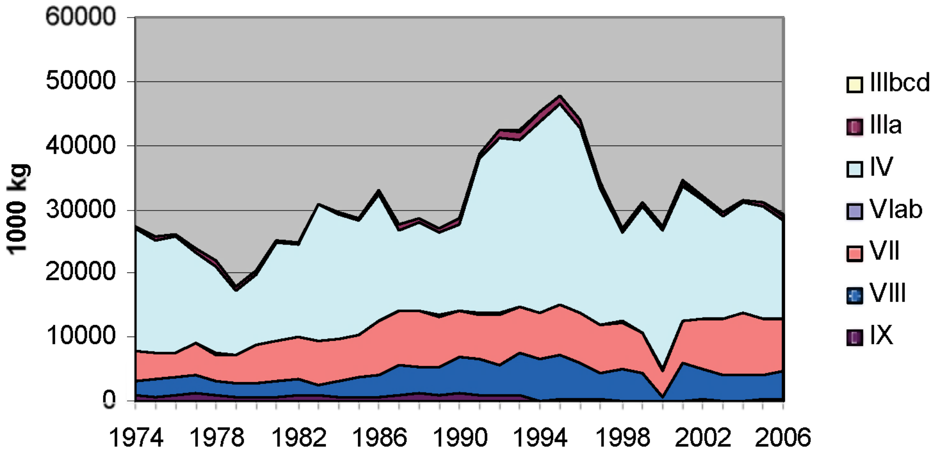


Figure 21.1. Trends in landings of sole in different management areas (ICES areas): IIIb, c, and d = Baltic; IIIa = Skagerrak–Kattegat; IV = North Sea; VIa and b = West of Scotland; VII = Celtic Sea and English Channel; VIII = Bay of Biscay; and IX = Portugal.

21.4 Observed changes in production

International annual landings demonstrated an increasing trend since 1974, from ca. 20 000 to 30 000 t. Time-series in separate areas demonstrate that North Sea (Subarea IV) landings demonstrated a temporary high level in the early 1990s (Figure 21.1). An increase in sole landings occurred in the northern areas off the west coast of Scotland (Divisions VIa and b), the Skagerrak–Kattegat (Division IIIa), and the Baltic (Divisions IIIb, c, and d), and also in the Bay of Biscay (Subarea VIII) and the Celtic Sea–English Channel (Subarea VII). The landings off Portugal suggest a sudden decrease in 1994, but this may be the result of the inclusion of other sole species prior to 1994 (Figure 21.2).

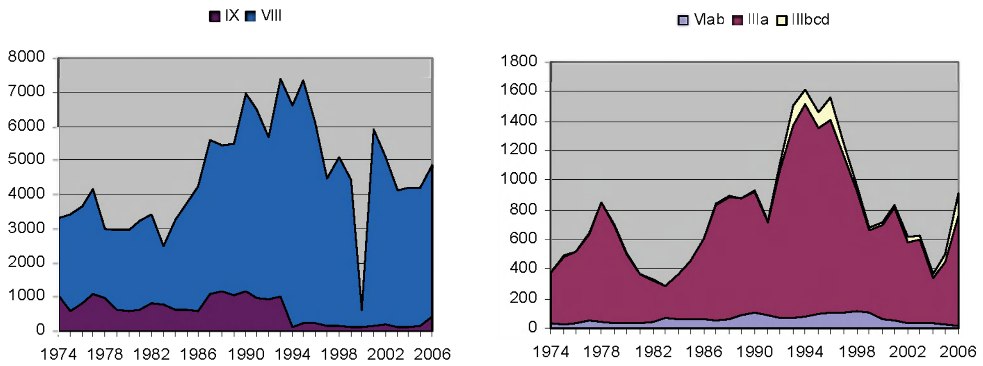


Figure 21.2. Time-trends in landings in ICES Areas. Left panel: southern areas: IX = Portugal; VIII = Bay of Biscay. Right panel: northern areas: VIa and b = West of Scotland; IIIa = Skagerrak–Kattegat; IIIb, c, and d = Baltic.

21.5 Observed changes in distribution

The trends in landings tentatively suggest that the northern limit of sole has shifted northwards. With increasing landings from the Skagerrak–Kattegat and the west coast of Scotland, the possibility of the changes being caused by increased fishing effort cannot be excluded. Perry *et al.* (2005), using data collected during English summer groundfish surveys, demonstrated a southward shift in sole distribution in the North Sea, opposite to the expected change caused by the increase in temperature, and suggested that this might be caused by improved environmental conditions in the rivers. However, as sole is not only confined to coastal areas under the influence of rivers, this explanation seems unlikely.

In French nursery grounds in the Baie de Vilaine (Bay of Biscay), an analysis of trends in sole abundance revealed no significant change, apart from irregular interannual variations. In contrast, two northern, winter-spawning flatfish species, plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*), demonstrated a decline, and the southern, summer-spawning wedge sole (*Dicologlossa cuneata*) increased in abundance (Désaunay *et al.*, 2006).

21.6 Processes underlying observed changes

21.6.1 Productivity

Sole are known to suffer high mortality in winters when the temperature falls below 3°C for a prolonged period (Woodhead, 1964a). Natural mortality in the severe winter year of 1963 was ca. 60%, compared with 10% during a normal year (Horwood and Millner, 1998). On the other hand, cold years generally coincide with good recruitment (see Section 21.6.2). Cold winters, therefore, temporarily decrease productivity.

Changes in growth rate have been observed in several sole stocks. The increase in growth rate of North Sea sole in the 1960s and 1970s coincided with an increase in eutrophication as well as an increase in bottom disturbance caused by beam trawling (de Veen, 1976, 1978b; Rijnsdorp and van Beek, 1991; Millner and Whiting, 1996; Rijnsdorp and van Leeuwen, 1996). In the 1990s, a decrease in growth rate was observed in several sole and plaice stocks, suggesting that changes in growth rate are governed by broad-scale processes (Millner *et al.*, 1996). Growth of age-0 sole is positively affected by temperature. The effect is the result of an increase in both the growth rate at higher water temperatures and the duration of the growth period (Teal *et al.*, 2008). No relationship between adult growth and temperature has been reported.

In the Bay of Biscay, Le Pape *et al.* (2003) demonstrated that the quantity and quality of the nursery area was positively affected by river run-off. In the Mediterranean, run-off from the River Rhône is positively correlated with sole landings, with a time-lag of 2 years (Salen-Picard *et al.*, 2002). Darnaude *et al.* (2004) identified two different benthic foodwebs off the River Rhône: one based on marine planktonic carbon and the other based on terrestrial particulate organic matter (POM) carried by the river. Deposit-feeding polychaetes were responsible for the main transfer of terrestrial POM to upper trophic levels, linking sole population dynamics to river run-off fluctuations.

The onset of sexual maturity is positively influenced by growth rate during the juvenile phase (Mollet *et al.*, 2007) and, thus, will also be influenced by temperature.

21.6.2 Recruitment

Time-series of recruitment derived from virtual population analysis (VPA) do not indicate any increasing or decreasing trends in normalized recruitment (Figure 21.3). Recruitment variability in sole stocks increases with latitude (Philippart *et al.*, 1998). In southern populations, recruitment is rather stable, but in northeastern populations, recruitment is more variable, owing to the occurrence of cold winters causing extra mortality (Woodhead, 1964a, 1964c; Rijnsdorp *et al.*, 1992). When recruitment patterns of different sole stocks are compared, correlations are found between neighbouring stocks, but the correlations break down if stocks farther away are compared, suggesting that local conditions are more important than large-scale processes (Rijnsdorp *et al.*, 1992).

In the North Sea, strong year classes are produced in years when the spring water temperature is low, but a low temperature does not guarantee a strong year class. The effect of temperature on recruitment may be related to the effect on the timing of spawning. Low temperatures in March delay spawning (van der Land, 1991; Rijnsdorp and Witthames, 2005). Year-class strength in sole appears to be determined by autumn of their first year, although a severe winter may increase mortality of prerecruits (Rijnsdorp *et al.*, 1992; van der Veer *et al.*, 2000) and adults (Woodhead, 1964a). The extent to which recruitment is determined during the pelagic egg and larval stages, or during the early demersal stage, is unknown. In sea areas more strongly influenced by the Atlantic Ocean, there is no indication that recruitment is negatively related to winter temperature. On the contrary, in the Bristol Channel (Subareas VIIf and g), recruitment appears to be positively related to both water temperature and growth rate. High temperatures allow faster development, and a positive North Atlantic Oscillation (NAO) index increases productivity and offers more food. Both of these positive influences act to reduce mortality, resulting in stronger year classes (Henderson and Seaby, 2005).

Recruitment to a local stock is significantly correlated with the size of the available nursery grounds (Rijnsdorp *et al.*, 1992). In the Bay of Biscay and the northwestern Mediterranean Sea, recruitment, as well as the size of nursery grounds, varies in relation to run-off of the major rivers (Salen-Picard *et al.*, 2002; Le Pape *et al.*, 2003; Darnaude *et al.*, 2004).

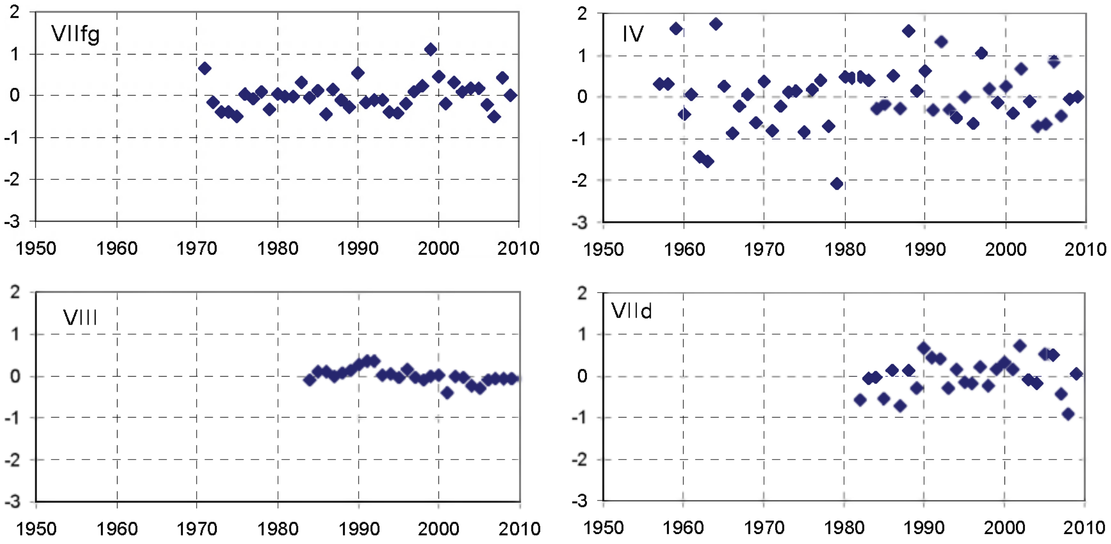


Figure 21.3. Normalized time-trends in age-1 recruitment of sole stocks in ICES Areas: VIIf and g = Bristol Channel; VIII = Bay of Biscay; IV = North Sea; and VIId = eastern English Channel.

21.6.3 Distribution

Sole avoid low temperatures and, in autumn, demonstrate an offshore migration to deeper and warmer waters (de Veen, 1978a). In severe winters, when temperatures of shallow waters decrease to lethal levels (<3°C), sole concentrate in deep pits in the western North Sea (Woodhead, 1964c; Horwood and Millner, 1998).

21.7 Conclusion

Climate change is expected to affect sole populations through a number of different mechanisms. The most important environmental factors involved are temperature and river run-off. Warmer conditions will improve the survival of demersal stages because the probability of high winter mortality caused by cold winters will decrease. This will apply particularly to northern areas characterized by a relatively large temperature range. The timing of spawning will be advanced, particularly in areas such as the North Sea, where the range of the seasonal cycle in water temperature is relatively large, resulting in a longer growth period for age-0 fish. In combination with higher temperatures during the growth period, this will result in a higher growth rate. In sea areas such as the Mediterranean and Bay of Biscay, where the size and quality of the nursery grounds are affected by river run-off, changes in rainfall and river run-off will affect recruitment and growth.

How climate change will affect the pelagic life stages and their transport to the coastal nursery grounds remains to be studied. The temperature tolerance limits of eggs and larvae suggest that an increase in temperature will have no significant impact. The above conclusions are uncertain, because the potential effects of an increase in temperature on the productivity of pelagic and benthic food are unknown.

22 Brown shrimp

Marc Hufnagl and Axel Temming

22.1 Introduction

This section reviews the stock development of the commercially exploited brown shrimp (*Crangon crangon*; phylum Crustacea, order Decapoda, infraorder Caridea, family Crangonidae). The focus is on recent changes observed in the North Sea stock and the direct and indirect roles that climate-driven changes in temperature may have on the productivity and distribution of this shrimp via habitat alteration and changes in key predator populations.

22.2 General biology

The brown shrimp inhabits shallow coastal and estuarine areas and is distributed from Iceland in the north (Gunnarson *et al.*, 2007) to Spain (Cuesta *et al.*, 2006) and the north coast of Africa in the south. It tolerates a wide range of salinity levels, although it is unable to reproduce in waters with a salinity of <5 psu. It is found in near-freshwater habitats (Gelin *et al.*, 2001), in estuarine areas, such as the Baltic Sea (Lapinska and Szaniawska, 2006), and in marine areas with relatively high salinities, such as the Mediterranean Sea (Bulnheim and Schwenzer, 1993). The core of its distribution is located in the southern and eastern parts of the North Sea, including the Wadden Sea along the coasts of the Netherlands, Germany, and Denmark. Although brown shrimp can live at depths up to 120 m (Wollebaek, 1908), they mainly concentrate in highly productive, tidally influenced waters of <10 m depth.

The longevity of the brown shrimp is approximately 2 years, and it reaches a mean maximum total length of 80 mm, although individuals up to 110 mm are sometimes found (German demersal young fish survey 2005). Hatching occurs mainly in winter and summer, but egg-bearing females can be captured throughout the year, except in October and November (Kuipers and Dapper, 1984; Neudecker and Damm, 1992). Post-larvae of 5–15 mm length mainly invade intertidal areas from May until June (Temming and Damm, 2002), growing to a marketable size of 50 mm by October or November. Small individuals tolerate temperatures up to 27 °C. When temperatures exceed 27 °C, individuals leave the tidal flats in large numbers (Berghahn, 1983). Shrimp that are 40 mm or longer avoid the tidal flats and are mainly caught within gullies and tidal creeks, where the water is colder (Janssen and Kuipers, 1980). Experiments have demonstrated that the optimum salinity at 6 °C is 35 psu and that lower salinities are favoured at higher temperatures (Caudri, 1937). The brown shrimp is an opportunistic omnivore, but feeds mainly on small crustaceans, copepods, mussels, dead fish, algae, and detritus (Plagmann, 1939; Pihl and Rosenberg, 1984).

22.3 Fisheries

Brown shrimp are caught throughout the year, mainly by fisheries in Germany and the Netherlands and, to a lesser extent, in the UK, Denmark, Belgium, and France. The highest landings are normally in autumn, coinciding with the timing of the peak in abundance of shrimp >50 mm (Maes *et al.*, 1998), whereas the catch during winter is relatively low (ICES, 2009). Fishing effort is also lowest during winter, although catches at this time of year yield higher prices. The price for the fishers in 2006 was €2–3 kg^{-1}. Shrimping in the North Sea is mainly performed by small- and medium-sized cutters equipped with 9 m beam trawls, with or without tickler chains. At present, the *Crangon* fishery is not regulated, and the minimum catch size is mainly driven by market factors, such as the sizes preferred for processing.

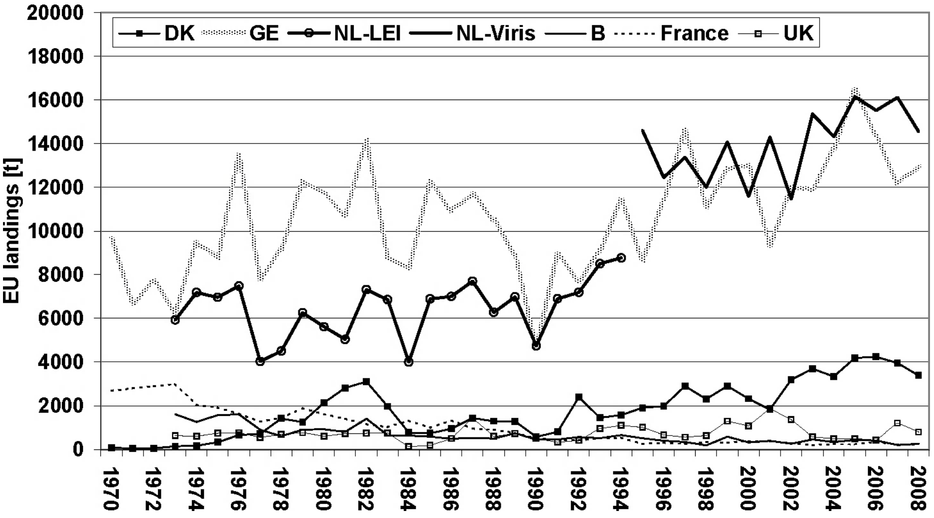


Figure 22.1. Landings of *Crangon crangon* from the North Sea (in t) by country. (Source: ICES, 2009.)

22.4 Observed changes in production

Annual landings for the entire North Sea were ca. 10 000 t in 1970 and increased constantly from 1990 until 2006, when landings were 35 000 t (Figure 22.1). This increase was achieved with hardly any, or only a low, increase in fishing effort. For the two main fishing nations, Germany and the Netherlands, effort in these years averaged ca. 9–10 million and 4 million horse power days (hpd), respectively (ICES, 2009).

In recent years, increased densities were observed in the northern part of the North Sea. In Denmark, landings per unit effort (lpue) increased from 1 kg hpd^{-1} in 2001 to 6 kg hpd^{-1} in 2006, followed by a decrease to 3 kg hpd^{-1} in 2008. Additionally, a recent rapid increase in abundance of brown shrimp in Icelandic waters was observed (Gunnarson *et al.*, 2007). Although the establishment of this species in Iceland might be the result of introduction via ballast water, it has found favourable conditions and rapidly colonized this area.

22.5 Processes underlying observed changes

Although the annual landings of brown shrimp from the North Sea have fluctuated considerably over the past three decades, there is clear evidence of a general increase since 1990 (Figure 22.1). This increase might be caused by several factors, the most likely being a release from predation pressure. Adult brown shrimp are mainly consumed by Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), and mackerel (*Scomber scombrus*), which are all fish species that have declined dramatically in the North Sea (Cook *et al.*, 1997), especially since the mid-1990s (see also Section 17). The increase in brown shrimp landings in the northern part of the North Sea by both Denmark and Iceland may have been partly the result of increasing water temperatures, although fishing effort has also shifted into these areas from other regions. However, because German, Belgian, and Dutch vessels were also fishing in Danish waters, increased abundance of brown shrimp over the whole area is likely.

The northward shift of brown shrimp may be caused by increasing water temperatures. For example, mean sea surface temperature increased between 2001 and 2006, and this increase has been especially apparent during August and September (see also Section 6). Danish lpue was low in 2001 and much higher in 2006, when temperatures during October were >2°C warmer along areas of the Danish coast. However, temperature and predation are probably acting simultaneously to influence the stock dynamics. For example, in 1997, the lpue was only about half that in 1996, despite relatively high temperatures, a difference probably attributable to the presence of larger numbers of predators in 1997. Furthermore, because the *Crangon* fishery is not regulated, market factors might also play an important role.

22.6 Future stock development

At present, there is no indication that the populations of the main predators of brown shrimp are recovering and, according to Welleman and Daan (2001), the shrimp fishery has been sustainable in recent times. Therefore, it can be assumed that landings will remain at a high level (since 2003, total annual landings have been above 30 000 t). Henderson *et al.* (2006) suggest that a shortage of suitable substrata could be a factor limiting the increase in brown shrimp stock. If the availability of habitat is limited, density-dependent factors, such as cannibalism, might play a greater role in controlling the population. Further increases in temperature will most probably stabilize or even increase landings as a result of the expansion of the distribution area of brown shrimp farther northwards, mainly into Danish waters, but also into southern Swedish and Norwegian waters. Increased temperatures will also increase the growth rate of brown shrimp at higher latitudes. Currently, winter-hatched larvae take ca. 1 year to reach marketable size by October.

Kuipers and Dapper (1984) reviewed the spawning activity of brown shrimp in relation to latitude and demonstrated that, in more northern regions, only one spawning season (in autumn) is observed, as opposed to two spawning peaks in southern areas, such as the Wadden Sea. Higher temperatures in northern areas would therefore influence not only growth rates, but also reproduction of the shrimp. This higher productivity will only be possible if fuelled by sufficient levels of primary and secondary production. Pihl and Rosenberg (1984) observed that food consumption rates increased by 6% for each 1°C increase in temperature over a range of 10–20°C. Therefore, higher growth rates in response to increasing water temperatures (especially in warmer areas) may only be possible in highly productive areas, such as the Wadden Sea, as suggested by reports linking the increase in the brown shrimp population with eutrophication (Boddeke and Hagel, 1995: Boddeke, 1996). However, zooplankton time-series from corresponding areas would be necessary in order to test whether or not brown shrimp populations may become food-limited. In the north, although brown shrimp densities may be lower, owing to food limitations, overall landings should increase and, barring additional ecosystem changes, could eventually reach a higher, stable plateau.

The effects of temperature on stock size are not only positive. Increased temperatures translate into higher moulting rates and increased frequency of periods when the shrimp are more vulnerable to cannibalism, predation, and influences of pollutants. Moreover, preferred habitats may become unsuitable because tolerance of low salinity is reduced at higher temperatures, and mortality, especially of larger shrimp, would be expected to increase. Increased temperatures are associated with decreases in oxygen content and increases in the concentration of harmful substances in the water, such as H_2S; brown shrimp are particularly sensitive to low concentrations of the former and high concentrations of the latter (Hagerman and Vismann, 1995).

22.7 Conclusions on climate effects

At present, it is difficult to establish whether the steady, high landings reported for brown shrimp in recent years are the result mainly of an increase in temperature or a decrease in the main predators, such as Atlantic cod and whiting. Under *ad libitum* feeding conditions, increasing temperatures will increase the growth rates of the shrimp, allowing a larger proportion of the juveniles invading intertidal areas of the North Sea in spring to reach reproductive size by autumn. This will not only increase landings, but will also alter or increase the spawning-stock biomass. A northward shift of the population has been discussed, but until now, the only indications are higher lpue in northern areas and an increasing stock on the coast of Iceland. Increased productivity may result from a shortening of the life cycle caused by higher growth rates and, therefore, a decrease in cumulative mortality. Furthermore, the number of breeding seasons at higher latitudes may increase from only one (during summer) to two (during summer and winter), as currently described for populations of brown shrimp in the southern North Sea.

On the other hand, there is some indication that bottlenecks exist for the productivity of brown shrimp populations in the form of a lack of suitable habitat (space limitation) and/or sufficient prey resources. Habitat and/or prey limitation can play important roles in the stock dynamics, and both would be exacerbated by increased warming: the former by increased hypoxy in benthic habitats, and the latter by increased metabolic demands. Moreover, brown shrimp populations may benefit indirectly from increasing temperature via decreases in predator populations. This appears to be the case with Atlantic cod, but the effect of increasing temperature on whiting populations is unknown.

23 Nephrops

Georg H. Engelhard and John K. Pinnegar

23.1 Introduction

This section reviews knowledge of the Norway lobster (*Nephrops norvegicus*; phylum Crustacea, order Decapoda, family Nephropidae), with particular focus on the possible effects of climate change. It summarizes the general biology and then addresses recent developments of landings, including apparent differences in trends between the more northern and southern parts of the distribution range. It concludes by hypothesizing climate change as a possible factor in these changes, but also proposes three alternative hypotheses that are not mutually exclusive.

23.2 General biology

The Norway lobster, widely marketed as scampi, langoustine, or Dublin Bay prawn, is a relatively small, elegant lobster up to 24 cm long. As in other lobsters, the thorax bears 10 legs, or pereiopods; the first pair is modified into two long, slender claws and the others are stout walking legs. If it needs to escape, this walking decapod can also swim rapidly backwards by fast flexing of the powerful abdomen (Hayward *et al.*, 1996).

Norway lobster live in dense aggregations on the flat, muddy bottoms of the European continental shelves and slopes of the Atlantic and Mediterranean. After 6 months as larvae and post-larvae in the water column, individuals settle on the seabed, notably where temperatures are ca. 13–14°C and the bottom consists of silt and clay of specific particulate dimensions (Farmer, 1975; Aguzzi and Sardà, 2008). These two factors confine the species to the shallower depths of the continental shelf of the North Atlantic, but to much deeper shelves and slopes of the Mediterranean (Farmer, 1975; Abelló *et al.*, 2002). In the seabed, the lobsters dig extensive, branching tunnels, which have a depressed, crater-like entrance, tubes that travel horizontally ca. 20–30 cm under the seabed surface, and between one and eight ventilation shafts (Rice and Chapman, 1971).

The lobsters spend most of the time in the burrows, which they leave only to feed and to mate. These emergence patterns are very important because most *Nephrops* fishing is by trawling (although creels are used in many sheltered Scottish sea lochs), and the lobsters are protected from trawling while they are in the burrows. Emergence appears to be related to light levels, and the greatest catches are often taken at dawn and dusk, although this may vary according to water depth and clarity (Aguzzi and Sardà, 2008). Females carrying eggs (so-called "berried" females) rarely come out of their burrows and are therefore naturally protected from trawlers; as a result, males dominate the catches during most of the year and are more heavily exploited than females (Bell *et al.*, 2006).

A small fish, Fries' goby (*Lesueurigobius friesii*; order Perciformes, family Gobiidae) is a common cohabitant of *Nephrops* burrows.

23.3 Fisheries

Nephrops are mainly caught by trawlers, but other methods are used in inshore areas (e.g. creeling is important along the Scottish west coast). The fishery has especially developed since the 1960s and is currently of particular importance to the UK, especially Scotland. This has been attributable to (i) a redirection of fishing effort away from traditional species, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), which have recently declined markedly and hence become less available to the fishery; and (ii) the very high market price of *Nephrops*. In Scotland, it is now one of the most valuable fisheries (landings valued at ca. £50 million in recent years).

Of the total nominal catches from the Northeast Atlantic (excluding the Mediterranean) during the period 2000–2005, ca. 53% was landed in the UK (39% in Scotland alone). The next-most important countries were France and Ireland (13% each), Denmark (10%), and Iceland (3%). Landings in Spain and Portugal were much higher in the 1970s to 1980s, but currently are only 1–2 % of the total for the Atlantic.

The most important fishing regions for Norway lobster in the Northeast Atlantic include: the North Sea (ICES Subarea IV: 42% of total landings during 2000–2005); the English Channel and Celtic and Irish seas (Subarea VII: 28%); West of Scotland (Division VIa: 19%); Bay of Biscay (Subarea VIII: 7%); and to a lesser extent, the Portuguese coastal region (Division IXa: 1.2%), notably the Galician coast. However, it is of note that, within these regions, *Nephrops* fisheries are highly localized and tightly linked to the specific habitat requirements of the species (i.e. the need for muddy and/or silty substrata).

23.4 Observed changes in production and distribution

Northeast Atlantic *Nephrops* landings increased dramatically from the 1950s to the mid-1980s and have since stabilized (Figure 23.1). Notably, there appears to have been a latitudinal shift in the regions where most of the landings were taken. The relative importance of southern countries (Portugal, Spain, and France; Figure 23.1 left panel) or southern fishing regions (Portuguese coast, Bay of Biscay; Figure 23.1 right panel) has decreased, whereas that of northern countries (Ireland, UK, Denmark) or fishing regions (West of Scotland, North Sea) has increased.

There are indications that geographic differences in *Nephrops* population trends at least partly reflect those of the landings. The population along the Portuguese coast has collapsed since the 1980s, with an estimated decline in spawning-stock biomass (SSB) from ca. 2000 t in 1988 to ca. 400 t in 2004 (ICES, 2006f). No such drastic declines are evident in the North Sea and West of Scotland, based on television-survey methods and landings per unit effort (lpue) data, although, admittedly, the population sizes are not properly known; lpue data are difficult to interpret because of highly localized and targeted fishing (Bell *et al.*, 2005; ICES, 2006d).

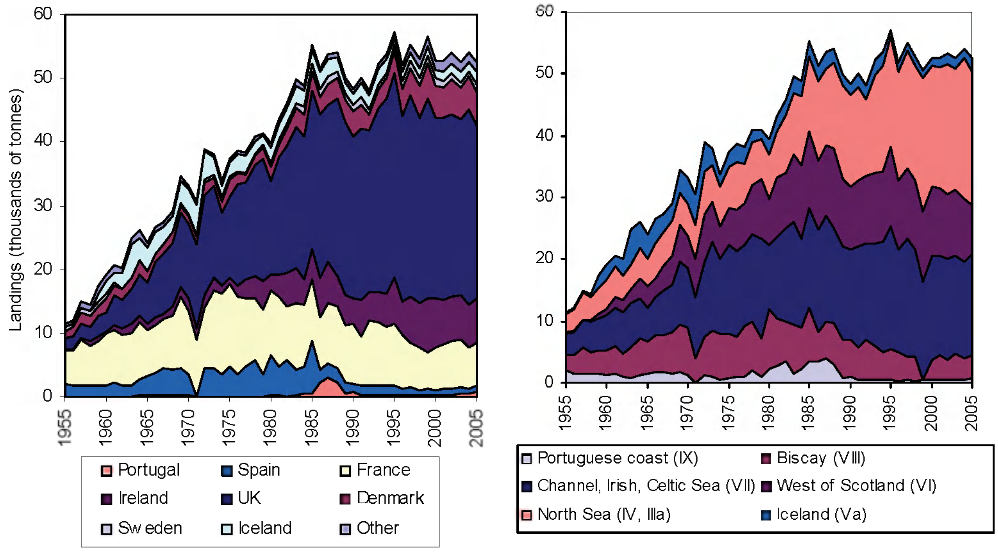


Figure 23.1. Northeast Atlantic *Nephrops*: trends in total landings: (left panel) by country of landing, and (right panel) by fishing region. "Other" in the left panel includes, in decreasing order of average annual landings over this time-series, Belgium, the Netherlands, Norway, and the Faroes. (Data from ICES Fisheries Statistics.)

23.5 Processes underlying observed changes

Four hypotheses may be adduced to explain why, over the past three decades, *Nephrops* landings from southern populations have generally decreased, while landings from more northern populations have either increased or remained stable (Figure 23.1 right panel). These hypotheses, which are not mutually exclusive, relate to:

1) climate change,
2) differences in fishing pressure,
3) trends in targeted fishing effort, and
4) indirect effects of fishing through reduction in natural predators.

The trends are in line with hypothesis 1 (climate change), where species are expected to decrease in abundance at their southern distribution limits and increase at their northern limits (for examples, see Beare *et al.*, 2004; Perry *et al.*, 2005). Indeed, experiments on Irish Sea *Nephrops* demonstrated that, at higher temperatures, larval stages are of shorter duration there (Dickey-Collas *et al.*, 2000), hinting that climate warming would speed up growth rates. Moreover, species with spatially restricted habitat requirements during a crucial part of their life history may be more sensitive to climate change than species without such specific habitat requirements (i.e. if temperature changes occur at sites with suitable substrata, but animals cannot redistribute to other such sites, because of geographic constraints; Rijnsdorp *et al.*, 2009; see also Section 1). In such species, climate change is unlikely to result in rapid distribution shifts, but may cause local decline or disappearance, with recolonization likely to occur only at a slow pace. Given that adult *Nephrops* are closely associated with silty and muddy bottoms in waters of 13–14°C (Farmer, 1975), they are vulnerable to a warming climate if this would lead to a mismatch between suitable temperatures and substrata types.

However, climate effects on population trends were not found by Zuur *et al.* (2003), who analysed lpue series for 13 *Nephrops* populations around northern and central Europe. Using dynamic-factor analysis, they were able to detect six groups of populations demonstrating similar temporal patterns, but found no evidence that any of the trends were related to such climatic drivers as the North Atlantic Oscillation (NAO) or to sea surface temperatures.

Higher and historically more sustained, fishing pressures on southern populations (hypothesis 2) might also explain the declining catches compared with the north. In southern Europe, *Nephrops* have been marketed for many decades, whereas the targeted fisheries in the north expanded more recently; even now, the catches are mainly exported to the south.

It is unclear to what extent the shifts in landings relate to abundance changes of *Nephrops* itself or to changes in fishing patterns leading to regional differences in fishing effort (hypothesis 3). This difference occurs mainly in the north where cod-targeted fishing effort has been redirected towards *Nephrops* (most notably in the central and northern North Sea; Pawson *et al.*, 2002). In contrast, off Portugal, a mixed fishery, which targeted *Nephrops* (among other species), has declined and *Nephrops* landings have decreased steeply, but the decline in effort appears to have preceded, not followed, the decline in *Nephrops*. It has been tentatively suggested that reduced discards might have limited the feeding opportunities of *Nephrops* and thereby contributed to its population decline.

Finally, hypothesis 4 suggests that the increases in *Nephrops* in the Irish Sea, North Sea, and possibly other northern populations may be related to a reduction in predation mortality from demersal fish, notably cod. In the Irish Sea, cod was the predominant predator of *Nephrops* during the 1970s to 1980s (Armstrong, 1979, 1982; Patterson, 1983), and Brander and Bennett (1986) estimated that cod, at biomass levels typical of that time, imposed on it an instantaneous predation mortality of 0.2 year^{-1}, as part of an estimated natural mortality of 0.3 year^{-1}. Furthermore, strong evidence of a close predator–prey relationship was given by Brander and Bennett (1989), who demonstrated that the catch rates of Irish Sea *Nephrops* in the 1970s to 1980s were inversely related to cod biomass levels in the following years. Similar, top–down regulation of a crustacean by cod has been reported for shrimp (Worm and Myers, 2003).

Cod is also the main *Nephrops* predator in Icelandic waters (Dombaxe, 2002), and possibly in most of the stocks living north of the English Channel (Björnsson and Dombaxe, 2004). However, *Nephrops* are relatively low-quality food for cod, compared with pelagic fish such as capelin (*Mallotus villosus*; Björnsson and Dombaxe, 2004) because of their hard exoskeleton and low fat content. This implies that more *Nephrops* than fish would be required to sustain the same growth. Given that, largely through overfishing, cod stocks have declined substantially over the past two to three decades almost throughout their range, from the English Channel northwards, a positive effect through significant release of predation mortality on the *Nephrops* populations of the area is likely to have occurred.

23.6 Conclusions on climate effects

Over the past three decades, *Nephrops* landings from southern populations have generally decreased, whereas landings from more northern populations have either increased or remained stable. Four complementary hypotheses are proposed here to account for these changes, related to (i) climate change, (ii) differences in fishing pressure, (iii) trends in targeted fishing effort, and (iv) indirect effects of fishing through reduction in predation mortality.

Further studies are needed that address the relative contributions of climate and fishing to the geographically different trends in landings and population sizes, both now and in the future. However, for this species, it will also be particularly important to examine whether its highly specific habitat requirements may make it particularly vulnerable to climate change.

24 Synthesis and working hypotheses

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24.1 Introduction

Resolving the effect of climate change on fish populations is complicated because climate change will affect a multitude of environmental factors that may, in turn, affect various processes at different levels of biological organization. For example, even if the effect of changes in an environmental factor on the physiology of an organism is known, it will be difficult to evaluate the outcome of this organismal-level physiological response at the level of the population or ecosystem (MacKenzie and Köster, 2004). Statistical analysis of available time-series revealed changes in the distribution and abundance of fish species that correlate with environmental variables (Murawski, 1993; Beaugrand, 2003; Köster *et al.*, 2005; Weijerman *et al.*, 2005). However, statistical correlations do not necessarily reflect underlying processes.

It may be argued that it will be impossible to detect generalities because the number of interactions in the system is too large and individual species may differ too widely in their response. Nevertheless, we believe that it is possible to derive generalities by developing hypotheses about the impact of climatic factors (abiotic variables) on fish populations based on first principles and by taking account of different levels of biological organization (from cellular- and organismal-level ecophysiology to population- and ecosystem-level responses). In this section, we will:

i) review the environmental variables and oceanographic features relevant to fish that will be affected by climate change;

ii) derive theoretical expectations from first principles and from physiological and ecological theory;

iii) derive working hypotheses for future research; and

iv) review the empirical evidence against this theoretical background.

An extended version of this section is published in *ICES Journal of Marine Science* (Rijnsdorp *et al.*, 2009).

24.2 Climate change

The effects of climate change differ among geographic areas (IPCC, 2007), and a review of the observed changes in ocean climate is given in Section 6. Predictions indicate the following.

i) High-latitude areas will experience the largest increase in air temperature and melting of sea ice. The Norwegian, Barents, and Baltic seas will demonstrate an intermediate increase in temperature, whereas the more southern areas, including the North and Mediterranean seas, will demonstrate the most modest increases. Ocean temperature will follow increases in air temperature, although, to a lesser extent, this will be caused by the high heat-storage capacity of oceanic water masses. Shallow areas will demonstrate a larger increase in sea temperature than deeper waters.

ii) In western Europe, there will be an decrease in the frequency of very cold winters and an increase in the frequency of very hot.

iii) Changes in the strength and prevailing direction of winds over European marine areas remain uncertain, although average and extreme windspeeds over northern Europe are expected to increase.

iv) Precipitation and river run-off will increase in northern Europe and decrease in southern Europe. Also, the seasonality of run-off will change, increasing in winter, but decreasing in spring in northwestern Europe. In warmer regions, such as the Mediterranean, differences in the magnitude of river run-off between winter and summer will increase.

Abiotic variables that will be influenced by climate change and, in turn, affect the production and distribution of fish, will differ among regions, such as the open ocean, shelf areas, and coastal waters. Although the importance of the variables changes regionally, some general conclusions can be reached.

i) Temperature, because of its pervasive effect on organisms, will be of crucial importance in all regions.

ii) Stratification will be of major importance in all regions because of its impact on the vertical structure of ecosystems and on bottom–up processes.

iii) The effect of winds is usually through mixing and circulation changes in the open ocean, but in shelf and coastal regions, upwelling may become more important, depending on wind direction and coastal orientation.

iv) Sea ice is only important in the more northern regions, such as the Barents and Baltic seas, but ice cover there does act as a key factor in the system.

v) Changes in salinity will generally have less of a direct effect on most organisms, although this is an important factor in the Baltic Sea.

24.3 Theoretical expectations

Fish have complex life cycles comprising egg, larva, juvenile, and adult stages, in which body size is increased by a factor of 10^5 (Rothschild, 1986). Successive life-history stages require different habitats, which are often spatially separated. A prerequisite for population persistence is that the successive habitats are connected, allowing the survivors to metamorphose, mature, and return to the spawning grounds to reproduce successfully (life cycle closure: Sinclair, 1988). Within stage-specific habitats, fish must be able to experience suitable abiotic conditions as well as find food for growth and shelter to escape predation or disease.

Climate-driven changes in fish populations may result from five, often interlinked, mechanisms:

i) physiological responses to changes in environmental parameters, such as temperature;

ii) behavioural responses, such as avoiding unfavourable conditions and moving into new suitable areas;

iii) population dynamics resulting from changes in the balance between rates of mortality, growth, and reproduction, in combination with dispersal, which can lead to the establishment of new populations in new areas or the abandonment of traditional sites;

iv) ecosystem-level changes in productivity and/or trophic interactions; and

v) commercial exploitation, which greatly affects the abundance and distribution of fish and may interact with impacts of climate change.

In the following sections, we expand on each of these five themes with regard to potential climate impacts in order to derive a suite of testable hypotheses.

24.3.1 Physiological response

In order to interpret observations in terms of underlying mechanisms, insight regarding ecophysiological responses will be important (Section 3). Species can tolerate only limited ranges of environmental conditions, and this will influence their distribution ranges. A classification scheme based on the biogeographic affinities of species (Arctic, Boreal, Lusitanian, Tropical, Atlantic) may be a powerful tool in evaluating the expected response (Section 2).

A review of the upper and lower lethal temperatures for fish species indicated that tolerance range changed with latitude, being narrow at the equator and the poles, and wide in intermediate latitudes (Section 3). Although estimates of thermal preference gauged from fish in the field should not be oversimplified, because other environmental factors can modify preferred temperatures, such estimates may give a first approximation of the general patterns. There are indications of an ontogenetic shift in the temperature tolerance of species, so that optimum temperatures for growth decrease with increasing body size of juveniles and adults (Kuipers and Fonds, 1978; Fonds *et al.*, 1992; Imsland *et al.*, 1996; Yamashita *et al.*, 2001).

The observed relationship between fish size and depth distribution (Heincke's law; Heincke, 1913) may be a reflection of the decrease in the upper thermal limit with increasing fish size. This mechanism could explain the ontogenetic shift in habitats observed in several fish species, where young stages occur in shallower waters than larger stages. In some species, larval stages have been observed to have a narrower temperature-tolerance range than other life-history stages, making them more vulnerable to changes in temperature (Irvin, 1974). If this is a general phenomenon, it may provide a powerful basis for predicting the response of a species to changes in temperature, but further research is needed to test its general application. The sensitivity of larval stages to climate change may be further increased by their small body size, which will make them less capable of selecting a suitable habitat and more vulnerable to mortality during periods of adverse environmental conditions, such as food shortage.

Several authors have stated that marine fish are less likely to be affected by an increase in oceanic CO_2 and a corresponding decrease in pH than invertebrate groups, such as molluscs and corals (Feely *et al.*, 2004; Orr *et al.*, 2005; Fabry *et al.*, 2008). However, laboratory studies have revealed that manipulation of pH and CO_2 can have dramatic consequences on physiology, metabolism, and reproductive biology, with egg fertilization and survival of early developmental phases being primarily affected (Ishimatsu *et al.*, 2005).

It is worth noting that responses to climate change at higher levels of organization (population, community, ecosystem) are ultimately driven by differences in physiological responses that affect trophodynamic relationships. For example, physiological responses to a change in temperature can differ between primary, secondary, and tertiary consumers, thereby influencing trophic coupling (Freitas *et al.*, 2007) via changes in productivity or phenological shifts and match–mismatch dynamics (Cushing, 1990).

24.3.2 Behavioural response

Organismal-level responses, such as changes in behaviour, can result from changes in key abiotic factors, such as temperature or O_2 levels, but the presence (and/or strength) of the response will depend on the ability of the animal to detect environmental gradients and navigate accordingly. In contrast to early-feeding larvae of tropical marine fish, which can exhibit relatively strong swimming capacity (e.g. Leis, 2006), larvae of most temperate marine fish species have little or no swimming ability. Temperate marine fish larvae can respond to relatively intensive environmental signals (e.g. turbulence avoidance: Franks, 2001) but have little capacity to avoid unfavourable environments if the situation requires swimming over large (km) distances.

In later (juvenile and adult) life stages, individual fish can clearly respond to a change in temperature (Woodhead, 1964a; Berghahn, 2000) and, in many cases, exhibit active temperature preference (e.g. Tsuchida, 1995). Some elasmobranchs are extremely sensitive to temperature variation (i.e. they can respond to changes of <0.001 °C: Brown, 2003), and some sharks are able to move to deeper water before the onset of severe storms (Heupel *et al.*, 2003). Even for individuals in these later life stages that have strong swimming capacity, information concerning the location of optimal habitats will be imperfect. Field studies on thermal habitat revealed that fish may inhabit suboptimal temperatures even if more optimal temperatures are within reach (Neat and Righton, 2007); however, optimal habitat is also determined by other factors, such as food. Behavioural changes may have unexpected consequences. For example, as a result of an increase in temperature, fish swimming speed increases (e.g. Peck *et al.*, 2006), and fish may behave differently in response to oncoming fishing gear, making them more (or less) vulnerable to capture (Winger, 2005).

Finally, at longer temporal scales, climate-driven changes in temperature can modify the phenology of annual migrations to feeding and/or spawning grounds, as observed (Carscadden *et al.*, 1997; Sims *et al.*, 2004) and predicted (Huse and Ellingsen, 2008) for temperate marine species. It can be inferred that the behavioural response to changes in environmental conditions depends on the rate of change and/or the spatial scale over which conditions change relative to fish body size or developmental stage, because the capacity for avoidance responses increases with increasing body size.

24.3.3 Population dynamic response

Productivity of fish populations, in terms of biomass, is determined by recruitment, growth, and mortality. Most commercially important species are broadcast spawners, producing millions of eggs (Rothschild, 1986). Mortality rates of early life-history stages are very high and variable, generating large fluctuations in annual recruitment. Relatively small changes in rates of growth and mortality during the egg and larval phases can have a large impact on recruitment success of populations (Houde, 1987). As the early life-history stages are likely to be more sensitive to climate change, climate change can be expected to have a major effect on the distribution and abundance of fish because of its influence on recruitment. The mechanism will be either the match–mismatch between the timing of reproduction relative to the production of larval food and/or predators (Cushing, 1990; van der Veer *et al.*, 2000; Platt *et al.*, 2003; Temming *et al.*, 2007) or the connectivity (retention or transport) between spawning and nursery areas (Sinclair, 1988; Wilderbuer *et al.*, 2002).

Interstock comparisons indicate a dome-shaped pattern in the relationship between the recruitment strength and spawning temperature experienced during the spawning season, with maximum recruitment at an intermediate temperature in cod (*Gadus morhua)* and sprat (*Sprattus sprattus*; Brander, 2000; MacKenzie and Köster, 2004). In cod, this temperature was close to the optimal temperature for growth of larvae (Brander, 2000). However, the impacts of climate on recruitment are not limited to processes acting during the egg and larval stages, but may extend to later (juvenile and adult) life stages. For example, year-class strength in sprat appears to be established during the post-larval or juvenile period (Köster *et al.*, 2003b), and low growth rates and poor condition of juvenile sprat can result from top–down control of their zooplankton prey resources (Baumann *et al.*, 2007).

Productivity is also influenced by the effect of temperature on growth rate (Brander, 1995; Teal *et al.*, 2008). In a comparative study of 15 cod stocks, the sevenfold differences in productivity among stocks corresponded to differences in temperature in the environment (Dutil and Brander, 2003). Fish species are generally plastic in the age and size at which they become sexually mature. An increase in juvenile growth, as well as an increase in temperature, may result in a decrease in the length and/or age of first maturation, affecting growth of adults, as surplus energy is channelled into reproduction at an earlier age and/or smaller size (Heino *et al.*, 2002b).

High mortality may occur when temperature conditions reach extreme values. Low temperatures during winter may increase mortality, especially of smaller fish, which have relatively fewer energy reserves than larger conspecifics (Post and Evans, 1989; Sogard, 1997). During severe winters in the North Sea, high mortality has frequently been reported for Lusitanian species, such as sole (*Solea solea*) and conger eel (*Conger conger*), but only rarely for Boreal species, such as cod, plaice (*Pleuronectes platessa*), and dab (*Limanda limanda*; Woodhead, 1964a). High mortality may also occur during hypoxic or anoxic conditions, as has been reported for the Kattegat (Diaz, 2001). Although mass mortalities during summer in relation to harmful algal blooms have been reported elsewhere (Yin *et al.*, 1999; Heil *et al.*, 2001), no records are known for the Northeast Atlantic. Climate change may have the most dramatic (negative) impacts on the productivity of fish populations by increasing the frequency of these "episodic" extreme events.

For some broadcast-spawning fish species, there is evidence that the size of populations is determined by the size and availability of spawning and/or nursery habitats (Rijnsdorp *et al.*, 1992; Gibson, 1994; Sparholt, 1996; MacKenzie *et al.*, 2000). Limits on the availability of these habitats may act as a bottleneck for population size (and/or productivity). In these cases, the focus should be on the impact of climate change on the critical life-history stage(s). Whether this relationship is applicable will depend on the relative size of the habitat in relation to that of other life-history stages, and is determined by the specific geographic setting.

Life-cycle closure may be affected if climate change influences the connectivity between habitats of successive life-history stages (Sinclair, 1988). For example, changes in ocean climate may affect the transport of eggs and larvae between spawning grounds and nursery areas (Corten, 1986; van der Veer *et al.*, 2000; Wilderbuer *et al.*, 2002), or the timing of spawning migrations, which may influence the arrival of adults at the spawning grounds (Sims *et al.*, 2004).

24.3.4 Ecosystem response

Climate change can affect all trophic levels of marine ecosystems, eventually resulting in changes in the productivity and distribution of fish stocks. At lower trophic levels, climate is expected to affect primary and secondary productivity through its effect on physiological rates of species, availability of nutrients (upwelling or stratification), and advection of water into shelf areas and enclosed basins (Section 8).

At a qualitative level, the increase in average and extreme winds over European marine areas may increase upwelling, enhance primary production, and eventually increase fish productivity (Dickson *et al.*, 1988; Jahncke *et al.*, 2004; Rykaczewski and Checkley, 2008). A further effect will be the translocation of deep-water species into shelf seas (Blanchard and Vandermeirsch, 2005). Within shelf areas, increased warming will result in earlier water-mass stratification (if not balanced by increased wind mixing), that will affect the timing of the spring bloom and the level and composition of primary production. Primary productivity may also be influenced by changes in precipitation and river run-off. In areas where coastal production is enhanced by nutrient input (from either organic matter or nutrients through rivers), changes in precipitation will probably affect coastal fish production. Hence, in the Bay of Biscay, an increase in river run-off may enhance the productivity of sole, whereas, in the Mediterranean, a decrease in run-off could lead to a decrease in the productivity of sole (Salen-Picard *et al.*, 2002; Le Pape *et al.*, 2003; Darnaude *et al.*, 2004; see also Section 21).

Climate-driven changes in the level of primary productivity will probably be accompanied by phenological changes that affect lower trophic-level coupling and eventually the recruitment success of marine fish (Cushing, 1990). Changes in phenology and a resulting trophic mismatch have been reported for the North Atlantic plankton community, where the level of response differs throughout the community and the seasonal cycle, leading to a mismatch between trophic levels and functional groups (Platt *et al.*, 2003; Beaugrand *et al.*, 2003; Edwards and Richardson, 2004). This trophic mismatch can eventually affect fish-stock recruitment, as demonstrated for the interaction between North Sea cod and the copepod *Calanus finmarchicus* (Durant *et al.*, 2005; Section 17). To some extent, biophysical modelling approaches can be used to identify "mediator chains" (Dippner, 2006), describing how climate-induced changes in physical factors (e.g. stratification) are propagated up the foodweb to affect processes (e.g. match–mismatch dynamics) important to the survival of marine fish (e.g. Daewel, 2008; Daewel *et al.*, 2008a, 2008b; Section 4).

Beyond a strict bottom–up control, a number of different control patterns exist within foodwebs (i.e. top–down and wasp-waist controls), and climate-induced changes will depend on the prevailing control pattern, making it challenging to predict how climate change will affect marine fish stocks within those foodwebs (Stenseth *et al.*, 2002; Jennings *et al.*, 2008; Section 8). There is a lasting discussion about whether ecosystems are primarily regulated by bottom–up or top–down processes (Frank *et al.*, 2007). The traditional view in marine ecology of a bottom–up control (Strong, 1992) is supported by a number of recent studies (Ware and Thomson, 2005; Greene and Pershing, 2007). Other studies, however, suggest that the dominance of bottom–up control can switch to top–down control, leading to trophic cascades initiated by overfishing (Worm and Myers, 2003; Frank *et al.*, 2005; Daskalov *et al.*, 2007; Möllmann *et al.*, 2008).

Moreover, recent studies emphasize the simultaneous importance of both climate-induced (bottom–up) and fisheries-induced (top–down) effects in marine ecosystem reorganizations (Möllmann *et al.*, 2008, 2009). The strength of these processes also appears to depend on foodweb complexity and thermal conditions (Frank *et al.*, 2007), and may oscillate between bottom–up and top–down control (Hunt *et al.*, 2002; Hunt and McKinnell, 2006). The control change can be triggered by both climate changes and overfishing (Litzow and Ciannelli, 2007; Casini *et al.*, 2008a, 2008b). Hence, predicting the effect of climate changes on marine ecosystem development and, hence, the productivity of different fish stocks, particularly in light of the additional (interacting) pressure of exploitation, is a major challenge for the future (Greene and Pershing, 2007).

24.3.5 Effects of fishing

Fisheries may interact with climate change by causing changes in fish populations through various mechanisms (Sections 8 and 9). Climate change may affect the distribution of particular species and hence their susceptibility to particular fishing fleets, making them more or less "catchable" (Section 10). Similarly, climate-related distribution shifts may affect the protective capabilities of closed areas, because species or life stages may shift outside the boundaries of the protected area and so become vulnerable to fishing (e.g. the North Sea "Plaice Box": van Keeken *et al.*, 2007).

Extensive fishing may render fish populations more vulnerable to short-term, natural climate variability (O'Brien *et al.*, 2000; Walther *et al.*, 2002; Beaugrand *et al.*, 2003; Anderson *et al.*, 2008) by making such populations less able to "buffer" the effects of occasional poor year classes. During recent decades, there has been a clear, positive correlation between temperature and recruitment in northeast Arctic cod; however, this link was weak or non-existent in earlier periods (Ottersen and Stenseth, 2001). A major implication is that fishery-induced impoverishment of stock structure (reduced and fewer ages, smaller sizes) can increase the sensitivity of a previously robust stock to climate change (Ottersen *et al.*, 2006). Conversely, long-term climate change may make stocks more vulnerable to fishing by reducing the overall carrying capacity of the stock, so that it might not be sustained at, or expected to recover to, levels observed in the past (Jennings and Blanchard, 2004).

Fishing will have a major influence on the size structure and species composition of the fish assemblage and, thus, will affect predator–prey relationships (Rice and Gislason, 1996; Daan *et al.*, 2005). Fishing will interact with global warming, because body size generally increases with latitude (Belk and Houston, 2002) and small fish species may take advantage of the removal of larger predatory fish (Daan *et al.*, 2005). Fishing may also affect ecosystem control, causing bottom–up systems to become top–down controlled systems. How climate change will interact with fishing will depend on the species affected and, eventually, on the prevailing patterns of ecosystem structure and function (Heath, 2005). Hence, the response of ecosystems to climate change and fishing pressure is currently difficult to predict.

24.4 Working hypotheses

The response of fish populations to climate change will differ between species. The difference may be related to their adaptations to the environmental conditions in their respective habitats. As such, the biogeographic affinities of the species may be used as a proxy for their expected response to a change in temperature (e.g. Section 2 and Annexes 1–4 on the biogeographic affinities of North Sea, Baltic, Irish Sea, and other European marine fish species). Populations living near the limits of their distribution area are probably also living close to the limits of their physiological tolerance range and are therefore more vulnerable to changes in abiotic conditions than populations living at the centre of their distribution area (Miller *et al.*, 1991). As water temperature is correlated with water depth, fish may move into deeper waters during summer in order to avoid the warmer waters in shallow areas (Dulvy *et al.*, 2008). This leads to the first set of working hypotheses.

- **H1a**. Populations at the limits of their latitudinal range will demonstrate stronger responses than those at the centre of their latitudinal distribution.
- **H1b**. Northern species at the southern limits of their distribution will decrease in abundance, and southern species at the northern limits of their range will increase in abundance.
- **H1c**. Species will shift into deeper, cooler waters in response to an increase in water temperature.

The responses of species to climate change are expected to be influenced by their habitat requirements (pelagic, demersal, deep-water species), life-history characteristics (short-lived or long-lived; specialist or generalist), and trophic position within the ecosystem (apex predators or forage fish). Although the early life stages of many pelagic fish species reside in demersal habitats, and those of many demersal fish are pelagic, fish that are strictly pelagic (all life stages) inhabit water masses with certain abiotic conditions whose spatial distribution may change as a result of climate change. On the other hand, demersal fish may have specific habitat requirements that are geographically fixed by their seabed characteristics.

Environmental conditions tend to be more constant at greater depths, although deep-water fish may be influenced indirectly by changes in productivity in levels above (food availability) and by changes in deep-water currents. Generalists can adapt to prevailing patterns of food availability, whereas specialists depend strongly on the success of particular prey organisms. Short-lived species, characterized by high reproductive rates (so-called *r*-strategists), are likely to respond to changes in their environment relatively rapidly, whereas long-lived species (*K*-strategists) will be slower (Perry *et al.*, 2005). The ability to respond to changes in their environment will apply to both an improvement and a deterioration in environmental conditions. This leads to the second set of hypotheses.

- **H2a**. Pelagic and demersal species will differ in their distributional responses, because the former can respond to changes in water masses more easily than the latter, which may have more geographically fixed habitat requirements.
- **H2b**. Deep-water fish species will be less affected by climate change than shelf or coastal species.
- **H2c**. Fish species with narrow dietary preferences will be more sensitive to climate change than generalists.
- **H2d**. Short-lived species will demonstrate stronger responses and will be better equipped to adapt to changes in their environment than long-lived species.

Populations can survive in systems where habitats suitable for different life-history stages are available and connected, allowing life cycle closure (Sinclair, 1988). If the habitat for a particular life-history stage is spatially restricted, a change in habitat suitability of this stage will make the species more sensitive to climate change than species, which do not have spatially restricted habitat requirements. Populations living in areas with a large heterogeneity in environmental conditions, or which migrate over large distances, will be more able to survive by selecting appropriate environments than populations , which live in large areas with a more homogeneous environment. This leads to the third set of hypotheses.

- **H3a**. Species with spatially restricted habitat requirements during part of their life history will be more sensitive to climate change than species without specific habitat requirements.
- **H3b**. Fish populations in oceanographic systems with a high variety of mesoscale features will be less sensitive to climate change.

Fishing will reduce the size and age structure of a population and reduce its "bet hedging" capabilities, thus allowing it to respond to conditions suitable for the survival of eggs and larvae (Rothschild, 1986; Ottersen *et al.*, 2006). Also, fishing may lead to a reduction in genetic variability that would negatively affect the possibilities of an evolutionary response to climate change and the ability of depleted stocks to recover (Anderson *et al.*, 2008).

- **H4**. Fish stocks under climate change will be more vulnerable to fishing pressure.

The ecosystem response to climate change will depend on the response of the individual species and the resulting effect on trophodynamic interactions among species. Different species within a foodweb will not all respond the same way to climate change. Species-rich systems, characterized by many weak, readily interchangeable feeding links rather than a few strong links, will probably be more stable, because different species may take over vacant ecological functions (Link, 2002) and may be more resilient (Frank *et al.*, 2007) in light of climate change. Climate change will not necessarily lead to gradual and predictable changes in fish populations and ecosystem state. Ecosystems may demonstrate multiple stable equilibriums, and climate change may push systems into a new equilibrium (Scheffer and Carpenter, 2003). Once a regime shift has occurred, it may be disproportionately difficult to return to the original state (Beaugrand, 2004; Daskalov *et al.*, 2007; Möllmann *et al.*, 2008).

- **H5a**. Ecosystems with a simple trophic structure will demonstrate more rapid responses to climate change than ecosystems with a more complex trophic structure.
- **H5b**. Changes in ecosystem structure caused by climate change will be abrupt.

The introduction of non-native species to a marine ecosystem and its subsequent establishment may cause effects that range from almost undetectable to marked (e.g. the complete domination and displacement of native communities; Eno *et al.*, 1997). Improved environmental conditions, as well as new shipping routes, will facilitate the spread of warm-water fish species and pathogens. New species may be introduced to the Arctic as a result of ice-free shipping routes (ACIA, 2004), and further colonization of the Mediterranean by tropical species through the Suez Canal can be anticipated.

- **H6**. With improved local conditions, an increasing number of exotic warm-water fish species (and fish pathogens) will become established in European waters.

24.5 Observed changes in distribution and abundance

This section reviews changes in distribution, abundance, and growth of a selection of fish species in the Northeast Atlantic (Table 24.1) against the background of the above working hypotheses. The species selected were those for which sufficient data were available (commercially important species) and those which represented different ecotypes, combining biogeographic affinity (Lusitanian, Boreal, Atlantic), habitats (pelagic or demersal; Atlantic or shelf), and longevity (short, medium, long).

Changes in abundance and distribution of Northeast Atlantic marine species support the first set of hypotheses. Lusitanian species have increased in recent decades (sprat, anchovy (*Engraulis encrasicholus*), horse mackerel (*Trachurus trachurus*), red mullet (*Mullus surmuletus*), John dory (*Zeus faber*)), particularly at the northern limit of their distribution areas, whereas Boreal species generally decreased at the southern limit of their distribution area (cod, plaice), but increased at the northern limit (cod). A shift in distribution to deeper waters was recorded in the Boreal species cod and plaice (Hedger *et al.*, 2004; Perry *et al.*, 2005; van Keeken *et al.*, 2007; Dulvy *et al.*, 2008).

Comparison of the changes in distribution between pelagics and demersals provides support for the second set of hypotheses. For the pelagic species, changes in distribution patterns have been observed that are related to climate-induced changes in the distribution of their food (herring (*Clupea harengus*), Toresen and Østvedt, 2000; Corten, 2001a, 2001b; horse mackerel, Borges *et al.*, 1996; Iversen *et al.*, 2002; mackerel (*Scomber scombrus*), Reid *et al.*, 2001b; ICES, 2007i). Changes in plankton have been linked to changes in climate (Beaugrand *et al.*, 2002; Richardson and Schoeman, 2004). A comparison between demersal and pelagic species tentatively suggests that changes in the distribution of the former are smaller than those of the latter. The northward shifts in cod have been related to the transport of eggs and larvae (pelagic life stages), but not to a northward movement of the later (demersal) life stages (Rindorf and Lewy, 2006).

With regard to the underlying mechanisms, available evidence suggests that observed changes in productivity are, at least partly, related to a climate-related change in recruitment (herring, anchovy, sprat, cod, plaice, sole), either because of higher production or survival in the egg or larval stage (herring, anchovy, sprat, cod), or because of a change in the quality or quantity of the nursery habitat (plaice, sole). In sole and plaice, there is evidence that the timing of spawning is influenced by temperature during the spawning period (Teal *et al.*, 2008). In the Northwest Atlantic, such an effect is also reported for cod (Hutchings and Myers, 1994b). The negative relationship between recruitment and temperature in sole in the North Sea contrasts to the expected positive relationship in this Lusitanian species.

Temperature-related changes in growth were reported for cod (Brander, 1995; Dutil and Brander, 2003; Section 17) and age-0 sole and plaice (Teal *et al.*, 2008; Sections 20 and 21). The mean length of sole, a Lusitanian species, has increased in autumn because of an increase in growth rate as well as an increase in duration of the growing season. However, no change in mean length was observed in plaice, a Boreal species that exhibited an increased growth rate early in the season but a reduced growth rate during summer, when temperature exceeded its optimal temperature. Growth rates of older age groups of sole and plaice demonstrate a dome-shaped pattern since the late 1950s, with relatively high growth rates between the mid-1960s and mid-1980s, which were not correlated with changes in temperature (Millner and Whiting, 1996; Rijnsdorp and van Leeuwen, 1996). Available data do not allow a quantitative comparison of the relative effects of climate-induced changes in recruitment and in juvenile and adult growth rates on productivity. The results of the selected species did not allow hypotheses 3–5 to be tested.

With regard to the hypothesis on invasive species (hypothesis 6), there is strong evidence that increasing connectivity between geographically distinct areas may result in major changes in ecosystems (see also Section 10). The opening of the Suez Canal in 1869 allowed entry of Indo-Pacific and Red Sea biota into the southeastern Mediterranean, where these so-called "Lessepsian migrants" now dominate the fish community (50–90% of fish biomass). For many decades, this migration was very limited, partly because of extremely high salinity within the Suez Canal, where dry salt valleys had existed previously. With the warming trend of seawater and a significant drop in the canal's salinity to normal marine levels (Mavruk and Avsar, 2007), record numbers of newly established non-native fish species have recently been observed in the southeastern Mediterranean, leading to the creation of a human-assisted Erythrean (Red Sea) biotic province (Goren and Galil, 2005). Trans-local fish species, such as the round goby (*Neogobius melanostomus*), have also become established in the Baltic Sea (Karlson *et al.*, 2007).

24.6 Discussion

We propose a framework for the study of the impact of climate change on fish populations and derive a set of testable hypotheses based on first principles. Similar to that of Harley *et al.* (2006), the framework recognizes that climatic factors will affect successive life-history stages (eggs, larvae, juveniles, adults) in different ways and via processes acting at all levels of biological organization (from organismal-level physiological responses to population-level disturbances to ecosystem-level/trophodynamic impacts). The different levels of organization can be viewed as a mechanistic chain. Population-level processes will only operate within the appropriate physiological envelope of abiotic conditions. Equally, ecosystem-level processes will only be relevant when life-cycle closure is possible within the specific geographic location, providing interconnection between suitable habitats of successive life-history stages. This framework structures the analysis of the published data and provides the basis for modelling studies to test hypotheses. In our analysis, we have focused mainly on the effects of temperature, although other factors may be incorporated.

Knowledge of the ecophysiology of different life stages will provide a strong basis from which to infer the response of a species to a change in temperature (and other climate-driven changes in abiotic factors). It will allow us to define the bioclimate envelope and to evaluate the change in habitat suitability for different life stages (Pearson and Dawson, 2003) or whether observed temperature changes may be responsible for the change in population abundance (e.g. for eelpout (*Zoarces viviparus*) in the Wadden Sea; Pörtner and Knust, 2007). Although we have dealt mainly with temperature, climate change may also affect oxygen, salinity, and ocean pH. These factors may load the metabolic scope and decrease the tolerance range of the organism (Fry, 1971), subsequently making it more vulnerable to climate change.

Ecophysiological data can also indicate whether or not species or species groups may differ in sensitivity to change in temperature affecting trophic relationships. A review of experimental data on optimum temperature and temperature-tolerance ranges of a number of fish and (epi-)benthic invertebrate species demonstrated clear species differences, suggesting that an increase in temperature will lead to a shift in predation pressure from cod and gobies to brown shrimp (*Crangon crangon*; Freitas *et al.*, 2007). If the temperature sensitivity of species groups, such as autotrophs and heterotrophs, ectotherms and endotherms, and taxonomic groups of different complexity, differ in a systematic manner, this will provide a basis for predicting the effects of temperature change on species and species interactions. Research into differences in sensitivity among species (groups), as well as the underlying mechanism, is needed.

Although climate change may influence vital rates and productivity of a fish stock (growth, mortality, and recruitment), we suggest that early life-history stages will be most sensitive to the effects of climate change. The underlying mechanisms may differ among species or stocks and will depend on trophic position (Frank *et al.*, 2007). The importance of processes affecting early life-history stages to the determination of productivity of a fish stock is corroborated by a literature review of a selected number of well-studied species in the Northeast Atlantic, indicating the importance of temperature effects on the level of recruitment (Table 24.1). Moreover, multi-decadal changes in ocean climate have been driving changes in recruitment and productivity in the North Atlantic and Pacific Ocean (Lehodey *et al.*, 2006). Climate-related changes in growth of recruited life-history stages may influence fish productivity (Dutil and Brander, 2003; Lehodey *et al.*, 2006), although this effect may be confounded by a change in intra- or interspecific competition for food. Global warming will reduce the probability of low winter temperatures, leading to improved survival of both southern species and fish of small body size (Post and Evans, 1989). A critical test of whether or not this inference holds true has yet to be performed. Most studies in the literature have focused on a specific part of the life cycle and did not attempt to study all processes in an integrated manner. Dutil and Brander (2003) distinguished between the effects of temperature on growth and recruitment, but were unable to measure recruitment independent of growth rate prior to recruitment to the fisheries.

Given the complexity of the problem, where climate change is a multifaceted driver and the affected fish population is also multifaceted, we believe that scientific progress will benefit from an approach whereby *a priori* hypotheses are formulated, based on first principles of the relevant levels of organization. The hypotheses proposed here are certainly not complete, but should be viewed as a first set. These hypotheses seek to compare species and species groups that have contrasting ecological characteristics and, therefore, are likely to differ in their responses to climate change. The classification of species into ecotypes, based on biogeographic affinity, habitat requirements, and life-history characteristics, may be an important starting point. The review of a number of well-studied fish species in the Northeast Atlantic did not allow us to test each of the working hypothesis, but supported the hypotheses that species exhibit distributional shifts (latitude and depth) in response to temperature increase, and that the response of pelagic species is stronger than that in demersal species, corroborating a number of recent studies on changes of fish assemblages (Attrill and Power, 2002; Beare *et al.*, 2004; Genner *et al.*, 2004).

We argue that understanding the complex impacts of climate on a species will require an integrated, life-cycle approach that examines the importance of different mechanisms acting on all life stages and identifies those developmental stages and mechanisms most critical for life-cycle closure and recruitment. Examples of this type of approach include the body of work performed on Baltic cod and sprat (e.g. Köster *et al.*, 2003b, 2005; Möllmann *et al.*, 2008), which highlights the possible complex feedback among elements of our framework (i.e. impacts of physiology on behaviour, behaviour on top–down processes, and climate-driven physical forcing on bottom–up processes).

Table 24.1. Review of the observed changes in distribution, abundance, and production related to climate change in a selection of commercially exploited fish and shellfish species of contrasting ecotypes (Section 2). Ecotypes were defined as a combination of the following characteristics: habitat (pelagic or demersal; Atlantic or Shelf), biogeographic affinity (Atlantic, Lusitanian, or Boreal), and longevity (long, medium, or short).

CHANGE	COMMENTS	SOURCE
Pelagic species		
Atlantic herring (*Clupea harengus*): Shelf, Boreal, Medium		
Herring populations demonstrate multidecadal variations	Multidecadal variations related to climate variations (Russell cycle) and fisheries. Great salinity anomaly affected larval transport in North Sea. Recruitment related to temperature; positive relationship in northern population (Norwegian spring-spawning herring)	Alheit and Hagen (1997), Cardinale *et al.* (2009), Corten (1986, 2001b), MacKenzie *et al.* (2007), Toresen and Østvedt (2000)
Norwegian spring-spawners: changes in overwintering, feeding, and spawning areas; North Sea herring: more northern distribution with warmer temperatures	Distribution changes related to changes in food distribution	Holst *et al.* (2002), Toresen and Østvedt (2000), Corten (2001a, 2001b)
Anchovy (*Engraulis encrasicolus*): Shelf, Lusitanian, Short		
Increase in abundance in northern areas (North Sea); decrease in Bay of Biscay	Increase in North Sea may be temperature-related; change in Bay of Biscay related to fishing; role of climate uncertain	Boddeke and Vingerhoed (1996), MacKenzie *et al.* (2007)
Sprat (*Sprattus sprattus*): Shelf, Lusitanian, Short		
Increase in abundance and production in Baltic; stock collapse in Black Sea	Increased recruitment at higher temperature (and reduced cod predation) at northern limit (Baltic) and decrease at higher temperature at southern limit (Black Sea)	Köster *et al.* (2003b), MacKenzie and Köster (2004), Möllmann *et al.* (2008), Daskalov *et al.* (2007)
Mackerel (*Scomber scombrus*): Atlantic, Atlantic, Long		
Northward shift in spawning and feeding areas; earlier spawning; increased variation in recruitment		Reid *et al.* (2001b), ICES (2007i)
Horse mackerel (*Trachurus trachurus*): Atlantic, Lusitanian, Long		
Increase in northern areas	Increase in north related to change in migration to feeding areas	Iversen *et al.* (2002), Borges *et al.* (1996)
Sandeel (*Ammodytes marinus*): Shelf, Boreal, Short		
Decrease in North Sea sandeel biomass in 2000s	Mismatch of larvae and their zooplankton food	Arnott and Ruxton (2002), ICES (2006o)
Demersal species		
Atlantic cod (*Gadus morhua*): Shelf, Boreal, Long		
Increase in abundance in northern areas at higher water temperatures	northeast Arctic cod: increase in recruitment at higher temperatures (overfishing increased sensitivity of the relationship); temperature-related shifts in spawning sites	Heath (2007a), Planque and Frédou (1999), Ottersen *et al.* (2006)
Growth	Body growth is strongly temperature related	Brander (1995)
Productivity changes in Baltic related to inflow of saline Atlantic water	Volume of spawning habitat where eggs and larvae can survive depends on inflow of saline water from North Sea	Sparholt (1996), MacKenzie *et al.* (2000)
Decrease in abundance in southern areas (e.g. North Sea)	Recruitment related to climate effects on zooplankton production and to temperature; also, high fishing pressure	O'Brien *et al.* (2000), Beaugrand *et al.* (2003)
Northward shift in distribution within North Sea	Likely owing to different fishing pressure and local survival of eggs/larvae	Hedger *et al.* (2004), Perry *et al.* (2005), Rindorf and Lewy (2006)

Change	**Comments**	**Source**
Shift to deeper waters in North Sea	No evidence for cod actively swimming north or to deeper water	Hedger *et al.* (2004), Neat and Righton (2007)
Red mullet (*Mullus surmuletus*): Shelf, Lusitanian, Medium		
Marked increase in northern parts of distribution, northward range expansion	Probably related to temperature; e.g. in North Sea, during summer mainly in (warmer) southeast, during winter mainly in northwest (then warmer); historically, has also had more northerly distributions during earlier warm periods	Beare *et al.* (2005), Enghoff (2000)
John dory (*Zeus faber*): Shelf, Lusitanian, Medium		
Marked increase in northern parts of distribution	Probably related to temperature; entering North Sea mainly from northwest	Beare *et al.* (2004)
Plaice (*Pleuronectes platessa*): Shelf, Boreal, Long		
Distribution shift to deeper waters (North Sea)	Temperature a likely cause, although other factors may have contributed	Perry *et al.* (2005), van Keeken *et al.* (2007)
Decrease in abundance in southern nursery grounds (Bay of Biscay)		Désaunay *et al.* (2006)
Recruitment negatively related to temperature in waters around UK		Fox *et al.* (2000b)
Timing of spawning advanced in warm years (North Sea)		Teal *et al.* (2008)
Changes in growth do not correlate with temperature, except in age-0 groups	Growth related to population abundance, eutrophication, and bottom trawling; growth of age-0 groups determined by temperature	Rijnsdorp and van Leeuwen (1996), Teal *et al.* (2008)
Sole (*Solea solea*): Shelf, Lusitanian, Long		
Recruitment related to river run-off (Bay of Biscay, Mediterranean Sea)	Nursery habitat quality/quantity increases	Salen-Picard *et al.* (2002), Le Pape *et al.* (2003), Darnaude *et al.* (2004)
Recruitment negatively related to temperature in North Sea and positively in the Bristol Channel		Rijnsdorp *et al.* (1992), Henderson and Seaby (2005)
Timing of spawning advanced in warm years (North Sea)		Teal *et al.*, 2008
Length at end of first year increases with temperature. Changes in growth of older fish do not correlate with temperature	Growth of age-0 group determined by temperature and length of growing season. Growth of older age groups related to population abundance, eutrophication, and bottom trawling	Teal *et al.* (2008), Millner and Whiting (1996)
Shellfish species		
Brown shrimp (*Crangon crangon*): Coastal , Boreal, Short		
Increase in abundance in North Sea and Iceland	Increase likely owing to higher temperature (Iceland, North Sea) and reduced predation (North Sea)	Hufnagl and Temming (2010), Gunnarson *et al.* (2007)
Norway lobster (*Nephrops norvegicus*): Shelf, Lusitanian, Medium		
Increase in northern areas, decrease in southern areas	Probably combination of reduced predation in north (owing to cod declines), temperature changes, and effort	Zuur *et al.* (2003), Björnsson and Dombaxe (2004)

25 References

Abella, A., Fiorentino, F., Mannini, A., and Orsi Relini, L. 2008. Exploring relationships between recruitment of European hake (*Merluccius merluccus* L. 1758) and environmental factors in the Ligurian Sea and the Strait of Sicily (Central Mediterranean). Journal of Marine Systems, 71: 279–293.

Abelló, P., Carbonell, A., and Torres, P. 2002. Biogeography of epibenthic crustaceans on the shelf and upper slope off the Iberian Peninsula Mediterranean coasts: implications for the establishment of natural management areas. Scientia Marina, 66(Suppl. 2): 183–198.

ACIA. 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment (ACIA). Cambridge University Press, Cambridge, UK. 139 pp.

ACIA. 2005. Arctic Climate Impact Assessment. Cambridge University Press, Cambridge, UK. 1042 pp.

Acosta, J. J., Muñoz, I., and Juárez, A. 2008. First record of *Chloroscombrus chrysurus* (Osteichthyes, Carangidae) in the Spanish waters of the Gulf of Cadiz, (ICES Division IXa South). Journal of the Marine Biological Association – Biodiversity Records. 3 pp. Available online at http://www.mba.ac.uk/jmba/pdf/5122pdf.

Aebischer, N. J., Coulsen, J. C., and Colebrook, J. M. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature, 347: 753–755.

Agnalt, A. L. 1989. Long-term changes in growth and age at maturity of mackerel, *Scomber scombrus* L. Journal of Fish Biology, 35(Suppl. A): 305–311.

Agostini, V., and Bakun, A. 2002. "Ocean triads" in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy (*Engraulis encrasicolus*)). Fisheries Oceanography, 11: 129–142.

Agostini, V. N., Hendrix, A. N., Hollowed, A. B., Wilson, C. D., Pierce, S. D., and Francis, R. C. 2008. Climate-ocean variability and Pacific hake: a geostatistical modelling approach. Journal of Marine Systems, 71: 237–248.

Aguzzi, J., and Sardà, F. 2008. A history of recent advancements on *Nephrops norvegicus* behavioral and physiological mechanisms. Reviews in Fish Biology and Fisheries, 18: 235–248.

Ahlmann, H. W. 1949. Introductory address. ICES Special Scientific Meeting on Climatic Changes in the Arctic in Relation to Plants and Animals. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 125: 9–16.

Aksnes, D. L., and Blindheim, J. 1996. Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. Ophelia, 44: 7–28.

Akyol, O., Unal, V., and Ceyhan, T. 2006. Lessepsian migrant fish, *Oxyurichthys petersi* (Gobiidae) and *Upeneus pori* (Mullidae), from the Aegean Sea. Cybium, 30: 389–390.

Alcock, R. 2003. The effects of climate change on rocky shore communities in the Bay of Biscay, 1895–2050. PhD thesis, Biodiversity and Ecology Division, University of Southampton, UK. 286 pp.

Alheit, J., and Hagen, E. 1996. The Bohuslän herring periods: are they controlled by climate variations or local phenomena? ICES Document CM 1996/O:6.

Alheit, J., and Hagen, E. 1997. Long-term climate forcing of European herring and sardine populations. Fisheries Oceanography, 6: 130–139.

Alheit, J., Wahl, E., and Cibangir, B. 1987. Distribution, abundance, development rates, production, and mortality of sprat eggs. ICES Document CM 1987/H:45.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science, 62: 1205–1215.

Alheit, J., Voss, R., Mohrholz, V., and Hinrichs, R. 2007. Climate drives anchovies and sardines into the North Sea. GLOBEC Newsletter, 13: 77–78.

Allain, G., Petitgas, P., and Lazure, P. 2001. The influence of mesoscale ocean processes on anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay estimated with a three-dimensional hydrodynamic model. Fisheries Oceanography, 10: 151–163.

Allain, G., Petitgas, P., Grellier, P., and Lazure, P. 2003. The selection process from larval to juvenile stages of anchovy (*Engraulis encrasicolus*) in the bay of Biscay investigated by Lagrangian simulations and comparative otolith growth. Fisheries Oceanography, 12: 407–418.

Allain, G., Petitgas, P., Lazure, P., and Grellier, P. 2007. Biophysical modelling of larval drift, growth and survival for the prediction of anchovy (*Engraulis encrasicolus*) recruitment in the Bay of Biscay (NE Atlantic). Fisheries Oceanography, 16: 489–505.

Allen, J. I., Blackford, J., Holt, J., Proctor, R., Ashworth, M., and Siddorn, J. 2001. A highly spatially resolved ecosystem model for the North West European Continental Shelf. Sarsia, 86: 423–440.

Allen, J. I., Somerfield, P. J., and Gilbert, F. J. 2007a. Quantifying uncertainty in high-resolution coupled hydrodynamic ecosystem models. Journal of Marine Systems, 64: 3–14.

Allen, J. I., Holt, J., Blackford, J., and Proctor, R. 2007b. Error quantification of a high-resolution coupled hydrodynamic-ecosystem coastal-ocean model. Part 2. Chlorophyll-*a*, nutrients and SPM. Journal of Marine Systems, 68: 381–404.

Allen, S. E., Dinniman, M. S., Klinck, J. M., Gorby, D. D., Hewett, A. J., and Hickey, B. M. 2003. On vertical advection truncation errors in terrain-following numerical models: comparison to a laboratory model for upwelling over submarine canyons. Journal of Geophysical Research, 108(C1), 3003, doi: 10.1029/2001JC000978.

Almeida, A. J., and Biscoito, M. 2007. New records of *Synaphobranchus* (Anguilliformes, Synaphobranchidae) from off the Azores (eastern Atlantic Ocean). Cybium, 31: 391–392.

Alshuth, S. 1988. Bestimmung von Alter und Wachstumsraten bei Larven und Juvenilen der Sprotte, *Sprattus sprattus* L. PhD thesis, Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven, Germany. 191 pp.

AMAP. 1998. AMAP Assessment Report: Arctic Pollution Issues. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. 859 pp.

Amara, R., Meziane, T., Gilliers, C., Hermel, G., and Laffargue, P. 2007. Growth and condition indices in juvenile sole *Solea solea* measured to assess the quality of essential fish habitat. Marine Ecology Progress Series, 351: 201–208.

Ambar, I., Fiuza, A., Boyd, T., and Frouin, R. 1986. Observations of a warm oceanic current flowing northward along the coasts of Portugal and Spain during Nov.–Dec. 1983. EOS Transactions of the American Geophysical Union, 67: 1054.

Andersen, K. H., and Beyer, J. E. 2006. Asymptotic size determines species abundance in the marine size spectrum. American Naturalist, 168: 54–61.

Anderson, C. N. K., Hsieh, C-H., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., *et al.* 2008. Why fishing magnifies fluctuations in fish abundance. Nature, 452: 835–839.

Andersson, H. C. 2002. Influence of long-term regional and large-scale atmospheric circulation on the Baltic sea level. Tellus, 54A: 76–88.

Aneer, G. 1985. Some speculations about the Baltic herring (*Clupea harengus membras*) in connection with the eutrophication of the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences, 42: 83–90.

Angilletta, M. J., and Dunham, A. E. 2003. The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. American Naturalist, 162: 332–342.

Angilletta, M. J., Steury, T. D., and Sears, M. W. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integrated Comparative Biology, 44: 498–509.

Anon. 1960. The sandeel story. World Fish, 9: 30–33.

Anon. 1997. Black Sea Transboundary Diagnostic Analysis. United Nations Publications, New York. 142 pp.

Anthony, V. C., and Fogarty, M. J. 1985. Environmental effects on recruitment, growth and vulnerability of Atlantic herring (*Clupea harengus harengus*) in the Gulf of Maine Region. Canadian Journal of Fisheries and Aquatic Sciences, 42: 158–173.

Arbault, S., and Lacroix, N. 1971. Aires de ponte de la sardine, du sprat et de l'anchois dans le golfe de Gascogne et sur le plateau celtique: résultats de 6 années d'étude. Revue des Travaux de l'Institut des Pêches Maritimes, 35: 35–56.

Arbault, S., Camus, P., and le Bec, C. 1986. Estimation du stock de sole (*Solea vulgaris*, Quensel 1806) dans le Golfe de Gascogne à partir de la production d'œufs. Journal of Applied Ichthyology, 4: 145–156.

Armstrong, M. J. 1979. The feeding ecology of a demersal fish community over a muddy substrate off the west coast of the Isle of Man. PhD thesis, University of Liverpool, Isle of Man.

Armstrong, M. J. 1982. The predator–prey relationships of poor cod (*Trisopterus minutus*), pouting (*T. luscus*), and cod (*Gadus morhua*). Journal du Conseil International pour l'Exploration de la Mer, 40: 135–152.

Arnott, S. A., and Ruxton, G. D. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Marine Ecology Progress Series, 238: 199–210.

Aro, E. 1989. A review of fish migration patterns in the Baltic. Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer, 190: 72–96.

Aro, E., and Plikshs, M. 2004. The ecosystem effects of Baltic cod (*Gadus morhua callarias* L.) abundance and distribution changes in 1977–2004: from top–down to bottom–up control. ICES Document CM 2004/L:01.

Arrhenius, F., and Hansson, S. 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Marine Ecology Progress Series, 96: 125–137.

Arvedlund, M. 2009. First records of unusual marine fish distributions – can they predict climate changes? Journal of the Marine Biological Association of the UK, 89: 863–866.

Arzel, O., Fichefet, T., and Goosse, H. 2006. Sea ice evolution over the 20th and 21st centuries as simulated by current AOGCMs. Ocean Modelling, 12: 401–405.

Astraldi, M., Bianchi, C. N., Gasparini, G. P., and Morri, C. 1995. Climatic fluctuations, current variability, and marine species distribution: a case study in the Ligurian Sea (north-west Mediterranean). Oceanologica Acta, 18: 139–149.

Astraldi, M., Balopulos, S., Candela, J., Font, J., Gacic, M., Gasparini, G. P., Manca, B., *et al.* 1999. The role of straits and channels in understanding the characteristics of Mediterranean circulation. Progress in Oceanography, 44: 65–108.

Attrill, M. J., and Power, M. 2002. Climatic influence on a marine fish assemblage. Nature, 417: 275–278.

Attrill, M. J., Wright, J., and Edwards, M. 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnology and Oceanography, 52: 480–485.

Aurich, H. J. 1941. Die Verbreitung der pelagischen Fischbrut in der südlichen Nordsee während der Frühjahrsfahrten 1926–1937 der Deutschen Forschungsschiffe Poseidon und Makrele. Helgoländer Wissenschaftlichen Meeresunters, 2: 184–225.

Axenrot, T., and Hansson, S. 2003. Predicting herring recruitment from young-of-the-year densities, spawning stock biomass, and climate. Limnology and Oceanography, 48: 1716–1720.

Bacher, C., and Gangnery, A. 2006. Use of dynamic energy budget and individual based models to simulate the dynamics of cultivated oyster populations. Journal of Sea Research, 56: 140–167.

Bagge, O., Thurow, F., Steffensen, E., and Bay, J. 1994. The Baltic cod. Dana, 10: 2–28.

Bailey, K. M., and Houde, E. D. 1989. Predation on eggs and larvae of marine fish and the recruitment problem. Advances in Marine Biology, 25: 1–83.

Bailey, R. S. 1980. Problems in the management of short-lived pelagic fish as exemplified by North Sea sprat. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 477–488.

Bainbridge, V., and Forsyth, D. C. T. 1972. An ecological survey of a Scottish herring fishery. Part V: the plankton of the northwestern North Sea in relation to the physical environment and the distribution of the herring. Bulletin of Marine Ecology, 8: 21–52.

Bakun, A. 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. California Sea Grant College System, NOAA. 291 pp.

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. Progress in Oceanography, 68: 271–288.

Balon, E. K. 1984. Patterns in the evolution of reproductive styles in fish. *In* Fish Reproduction: Strategies and Tactics, pp. 35–53. Ed. by G. W. Potts and R. J. Wootten. Academic Press, London.

Bannister, R. C. A. 1978. Changes in plaice stocks and plaice fisheries in the North Sea. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 172: 86–101.

Bariche, M., and Saad, M. 2005. Settlement of the Lessepsian blue-barred parrotfish *Scarus ghobban* (Scaridae) in the Mediterranean. Journal of the Marine Biological Association 2 – Biodiversity Records. 3 pp. Available online at http://www.mba.ac.uk/jmba/pdf/5122pdf.

Barot, S., Heino, M., O'Brien, L., and Dieckmann, U. 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecological Applications, 14: 1257–1271.

Barrett, J. H., Locker, A. M., and Roberts, C. M. 2004. The origins of intensive marine fishing in medieval Europe: the English evidence. Proceedings of the Royal Society of London, Series B, 271: 2417–2421.

Barton, A. D., Greene, C. H., Monger, B. C., and Pershing, A. J. 2003. The Continuous Plankton Recorder survey and the North Atlantic Oscillation: interannual- to multidecadal-scale patterns of phytoplankton variability in the North Atlantic Ocean. Progress in Oceanography, 58: 337–358.

Bartsch, J., and Knust, R. 1994a. Simulating the dispersion of vertically migrating sprat larvae (*Sprattus sprattus* (L.)) in the German Bight with a circulation and transport model system. Fisheries Oceanography, 3: 92–105.

Bartsch, J., and Knust, R. 1994b. Predicting the dispersion of sprat larvae (*Sprattus sprattus* (L.)) in the German Bight. Fisheries Oceanography, 3: 292–296.

Bas, C., Macpherson, E., and Sarda, F. 1985. Fish and fishermen: the exploitable trophic levels. *In* Key Environments: Western Mediterranean, pp. 296–316. Ed. by R. Margalef. Pergamon Press, Oxford.

Bauchot, M. L., and Pras, A. 1980. Guide des Poissons Marins d'Europe. Delachaux and Niestle, Paris. 427 pp.

Baumann, H., Hinrichsen, H-H., Möllmann, C., Koester, F. W., Malzahn, A. M., and Temming, A. 2006. Recruitment variability in Baltic sprat, *Sprattus sprattus*, is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Canadian Journal of Fisheries and Aquatic Sciences, 63: 2191–2201.

Baumann, H., Peck, M. A., Götze, E., and Temming, A. 2007. Starving early juvenile sprat, *Sprattus sprattus* L., in western Baltic coastal waters: evidence from combined field and laboratory observations in August/September 2003. Journal of Fish Biology, 70: 863–866.

Baumann, H., Voss, R., Malzahn, A., and Temming, A. 2009. The German Bight (North Sea) is a nursery area for both locally and externally produced sprat juveniles. Journal of Sea Research, 61: 234–243.

Baxter, I. G., and Hall, W. B. 1960. The fecundity of the Manx herring and a comparison of the fecundities of autumn-spawning groups. ICES Document CM 1960/H–Herring Committee: 55. 8 pp.

Beamish, R. J., Benson, A. J., Sweeting, R. M., and Neville, C. M. 2004. Regimes and the history of the major fisheries off Canada's west coast. Progress in Oceanography, 60: 355–385.

Beare, D., Burns, F., Greig, T., Jones, E., Peach, K., Kienzle, M., McKenzie, E., *et al.* 2004. Long-term increases in prevalence of North Sea fish having southern biogeographic affinities. Marine Ecology Progress Series, 284: 269–278.

Beare, D., Burns, F., Jones, E., Peach, K., and Reid, D. 2005. Red mullet migration into the northern North Sea during late winter. Journal of Sea Research, 53: 205–212.

Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fisheries Oceanography, 12: 270–283.

Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Progress in Oceanography, 60: 245–262.

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., and Edwards, M. 2002. Reorganisation of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692–1694.

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

Beckmann, A., and Doescher, R. 1997. A method for improved representation of dense water spreading over topography in geopotential coordinate models. Journal of Physical Oceanography, 27: 581–591.

Begon, M., Townsend, C. R., and Harper, J. L. 2006. Ecology. From Individuals to Organisms, 4th edn. Blackwell Publishing, Malden, MA, USA. 752 pp.

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., *et al.* 2006. Climate-driven trends in contemporary ocean productivity. Nature, 444: 752–755.

Bekkevold, D., André, C., Dahlgren, T. G., Clausen, L. A. W., Torstensen, E., Mosegaard, H., Carvalho, G. R., *et al.* 2005. Environmental correlates of population differentiation in Atlantic herring. Evolution, 59: 2656–2668.

Beldade, R., Van Tassell, J. L., and Goncalves, E. J. 2006. First record of *Chromogobius britoi* (Teleostei: Gobiidae) on the mainland European coast. Journal of Fish Biology, 68: 608–612.

Belk, M. C., and Houston, D. D. 2002. Bergmann's rule in ectotherms: a test using freshwater fish. American Naturalist, 160: 803–808.

Bell, M. C., Elson, J. M., and Addison, J. T. 2005. The effects of spatial targeting of fishing effort on the distribution of the Norway lobster, *Nephrops norvegicus*, on the Farn Deeps grounds, northeast England. New Zealand Journal of Marine and Freshwater Research, 39: 1023–1037.

Bell, M. C., Redant, F., and Tuck, I. 2006. *Nephrops* species. *In* Lobsters: Biology, Management, Aquaculture and Fisheries, pp. 412–461. Ed. by B. F. Phillips. Blackwell Publishing, Oxford, UK.

Bellerby, R. G. J., Olsen, A., Furevik, T., and Anderson, L. A. 2005. Response of the surface ocean CO_2 system in the Nordic Seas and North Atlantic to climate change. *In* Climate Variability in the Nordic Seas, pp. 189–198. Ed. by H. Drange, T. M. Dokken, T. Furevik, R. Gerdes, and W. Berger. American Geophysical Union Geophysical Monograph Series, 158.

Bellier, E., Planque, B., and Petitgas, P. 2007. Historical fluctuations in spawning location of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the Bay of Biscay during 1967–73 and 2000–2004. Fisheries Oceanography, 16: 1–15.

Ben Abdallah, A., Ben Souissi, J., Mejri, H., Capape, C., and Golani, D. 2007. First record of *Cephalopholis taeniops* (Valenciennes) in the Mediterranean Sea. Journal of Fish Biology, 71: 610–614.

Ben Rais Lasram, F., and Mouillot, D. 2009. Increasing southern invasion enhances congruence between endemic and exotic Mediterranean fish fauna. Biological Invasions, 11: 697–711.

Ben Souissi, J., Golani, D., Mejri, H., and Capape, C. 2005a. On the occurrence of *Cheilopogon furcatus* in the Mediterranean Sea. Journal of Fish Biology, 67: 1144–1149.

Ben Souissi, J., Mejri, H., Zaouali, J., and Capape, C. 2005b. On the occurrence of the Por's goatfish, *Upeneus pori* (Mullidae) in southern Tunisia (central Mediterranean). Cybium, 29: 410–412.

Ben Souissi, J., Golani, D., Mejri, H., Ben Salem, M., and Capape, C. 2007. First confirmed record of the Halave's Guitarfish, *Rhinobatos halavi* (Forsskål, 1775) (Chondrichthyes: Rhinobatidae) in the Mediterranean Sea with a description of a case of albinism in elasmobranchs. Cahiers de Biologie Marine, 48: 67–75.

Bengtsson, L., Semenov, V. A., and Johannessen, O. M. 2004. The early twentieth-century warming in the Arctic – a possible mechanism. Journal of Climate, 17: 4045–4057.

Ben-Tuvia, A. 1990. Mullidae. *In* Check-list of the Fish of the Eastern Tropical Atlantic (CLOFETA), Vol. 2, pp. 827–829. Ed. by J. C. Quéro, J. C. Hureau, C. Karrer, A. Post, and L. Saldanha. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B., and Slagstad, D. 2005. Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Marine Ecology Progress Series, 303: 167–175.

Berghahn, R. 1983. Untersuchungen an Plattfischen und Nordseegarnelen (*Crangon crangon*) im Eulitoral des Wattenmeeres nach dem Übergang zum Bodenleben. Helgoländer Meeresuntersuchungen, 36: 163–181.

Berghahn, R. 1984. Zeitliche und räumliche Koexistenz ausgewählter Fish- und Krebsarten im Wattenmeer unter Berücksichtigung von Räuber–Beute–Beziehungen und Nahrungskonkurrenz. PhD thesis, University of Hamburg, Germany.

Berghahn, R. 2000. Response to extreme conditions in coastal areas: biological tags in flatfish otoliths. Marine Ecology Progress Series, 192: 277–285.

Berghahn, R., Waltemath, M., and Rijnsdorp, A. D. 1992. Mortality of fish from the by-catch of shrimp vessels in the North Sea. Journal of Applied Ichthyology, 8: 293–306.

Berghahn, R., Bullock, A. M., and Karakiri, M. 1993. Effects of solar radiation on the population dynamics of juvenile flatfish in the shallows of the Wadden Sea. Journal of Fish Biology, 42: 329–345.

Bergmann, C. 1847. Über die Verhältnisse der wärmeökonomie der Tiere zu ihrer Grösse. Göttinger Studien, 3: 595–708.

Bergstad, O. A., Hoines, A. S., and Kruger, J. E. M. 2001. Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes marinus*, in the north-eastern North Sea and in unfished coastal waters off Norway. Aquatic Living Resources, 14: 293–301.

Berntsen, J., and Thiem, Ø. 2007. Estimating the internal pressure gradient errors in a sigma-coordinate ocean model for the Nordic Seas. Ocean Dynamics, 57: 417–429.

Berntsen, J., Skagen, D. W., and Svendsen, E. 1994. Modelling the drift of particles in the North Sea with reference to sandeel larvae. Fisheries Oceanography, 3: 81–91.

Béthoux, J. P., Gentili, B., Raunet, J., and Tailliez, D. 1990. Warming trend in the western Mediterranean deep water. Nature, 347: 660–662.

Béthoux, J. P., de Madron, X. D., Nyffeler, F., and Tailliez, D. 2002. Deep water in the western Mediterranean: peculiar 1999 and 2000 characteristics, shelf formation hypothesis, variability since 1970 and geochemical inferences. Journal of Marine Systems, 33: 117–131.

Beukema, J. J., and Dekker, R. 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: a possible role of climate change, predation on post larvae and fisheries. Marine Ecology Progress Series, 287: 149–167.

Beukema, J. J., Cadée, G. C., and Dekker, R. 2002. Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. Journal of Sea Research, 48: 111–125.

Beverton, R. J. H., and Lee, A. J. 1965. Hydrographic fluctuations in the North Atlantic Ocean and some biological consequences. *In* The Biological Significance of Climate Changes in Britain. Symposia of the Institute of Biology, 14, pp. 79–109. Ed. by C. G. Johnson and L. P. Smith. Academic Press, London.

Bez, N., Rivoirard, J., and Walsh, M. 1995. On the relation between fish density and sea surface temperature. Application to mackerel egg density. ICES Document CM 1995/D:6.

Bianchi, C. N. 1997. Climate change and biological response in the marine benthos. *In* Congresso dell'Associazione Italiana di Oceanologia e Limnologia 1, pp. 3–20. Ed. by M. Piccazzo. Associazione Italiana Di Oceanologia E Limnologia, Genova.

Bianchi, C. N., and Morri, C. 1994. Southern species in the Ligurian Sea (northern Mediterranean): new records and a review. Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova, 58–59: 181–197.

Bianchi, G., Carpenter, K. E., Roux, J-P., Molloy, F. J., Boyer, D., and Boyer, H. J. 1993. FAO Species Identification Field Guide for Fishery Purposes. The Living Marine Resources of Namibia. FAO, Rome. 250 pp.

Bilio, M., and Niermann, U. 2004. Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. Marine Ecology Progress Series, 269: 173–183.

Bissett, W. P., Walsh, J. J., Dieterle, D. A., and Carder, K. L. 1999a. Carbon cycling in the upper waters of the Sargasso Sea: I. Numerical simulation of differential carbon and nitrogen fluxes. Deep Sea Research Part I, 46: 205–269.

Bissett, W. P., Carder, K. L., Walsh, J. J., and Dieterle, D. A. 1999b. Carbon cycling in the upper waters of the Sargasso Sea: II. Numerical simulation of apparent and inherent optical properties. Deep Sea Research Part I, 46: 271–317.

Bissett, W. P., DeBra, S., and Dye, D. 2004. Ecological Simulation (EcoSim) 2.0 Technical Description. FERI Technical Document No. FERI-2004–0002-U-D, p. 27. 10 August 2004. Tampa, FL, USA.

Bjerkan, P. 1917. Age, maturity and quality of North Sea herrings during the years 1910–13. Report of Norwegian Fisheries and Marine Investigations, III, 1.

Bjerknes, J. 1962. Synoptic survey of the interaction of sea and atmosphere in the North Atlantic. Geofysiske Publikasjoner, 24: 115–145.

Björnsson, B., and Dombaxe, M. Á. D. 2004. Quality of *Nephrops* as food for Atlantic cod (*Gadus morhua* L.) with possible implications for fisheries management. ICES Journal of Marine Science, 61: 983–991.

Björnsson, B., and Steinarsson, A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 59: 494–502.

Björnsson, B., Steinarsson, A., and Oddgeirsson, M. 2001. Optimal temperatures for growth and food conversion of immature cod (*Gadus morhua* L.). ICES Journal of Marine Science, 58: 29–38.

Björnsson, H., and Pálsson, Ó. K. 2004. Distribution patterns and dynamics of fish stocks under recent climate change in Icelandic waters. ICES Document CM 2004/K:30.

Blackford, J. C., Allen, J. I., and Gilbert, F. J. 2004. Ecosystem dynamics at six contrasting sites: a generic modelling study. Journal of Marine Systems, 52: 191–215.

Blaikie, H. B., and Kerr, S. R. 1996. Effect of activity level on apparent heat increment in Atlantic cod, *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Sciences, 53: 2093–2099.

Blanchard, F., and Vandermeirsch, F. 2005. Warming and exponential abundance increase of the subtropical fish *Capros aper* in the Bay of Biscay (1973–2002). Comptes Rendus de l'Académie des Sciences, Biologies, 328: 505–509.

Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D., and O'Brien, C. M. 2005. Distribution–abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation vs. theory. Canadian Journal of Fisheries and Aquatic Sciences, 62: 2001–2009.

Blaxter, J. H. S. 1985. The herring: a successful fish? Canadian Journal of Fisheries and Aquatic Sciences, 42(Suppl. 1): 21–30.

Blaxter, J. H. S., and Hunter, J. R. 1982. The biology of the clupeid fish. Advances in Marine Biology, 20: 1–224.

Blindheim, J. 1989. Ecological features of the Norwegian Sea. *In* Proceedings of the Sixth Conference of the Comité Arctique International, 13–15 May 1985, Fairbanks, Alaska, pp. 366–401. Ed. by F. Rey and V. Alexander. E. J. Brill, New York.

Blindheim, J. 2004. Oceanography and climate. *In* The Norwegian Sea Ecosystem, pp 65–96. Ed. by H. R. Skjoldal. Tapir Academic Press, Trondheim.

Blindheim, J., and Østerhus, S. 2005. The Nordic Seas, main oceanographic features. *In* The Nordic Seas: An Integrated Perspective, pp. 11–37. Ed. by H. Drange, T. Dokken, T. Furevik, R. Gerdes, and W. Berger. American Geophysical Union Geophysical Monograph Series, 158.

Blindheim, J., Borovkov, V., Hansen, B., Malmberg, S-As., Turrell, W. R., and Østerhus, S. 2000. Upper layer cooling and freshening in the Norwegian Sea in relation to atmospheric forcing. Deep Sea Research Part I, 47: 655–680.

Boddeke, R. 1976. The seasonal migration of the brown shrimp *Crangon crangon*. Netherlands Journal of Sea Research, 10: 103–130.

Boddeke, R. 1980. Management on the brown shrimp (*Crangon crangon*) stock in Dutch coastal waters. *In* Marine Invertebrate Fisheries: Their Assessment and Management, pp. 35–62. Ed. by J. F. Caddy. John Wiley, London.

Boddeke, R. 1996. Changes in the brown shrimp (*Crangon crangon* L.) population off the Dutch coast in relation to fisheries and phosphate discharge. ICES Journal of Marine Science, 53: 995–1002.

Boddeke, R., and Hagel, P. 1995. Eutrophication, fisheries, and productivity of the North Sea continental zone. *In* Condition of the World's Aquatic Habitats. Proceedings of the World Fisheries Congress, Theme 1, pp. 290–315. Ed. by N. B. Armantrout and R. J. Wolotira. Oxford and IBH Publishing, New Delhi.

Boddeke, R., and Vingerhoed, B. 1996. The anchovy returns to the Wadden Sea. ICES Journal of Marine Science, 53: 1003–1007.

Boehlert, G. W., and Mundy, B. C. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. American Fisheries Society Symposium, 3: 51–67.

Boero, F. 1996. Episodic events: their relevance to ecology and evolution. Marine Ecology, 17: 237–250.

Boero, F. 2001. Adriatic ecological history: a link between jellyfish outbreaks, red tides, mass mortalities, overfishing, mucilages, and thaliacean plankton? *In* Gelatinous Zooplankton Outbreaks: Theory and Practice. CIESM Workshop Series, 14: 55–57.

Boeuf, G., and Payan, P. 2001. How should salinity influence fish growth? Comparative Biochemistry and Physiology, Part C, 130: 411–423.

Bolle, L. J., Dickey-Collas, M., van Beek, J. K. L., Erftemeijer, P. L. A., Witte, J. I. J., van der Veer, H. W., and Rijnsdorp, A. D. 2009. Variability in transport of fish eggs and larvae. III. Effects of hydrodynamics and larval behaviour on recruitment in plaice. Marine Ecology Progress Series, 390: 195–211.

Bologa, A. S., Bodeanu, N., Petran, A., Tiganus, V., and Zaitzev, Yu P. 1995. Major modifications of the Black Sea benthic and biotic biota in the last three decades. *In* Les Mers Tributaires de Méditerranée, pp. 85–110. Ed. by F. Briand. Bulletin de l'institut Océanographique, Monaco, Numéro Spécial 15.

Bond, N. A., and Harrison, D. E. 2000. The Pacific Decadal Oscillation, air–sea interaction and central north Pacific winter atmospheric regimes. Geophysical Research Letters, 27: 731–734.

Borges, L., van Keeken, O. A., van Helmond, A. T. M., Couperus, B., and Dickey-Collas, M. 2008. What do pelagic freezer-trawlers discard? ICES Journal of Marine Science, 65: 605–611.

Borges, M. D. F., Silva, A., Abaunza, P., Eltink, A., Lucio, P., Walsh, M., Poulard, J. C., *et al.* 1996. Changes in horse mackerel (*Trachurus trachurus*) catch distribution in the northeast Atlantic. ICES Document CM 1996/S:26. 8 pp.

Borisov, V. M. 1978. The selective effect of fishing on the population structure of species with a long life cycle. Journal of Ichthyology, 18: 896–904.

Borja, A., Uriarte, A., Egaña, J., Motos, L., and Valencia, V. 1998. Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay. Fisheries Oceanography, 7: 375–380.

Borja, A., Uriarte, A., and Egaña, J. 2002. Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north-east Atlantic coast of Europe. Fisheries Oceanography, 11: 116–127.

Borja, A., Fontan, A., Saenz, J., and Valencia, V. 2008. Climate, oceanography, and recruitment: the case of Bay of Biscay anchovy (*Engraulis encrasicolus*). Fisheries Oceanography, 17: 477–493.

Boucher, J. 1985. Caractéristiques: physiques et biologiques. *In* Peuplements profonds du Golfe de Gascogne, pp. 25–42. Ed. by L. Laubier and C. L. Monniot. Ifremer, Paris.

Boulcott, P., Wright, P. J., Gibb, F., Jensen, H., and Gibb, I. 2007. Regional variation in the maturation of sandeels in the North Sea. ICES Journal of Marine Science, 64: 369–376.

Bowers, A. B., and Williamson, D. I. 1951. Food of larval and early post larvae stage of autumn spawned herring in Manx waters. Annual Report of the Port Erin Marine Biology Station, 63: 17–26.

Boyd, P. W., and Doney, S. C. 2002. Modelling regional responses by marine pelagic ecosystems to global climate change. Geophysical Research Letters, 29: 1806.

Bradshaw, W. E., and Holzapfel, C. M. 2001. Genetic shift in photoperiodic response correlated with global warming. Proceedings of the National Academy of Sciences of the USA, 98: 14509–14511.

Brander, K. M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 52: 1–10.

Brander, K. M. 2000. Effects of environmental variability on growth and recruitment in cod (*Gadus morhua*) using a comparative approach. Oceanologica Acta, 23: 485–496.

Brander, K. M. 2003. What kinds of fish stock predictions do we need and what kinds of information will help us make better predictions? Scientia Marina, 67: 21–33.

Brander, K. M. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. ICES Journal of Marine Science, 62: 339–343.

Brander, K. M. 2007. The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970. ICES Journal of Marine Science, 64: 211–217.

Brander, K. M. 2010. Impacts of climate change on fisheries. Journal of Marine Systems, 79: 389–402.

Brander, K. M., and Bennett, D. B. 1986. Interactions between Norway lobster (*Nephrops norvegicus*) and cod (*Gadus morhua*) and their fisheries in the Irish Sea. Canadian Special Publication of Fisheries and Aquatic Sciences, 92: 269–281.

Brander, K. M., and Bennett, D. B. 1989. Norway lobsters in the Irish Sea: modeling one component of a multispecies resource. *In* Marine Invertebrate Fisheries: Their Assessment and Management, pp. 183–204. Ed. by J. F. Caddy. John Wiley, New York.

Brander, K. M., and Mohn, R. 2004. Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 61: 1558–1564.

Brander, K. M., Blom, G., Borges, M. F., Erzini, K., Henderson, G., MacKenzie, B. R., Mendes, H., *et al.* 2003. Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? ICES Marine Science Symposia, 219: 261–270.

Bremner, J., Paramor, O. A. L., and Frid, C. L. J. 2006. Developing a methodology for incorporating ecological structure and functioning into designation of Special Areas of Conservation (SAC) in the 0–12 nautical mile zone. School of Biological Sciences, University of Liverpool. Report to English Nature. 158 pp.

Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist, 11: 99–113.

Brett, J. R. 1979. Environmental factors and growth. *In* Fish Physiology, Vol. VIII. Bioenergetics and Growth, pp. 599–667. Ed. by W. S. Hoar, D. J. Randall, and J. R. Brett. Academic Press, London.

Brett, J. R., and Groves, T. D. D. 1979. Physiological energetics. *In* Fish Physiology. Vol. VIII. Bioenergetics and Growth, pp. 279–352. Ed. by W. S. Hoar, D. J. Randall, and J. R. Brett. Academic Press, London.

Bridger, J. P. 1961. On the fecundity and larval abundance of Down herring. Fisheries Investigations, Series II, 23: 1–30.

Briggs, J. C. 1974. Marine Zoogeography. McGraw-Hill, New York. 475 pp.

Broecker, W. S. 1991. The great ocean conveyor. Oceanography, 4: 79–89.

Brooks, C. F. 1938. The warming Arctic. Meteorological Magazine, 73: 29–32.

Brown, B. R. 2003. Sensing temperature without ion channels. Nature, 421: 495–495.

Brunel, T., and Boucher, J. 2007. Long-term trends in fish recruitment in the north-east Atlantic related to climate change. Fisheries Oceanography, 16: 336–349.

Brunel, T., and Dickey-Collas, M. 2010. Effects of temperature and population density on von Bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. Marine Ecology Progress Series, 405:15–28, doi:10.3354/meps08491.

Buckley, L. J., Caldarone, E. M., Lough, R. G., and St Onge-Burns, J. M. 2006. Ontogenetic and seasonal trends in recent growth rates of Atlantic cod and haddock larvae on Georges Bank: effects of photoperiod and temperature. Marine Ecology Progress Series, 325: 205–226.

Bückmann, A. 1961. Über die Bedeutung des Schollenlaichens in der südöstlichen Nordsee. Kurze Mitteilungen Institut Fischereibiologie, Universität Hamburg, 11: 1–40.

Buljan, M. 1974. Osnovne karakteristike Jadrana kao produkcionog bazena. Acta Adriatica, 16: 31–62.

Bulman, C., Althaus, F., He, X., Bax, N. J., and Williams, A. 2001. Diets and trophic guilds of demersal fish of the south-eastern Australian shelf. Marine and Freshwater Research, 52: 537–548.

Bulnheim, H-P., and Schwenzer, D. E. 1993. Zur Populationsgenetik von *Crangon crangon* und *C. allmanni* (Crustacea, Decapoda) im Bereich der europäischen Küsten. Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere, 97: 327–347.

Burd, A. C. 1978. Long term changes in North Sea herring stocks. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 137–153.

Burd, A. C. 1984. Density dependent growth in North Sea herring. ICES Document CM 1984/H:4.

Burd, A. C. 1985. Recent changes in the central and southern North Sea herring stocks. Canadian Journal of Fisheries and Aquatic Sciences, 42(Suppl. 1): 192–206.

Cabral, H. N., Costa, M. J., and Salgado, J. P. 2001. Does the Tagus estuary fish community reflect environmental changes? Climate Research, 18: 119–126.

Caddy, J. F. 2000. Marine catchment basin effects versus impacts of fisheries on semi-enclosed seas. ICES Journal of Marine Science, 57: 628–640.

Callaway, R., Alsvåg, J., de Boois, I., Cotter, J., Ford, A., Hinz, H., Jennings, S., *et al.* 2002. Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES Journal of Marine Science, 59: 1199–1214.

Callaway, R., Engelhard, G. H., Dann, J., Cotter, J., and Rumohr, H. 2007. A century of North Sea epibenthos and trawling: comparison between 1902–1912, 1982–1985 and 2000. Marine Ecology Progress Series, 346: 27–43.

Campos, J., and van der Veer, H. W. 2008. Autecology of *Crangon crangon* (L.) with an emphasis on latitudinal trends. Oceanography and Marine Biology: an Annual Review, 46: 65–104.

Cardinale, M., and Arrhenius, F. 2000. Decreasing weight-at-age of Atlantic herring (*Clupea harengus*) from the Baltic Sea between 1986 and 1996: a statistical analysis. ICES Journal of Marine Science, 57: 882–893.

Cardinale, M., Hjelm, J., and Casini, M. 2004. Effect of temperature on recruitment success of herring and sprat stocks in the North Atlantic. ICES Document CM 2004/K:01.

Cardinale, M., Möllmann, C., Bartolino, V., Casini, M., Kornilovs, G., Raid, T., Margonski, P., *et al.* 2009. Effect of environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea harengus* populations. Marine Ecology Progress Series, 388: 221–234.

Carl, H., Nielsen, J. G., and Møller, P. R. 2004. En kommenteret og revideret oversigt over danske fisk. Flora og Fauna, 110: 29–39.

Carpenter, K. E. (Ed). 2002. The living marine resources of the Western Central Atlantic. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists, Special Publication No. 5, Volumes I–III. 2127 pp.

Carpentier, A., Vaz, S., Martin, C. S., Coppin, F., Dauvin, J. C., Desroy, N., Dewarumez, J. M., *et al.* 2005. Eastern Channel Habitat Atlas for Marine Resource Management (CHARM). Atlas des Habitats des Ressources Marines de la Manche Orientale, INTERREG IIIA.

Carscadden, J., Nakashima, B. S., and Frank, K. T. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences, 54: 781–787.

Case, R. A. J., Hutchinson, W. F., Hauser, L., Van Oosterhout, C., and Carvalho, G. R. 2005. Macro- and micro-geographic variation in pantophysin (PanI) allele frequencies in NE Atlantic cod *Gadus morhua*. Marine Ecology Progress Series, 301: 267–278.

Casini, M., Cardinale, M., and Hjelm, J. 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? Oikos, 112: 638–650.

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J. C., and Kornilovs, G. 2008a. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society of London, Series B, 275: 1793–1801.

Casini, M., Hjelm, J., Molinero, J-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., *et al.* 2008b. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proceedings of the National Academy of Sciences of the USA, 106: 97–202.

Castelló, J. P., and Hamre, J. 1969. Age and growth of mackerel from the Skagerrak and the northern North Sea. ICES Document CM 1969/H:7.

Castonguay, M., Plourde, S., Robert, D., Runge, J. A., and Fortier, L. 2008. Copepod production drives recruitment in a marine fish. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1528–1531.

Castriota, L., and Andaloro, F. 2005. First record of the lessepsian fish *Siganus luridus* in the Tyrrhenian Sea. Journal of the Marine Biological Association 2 – Biodiversity Records. Available online at http://www.mba.ac.uk/jmba/pdf/5122pdf.

Caudri, L. W. D. 1937. Einfluss der Temperatur und des Salzgehalts auf die Sterblichkeit von Garnelen (*Crangon crangon* L.). Archives Néerlandaises de Zoologie, 3: 179–196.

Cech, J. J., Mitchell, S. J., Castleberry, D. T., and McEnroe, M. 1990. Distribution of California stream fish: influence of environmental temperature and hypoxia. Environmental Biology of Fish, 29: 95–105.

Cendrero, O., Cort, J., and Cardenas, E. 1981. Revisión de algunos datos sobre la biología de la anchoa, *Engraulis encrasicholus* (L.) del Mar Cantábrico. Boletín Instituto Español de Oceanografía, 311: 118–123.

Cerrano, C., Bavestrello, G., Bianchi, C. N., Cattaneo-Vietti, R., Bava, S., Morganti, C., Morri, C., *et al.* 2000. A catastrophic mass-mortality episode of gorgonians and other organisms in the Ligurian Sea (north-western Mediterranean), summer 1999. Ecological Letters, 3: 284–293.

Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E., and Tilman, D. 1997. Biotic control over the functioning of ecosystems. Science, 277: 500–504.

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

Checkley, D. M. 1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Marine Ecology Progress Series, 9: 245–253.

Chen, S., and Watanabe, S. 1989. Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi, 55: 205–208.

Cheung, W., Alder, J., Karpouzi, V., Watson, R., Lam, V., Day, C., Kaschner, K., *et al.* 2005. Patterns of Species Richness in the High Seas. Convention on Biological Diversity, Montreal, Technical Series No. 20. 31 pp.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., and Pauly, D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries, 10: 235–251.

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., and Pauly, D. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Global Change Biology, 16: 24–35.

Choi, J. S., Frank, K. T., Petrie, B. D., and Leggett, W. C. 2005. Integrated assessment of a large marine ecosystem: a case study of the devolution of the Eastern Scotian Shelf, Canada. Oceanography and Marine Biology: an Annual Review, 43: 47–67.

Christensen, A., and Andersen, K. H. In press. General classification of maturation reaction norm shape from size-based processes. Bulletin of Mathematical Biology.

Christensen, A., Daewel, U., Jensen, H., Mosegaard, H., St John, M., and Schrum, C. 2007. Hydrodynamic backtracking of fish larvae by individual-based modelling. Marine Ecology Progress Series, 347: 221–232.

Christensen, A., Jensen, H., Mosegaard, H., St John, M., and Schrum, C. 2008. Sandeel (*Ammodytes marinus*) larval transport patterns in the North Sea from an individual-based hydrodynamic egg and larval model. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1498–1511.

Christensen, V., and Walters, C. J. 2004. Ecopath with EcoSim: methods, capabilities and limitations. Ecological Modelling, 172: 109–139.

Christensen, V., Guenette, S., Heymanns, J. J., Walters, C. J., Watson, R., Zeller, D., and Pauly, D. 2003. Hundred-year decline of North Atlantic predatory fish. Fish and Fisheries, 4: 1–24.

Ciannelli, L., Chan, K-S., Bailey, K. M., and Stenseth, N. C. 2004. Nonadditive effects of the environment on the survival of a large marine fish population. Ecology, 85: 3418–3427.

Ciannelli, L., Bailey, K. M., Chan, K-S., Belgrano, A., and Stenseth, N. C. 2005. Climate change causing phase transitions of walleye pollock (*Theragra chalcogramma*) recruitment dynamics. Proceedings of the Royal Society of London, Series B, 272: 1735–1743.

CIESM. 2002. Alien species introduced by ships in the Mediterranean and Black Sea. CIESM Workshop Monographs 20. 136 pp.

Clarke, R. A., Fox, C. J., Viner, D., and Livermore, M. 2003. North Sea cod and climate change – modelling the effect of temperature on population dynamics. Global Change Biology, 9: 1669–1680.

Coelho, H. S., Neves, R. J. J., White, M., Leitao, P. C., and Santos, A. J. 2002. A model for ocean circulation on the Iberian coast. Journal of Marine Systems, 32: 153–179.

Coll, M., Palomera, I., and Tudela, S. 2009a. Decadal changes in a NW Mediterranean food web in relation to fishing exploitation. Ecological Modelling, 220: 2088–2102.

Coll, M., Santojanni, A., Palomera, I., and Arneri, E. 2009b. Food-web changes in the Adriatic Sea over the last three decades. Marine Ecology Progress Series, 381: 17–37.

Collie, J. S., Richardson, K., and Steele, J. H. 2004. Regime shifts: can ecological theory illuminate the mechanisms? Progress in Oceanography, 60: 281–302.

Compagno, L. J. V. 1984. FAO Species Catalogue, Vol. 4. Sharks of the World: an annotated and illustrated catalogue of shark species known to date. Parts 1 (Hexanchiformes to Lamniformes) and 2 (Carcharhiniformes). FAO Fisheries Synopsis, 125(4). 655 pp.

Compton, T. J., Rijkenberg, M. J. A., Drent, J., and Piersma, T. 2007. Thermal tolerance ranges and climate variability: a comparison between bivalves from differing climates. Journal of Experimental Marine Biology and Ecology, 352: 200–211.

Conover, D. O., and Munch, S. B. 2002. Sustaining fisheries yields over evolutionary time scales. Science, 297: 94–96.

Conover, D. O., and Schultz, E. T. 1995. Phenotypic similarity and the evolutionary significance of countergradient selection. Trends in Ecology and Evolution, 10: 248–252.

Constanza, R., and Sklar, F. H. 1985. Articulation, accuracy, and effectiveness of mathematical models: a review of freshwater wetlands applications. Ecological Modelling, 27: 45–68.

Conway, D. V. P., Coombs, S. H., and Lindley, J. A. 1996. Feeding of mackerel larvae (*Scomber scombrus*) to the west of the British Isles and the incidence of cannibalism and coprophagy. ICES Document CM 1996/S:20.

Cook, R. M., and Heath, M. R. 2005. The implications of warming climate for the management of North Sea demersal fisheries. ICES Journal of Marine Science, 62: 1322–1326.

Cook, R. M., Sinclair, A., and Stefánsson, G. 1997. Potential collapse of North Sea cod stock. Nature, 385: 521–522.

Coombs, S. H., Morgans, D., and Halliday, N. C. 2001. Seasonal and ontogenic changes in the vertical distribution of eggs and larvae of mackerel (*Scomber scombrus* L.) and horse mackerel (*Trachurus trachurus* L.). Fisheries Research, 50: 27–40.

Cooper, L. H. N. 1952. The boar fish, *Capros aper* (L.), as a possible biological indicator of water movement. Journal of the Marine Biological Association of the UK, 31: 351–362.

Corbin, P. G., and Vati, V. 1949. The post-larval sandeels (Ammodytidae) of the Celtic Sea and Plymouth area. Journal of the Marine Biological Association of the UK, 28: 287–313.

Corsini, M., Margies, P., Kondilatos, G., and Economidis, P. S. 2005. Lessepsian migration of fish to the Aegean Sea: first record of *Tylerius spinosissimus* (Tetraodontidae) from the Mediterranean, and six more fish records from Rhodes. Cybium, 29: 347–354.

Corsini, M., Margies, P., Kondilatos, G., and Economidis, P. S. 2006. Three new exotic fish records from the SE Aegean Greek waters. Scientia Marina, 70: 319–323.

Corten, A. 1986. On the causes of recruitment failure of herring in the central and northern North Sea in the years 1972–1978. Journal du Conseil International pour l'Exploration de la Mer, 42: 281–294.

Corten, A. 1999a. The reappearance of spawning Atlantic herring (*Clupea harengus*) on Aberdeen Bank (North Sea) in 1983 and its relationship to environmental conditions. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2051–2061.

Corten, A. 1999b. A proposed mechanism for the Bohuslän herring periods. ICES Journal of Marine Science, 56: 207–220.

Corten, A. 2001a. Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. Fisheries Research, 50: 189–204.

Corten, A. 2001b. Herring and climate. PhD thesis, Rijksuniversiteit Groningen, the Netherlands. 228 pp.

Corten, A. 2002. The role of "conservatism" in herring migrations. Reviews in Fish Biology and Fisheries, 11: 339–361.

Corten, A., and Lindley, J. A. 2003. The use of CPR data in fisheries research. Progress in Oceanography, 58: 285–300.

Corten, A., and van de Kamp, G. 1996. Variation in the abundance of southern fish species in the southern North Sea in relation to hydrography and wind. ICES Journal of Marine Science, 53: 1113–1119.

Costa, M. J., Vasconcelos, R., Costa, J. L., and Cabral, H. N. 2007. River flow influence on the fish community of the Tagus estuary (Portugal). Hydrobiologia, 587: 113–123.

Costello, M. J., Emblow, C., and White, R. (Eds). 2001. European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification. Collection Patrimoines Naturels, 50: 463 pp.

Costello, M. J., Bouchet, P., Boxshall, G., Emblow, C., and Vanden Berghe, E. 2004. European register of marine species. Available online at http://www.marbef.org/ data/erms.php.

Cotton, P. A., Sims, D. W., Fanshawe, S., and Chadwick, M. 2005. The effect of climate variability on zooplankton and basking shark (*Cetorhinus maximus*) relative abundance off southwest Britain. Fisheries Oceanography, 14: 151–155.

Couch, J. 1864. A History of the Fishes of the British Isles. Vol. I–IV. Goombridge and Sons, London.

Coutant, C. C. 1977. Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada, 34: 739–745.

Covill, R. W. 1959. Food and feeding habits of larvae and postlarvae of *Ammodytes americanus*. Bulletin of the Bingham Oceanographic Collection, Yale University, 17: 125–146.

Crawshaw, L. I., and O'Connor, C. 1997. Behavioural compensation for long-term thermal change. *In* Global Warming: Implications for Freshwater and Marine Fish, pp. 351–376. Ed. by C. M. Wood and D. G. McDonald. Cambridge University Press, London.

Creutzberg, F., Eltink, A. T. G. W., and van Noort, G. J. 1978. The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea. *In* Physiology and Behaviour of Marine Organisms, pp. 243–251. Ed. by D. S. McLusky and A. J. Berry. Pergamon Press, Oxford.

Cuenco, M. L., Stickney, R. R., and Grant, W. E. 1985. Fish bioenergetics and growth in aquaculture ponds. II. Effects of interactions among size, temperature, dissolved oxygen, unionized ammonia, and food on growth of individual fish. Ecological Modelling, 27: 191–206.

Cuesta, J. A., González-Ortegón, E., Rodríguez, A., Baldó, F., Vilas, C., and Drake, P. 2006. The decapod crustacean community of the Guadalquivir Estuary (SW Spain): seasonal and inter-year changes in community structure. Hydrobiologia, 557: 85–95.

Curry, R., Dickson, R., and Yashayaev, I. 2003. A change in the freshwater balance of the Atlantic Ocean over the past four decades. Nature, 426: 826–829.

Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Canadian Journal of Fisheries and Aquatic Sciences, 46: 670–680.

Cury, P., and Shannon, L. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguella. Progress in Oceanography, 60: 223–243.

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., and Verheye, H. M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine Science, 57: 603–618.

Cury, P., Shannon, L., and Shin, Y-J. 2003. The functioning of marine ecosystems: a fisheries perspective. *In* Responsible Fisheries in the Marine Ecosystem, pp. 103–123. Ed. by M. Sinclair and G. Valdimarsson. CAB International, Wallingford.

Cushing, D. H. 1955. On the autumn-spawned herring races in the North Sea. Journal du Conseil Permanent International pour l'Exploration de la Mer, 21: 44–59.

Cushing, D. H. 1967. The grouping of herring populations. Journal of the Marine Biological Association of the UK, 47: 193–208.

Cushing, D. H. 1982. Climate and Fisheries. Academic Press, London. 373 pp.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology, 26: 249–293.

Cushing, D. H. 1992. A short history of the Downs stock of herring. ICES Journal of Marine Science, 49: 437–443.

Cushing, D. H. 1996. Towards a science of recruitment in fish populations. *In* Excellence in Ecology, Vol. 7. Ed. by O. Kinne. Ecology Institute, Germany. 175 pp.

Cushing, D. H., and Bridger, J. P. 1966. The stock of herring in the North Sea, and changes due to fishing. Fisheries Investigations, Series II, 25: 1–123.

Cushing, D. H., and Burd, A. C. 1957. On the herring of the southern North Sea. Fisheries Investigations, Series II, 20: 1–31.

Cushing, D. H., and Dickson, R. R. 1976. The biological response in the sea to climate change. Advances in Marine Biology, 14: 1–122.

d'Elbée, J., Castège, I., Hémery, G., Lalanne, Y., Mouchès, C., Pautrizel, F., and D'Amico, F. 2009. Variation and temporal patterns in the composition of the surface ichthyoplankton in the southern Bay of Biscay (W. Atlantic). Continental Shelf Research, 29: 1136–1144.

Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Netherlands Journal of Sea Research, 6: 479–517.

Daan, N. 1978. Changes in cod stocks and cod fisheries in the North Sea. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 39–57.

Daan, N. 1997. TAC management in North Sea flatfish fisheries. Journal of Sea Research, 37: 321–341.

Daan, N. 2006. Spatial and temporal trends in species richness and abundance for the southerly and northerly components of the North Sea fish community separately, based on IBTS data 1977–2005. ICES Document CM 2006/D:02.

Daan, N., Rijnsdorp, A. D., and van Overbeeke, G. R. 1985. Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. Transactions of the American Fisheries Society, 114: 499–506.

Daan, N., Bromley, P. J., Hislop, J. R. G., and Nielsen, N. A. 1990. Ecology of North Sea fish. Netherlands Journal of Sea Research, 26: 343–386.

Daan, N., Gislason, H., Pope, J. G., and Rice, J. C. 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES Journal of Marine Science, 62: 177–188.

Daewel, U. 2008. Investigating the impacts of abiotic and biotic environmental factors on the life cycle dynamics and vital rates of marine organisms in the North Sea using biophysical models. PhD thesis, University of Hamburg, Germany. 132 pp.

Daewel, U., Peck, M. A., Kühn, W., St John, M. A., Alekseeva, I., and Schrum, C. 2008a. Coupling ecosystem and individual-based models to simulate the influence of environmental variability on potential growth and survival of larval sprat (*Sprattus sprattus* L.) in the North Sea. Fisheries Oceanography, 17: 333–351.

Daewel, U., Peck, M. A., Schrum, C., and St John, M. A. 2008b. How best to include the effects of climate-driven forcing on prey fields in larval fish individual-based models. Journal of Plankton Research, 30: 1–5.

Dalpadado, P., Ellertsen, B., Melle, W., and Dommasnes, A. 2000. Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. ICES Journal of Marine Science, 57: 843–857.

Danovaro, R., Dell'Anno, A., Fabiano, M., Pusceddu, A., and Tselepides, A. 2001. Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study. Trends in Ecology and Evolution, 16: 505–510.

Darnaude, A. M., Salen-Picard, C., Polunin, N. V. C., and Harmelin-Vivien, M. L. 2004. Trophodynamic linkage between river runoff and coastal fishery yield elucidated by stable isotope data in the Gulf of Lions (NW Mediterranean). Oecologia, 138: 325–332.

Daskalov, G. M. 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. Fisheries Research, 41: 1–23.

Daskalov, G. M. 2000. Mass-balance modelling and network analysis of the Black Sea pelagic ecosystem. Izvestiya IRR Varna, 25: 49–62.

Daskalov, G. M. 2002. Overfishing drives a trophic cascade in the Black Sea. Marine Ecology Progress Series, 225: 53–63.

Daskalov, G. M. 2003. Long-term changes in fish abundance and environmental indices in the Black Sea. Marine Ecology Progress Series, 255: 259–270.

Daskalov, G. M., Grishin, A. N., Rodionov, S., and Mihneva, V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Sciences of the USA, 104: 10518–10523.

Daunt, F., Wanless, S., Greenstreet, S. P. R., Jensen, H., Hamer, K. C., and Harris, P. H. 2008. The impact of sandeel fishery closure in the northwestern North Sea on seabird food consumption, distribution and productivity. Canadian Journal of Fisheries and Aquatic Sciences, 65: 362–381.

Davis, P., and Wheeler, A. 1985. The occurrence of *Pampus argenteus* (Euphrasen, 1788), (Osteichthyes, Perciformes, Stromateoidei, Stromateidae) in the North Sea. Journal of Fish Biology, 26: 105–109.

Dawson, W. A. 1986. Changes in western mackerel (*Scomber scombrus*) spawning stock composition during the spawning season. Journal of the Marine Biological Association of the UK, 66: 367-383.

Day, F. 1880–1884. The Fishes of Great Britain and Ireland. Vol. I–II. Williams and Norgate, London.

de Barros, P., and Holst, J. C. 1995. Identification of geographic origin of Norwegian spring-spawning herring (*Clupea harengus* L.) based on measurements of scale annuli. ICES Journal of Marine Science, 52: 863–872.

de Silva, C. D., and Tytler, P. 1973. The influence of reduced environmental oxygen on the metabolism and survival of herring and plaice larvae. Netherlands Journal of Sea Research, 7: 345–362.

de Silva, S. S. 1973a. Food and feeding habits of the herring *Clupea harengus* and the sprat *C. sprattus* in inshore waters of the west coast of Scotland. Marine Biology, 20: 282–290.

de Silva, S. S. 1973b. Abundance, structure, growth and origin of inshore clupeid populations of the west coast of Scotland. Journal of Experimental Marine Biology and Ecology, 12: 119–144.

de Veen, J. F. 1976. On changes in some biological parameters in the North Sea sole (*Solea solea* L.). Journal du Conseil International pour l'Exploration de la Mer, 37: 60–90.

de Veen, J. F. 1978a. On the selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa* L.) and other fish species. Netherlands Journal of Sea Research, 12: 115–147.

de Veen, J. F. 1978b. Changes in North Sea sole stocks (*Solea solea* (L.)). Rapports et Procès-Verbaux des Réunions Conseil International pour l'Exploration de la Mer, 172: 124–136.

Delhez, É. J. M., Damm, P., de Goede, E., de Kok, J. M., Dumas, F., Gerritsen, H., Jones, J. E., *et al*. 2004. Variability of shelf-seas hydrodynamic models: lessons from the NOMADS2 Project. Journal of Marine Systems, 45: 39–53.

Demirov, E., and Pinardi, N. 2002. Simulation of the Mediterranean Sea circulation from 1979 to 1993. Part I: the interannual variability. Journal of Marine Systems, 33–34: 23–50.

Deniel, C. 1981. Les poissons plats (téléostéens, Pleuronectiformes) en Baie de Douarnenez. PhD thesis, Université de Bretagne Occidentale, Brest, France.

Denman, K. L., and Peña, M. A. 2002. The response of two coupled one-dimensional mixed layer/planktonic ecosystem models to climate change in the NE Subarctic Pacific Ocean. Deep Sea Research Part II, 49: 5739–5757.

Désaunay, Y., Guerault, D., Le Pape, O., and Poulard, J. C. 2006. Changes in occurrence and abundance of northern/southern flatfishes over a 20-year period in a coastal nursery area (Bay of Vilaine) and on the eastern continental shelf of the Bay of Biscay. Scientia Marina, 70: 193–200.

Desbrosses, P. 1935. Contribution à la connaissance de la biologie du rouget barbet en Atlantique Nord (III). *Mullus barbatus* (rond) *surmuletus* (Fage). *Mode septentrional* Fage. Revue des Travaux de l'Office des Pêches Maritimes, 8: 351–376.

Despatie, S. P., Castonguay, M., Chabot, D., and Audet, C. 2001. Final thermal preferendum of Atlantic cod: effect of food ration. Transactions of the American Fisheries Society, 130: 263–275.

deYoung, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N., and Shannon, L. 2004a. Detecting regime shifts in the ocean: data considerations. Progress in Oceanography, 60: 143–164.

deYoung, B., Heath, M., Werner, F., Chai, F., Megrey, B., and Monfray, P. 2004b. Challenges of modeling ocean basin ecosystems. Science, 304: 1463–1466.

Diaz, R. J. 2001. Overview of hypoxia around the world. Journal of Environmental Quality, 30: 275–281.

Dickey-Collas, M., McQuaid, N., Armstrong, M. J., Allen, M., and Briggs, R. P. 2000. Temperature-dependent stage durations of Irish Sea *Nephrops* larvae. Journal of Plankton Research, 22: 749–760.

Dickey-Collas, M., Clarke, M., and Slotte, A. 2009a. "Linking Herring": do we really understand plasticity? ICES Journal of Marine Science, 66: 1649–1651.

Dickey-Collas, M., Bolle, L. J., van Beek, J. K. L., and Erftemeijer, P. L. A. 2009b. Variability in transport of fish eggs and larvae. II. The effects of hydrodynamics on the transport of Downs herring larvae. Marine Ecology Progress Series, 390: 183–194.

Dickey-Collas, M., Nash, R. D. M., Brunel, T., van Damme, C. J. G., Marshall, C. T., Payne, M. R., Corten, A., *et al.* 2010. Lessons learned from stock collapse and recovery of North Sea herring: a review. ICES Journal of Marine Science, 67. doi:10.1093/icesjms/fsq033

Dickmann, M., Möllmann, C., and Voss, R. 2007. Feeding ecology of Central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics – implications for survival. Marine Ecology Progress Series, 342: 277–289.

Dickson, R. R., and Brander, K. M. 1993. Effects of a changing windfield on cod stocks of the North Atlantic. Fisheries Oceanography, 3: 124–153.

Dickson, R. R., Kelly, P. M., Colebrook, J. M., Wooster, W. S., and Cushing, D. H. 1988. North winds and production in the eastern North Atlantic. Journal of Plankton Research, 10: 151–169.

Dickson, R. R., Lazier, J., Meincke, J., Rhines, P., and Swift, J. 1996. Long-term coordinated changes in the convective activity of the North Atlantic. Progress in Oceanography, 38: 241–295.

Dickson, R. R., Yashayaev, I., Meincke, J., Turrell, W., Dye, S., and Holfort, J. 2002. Rapid freshening of the deep North Atlantic Ocean over the past four decades. Nature, 416: 832–837.

Dickson, R. R., Curry, R., and Yashayaev, I. 2003. Recent changes in the North Atlantic. Philosophical Transactions of the Royal Society of London, Series A, 361: 1917–1934.

Dieckman, U., and Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Marine Ecology Progress Series, 335: 253–269.

Dinmore, T. A., Duplisea, D. E., Rackham, B. D., Maxwell, D. L., and Jennings, S. 2003. Impact of large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. ICES Journal of Marine Science, 60: 371–380.

Dinter, W. P. 2001. Biogeography of the OSPAR Maritime Area. A Synopsis and Synthesis of Biogeographical Distribution Patterns Described for the North-East Atlantic. Bundesamt für Naturschutz (BfN). 167 pp.

Dippner, J. W. 2006. Future aspects in marine ecosystem modelling. Journal of Marine Systems, 61: 246–267.

Dippner, J. W., and Ottersen, G. 2001. Cod and climate variability in the Barents Sea. Climate Research, 17: 73–82.

Dobzhansky, T. 1950. Evolution in the tropics. American Scientist, 38: 209–221.

Doescher, R., and Beckmann, A. 2000. Effects of a bottom boundary layer parameterization in a coarse-resolution model of the North Atlantic Ocean. Journal of Atmospheric and Oceanic Technology, 17: 698–707.

Dombaxe, M. Á. D. 2002. Predation intensity on the Norway lobster (*Nephrops norvegicus*) by cod (*Gadus morhua*), in Háfadjúp, southwest Iceland and the relative prey preference of cod fed on capelin (*Mallotus villosus*) and Norway lobster. MSc thesis, University of Iceland.

Dornheim, H., and Wegner, G. 1998. Unterschiedliche Trends beim Fischnachwuchs der Nordsee. Informationen für die Fischwirtschaft, 45: 103–108.

Dragesund, O., and Ulltang, Ø. 1978. Stock size fluctuations and rate of exploitation of the Norwegian spring-spawning herring, 1950–1974. Fiskeridirektoratets Skrifter, Serie Havundersøkelser, 16: 315–337.

Dragesund, O., Johannesen, A., and Ulltang, Ø. 1997. Variation in migration and abundance of Norwegian spring-spawning herring (*Clupea harengus* L.). Sarsia, 82: 97–105.

Drinkwater, K. F. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES Journal of Marine Science, 62: 1327–1337.

Drinkwater, K. F. 2006. The regime shift of the 1920s and 1930s in the North Atlantic. Progress in Oceanography, 68: 134–151.

Drinkwater, K. F. 2008. Comparison of the response of Atlantic cod (*Gadus morhua*) in the high-latitude regions of the North Atlantic during the warm periods of the 1920s–1960s and the 1990s–2000s. Deep Sea Research Part II, 56: 2087–2096.

Drinkwater, K. F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C. H., Ottersen, G., *et al.* 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. *In* The North Atlantic Oscillation: Climatic Significance and Environmental Impact, pp. 211–234. Ed. by J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck. American Geophysical Union Geophysical Monograph Series, 134.

Dubreuil, J., and Petitgas, P. 2009. Energy density of anchovy (*Engraulis encrasicolus*, L.) in the Bay of Biscay. Journal of Fish Biology, 74: 521–534.

Dulčić, J. 1998. Larval growth of sprat, *Sprattus sprattus phalericus*, larvae in the northern Adriatic. Fisheries Research, 36: 117–126.

Dulčić, J., and Grbec, B. 2000. Climate change and Adriatic ichthyofauna. Fisheries Oceanography, 9: 187–191.

Dulčić, J., Grbec, B., and Lipej, L. 1999. Information on the Adriatic ichthyofauna – effect of water warming? Acta Adriatica, 40: 33–43.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and Skjoldal, H. R. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of regional warming. Journal of Applied Ecology, 45: 1029–1039.

Dunbar, M. J. 1946. The state of the West Greenland Current up to 1944. Journal of the Fisheries Research Board of Canada, 6: 460–471.

Dunn, M. R. 1999. The exploitation of selected non-quota species in the English Channel. PhD thesis, University of Portsmouth, UK.

Dunn, M. R. 2001. The biology and exploitation of John dory, *Zeus faber* (Linnaeus, 1758) in the waters of England and Wales. ICES Journal of Marine Science, 58: 96–105.

Durant, J. M., Hjermann, Ø., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N., and Stenseth, N. C. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecology Letters, 8: 952–958.

Dutil, J. D., and Brander, K. 2003. Comparing productivity of North Atlantic cod (*Gadus morhua*) stocks and limits to growth production. Fisheries Oceanography, 12: 502–512.

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

Edwards, M., John, A. W. G., Hunt, H. G., and Lindley, J. A. 1999. Exceptional influx of oceanic species into the North Sea late 1997. Journal of the Marine Biological Association of the UK, 79: 737–739.

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

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

Edwards, M., Johns, D. G., Licandro, P., John, A. W. G., and Stevens, D. P. 2007. Ecological Status Report: results from the CPR survey 2005/2006. *In* Sir Alister Hardy Foundation for Ocean Science Technical Report, 4: 1–8.

Edwards, M., Johns, D. G., Beaugrand, G., Licandro, P., John, A. W. G., and Stevens, D. P. 2008. Ecological Status Report: results from the CPR survey 2006/2007. *In* Sir Alister Hardy Foundation for Ocean Science Technical Report, 5: 1–8.

Eide, A. 2008. An integrated study of economic effects of and vulnerabilities to global warming on the Barents Sea cod fisheries. Climate Change, 87: 251–262.

Einum, S., and Fleming, I. A. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. Nature, 405: 565–567.

Ekman, S. 1953. Zoogeography of the Sea. Sidgwick and Jackson, London. 417 pp.

Ellis, J. R. 2007. Occurrence of pelagic stingray *Pteroplatytrygon violacea* (Bonaparte, 1832) in the North Sea. Journal of Fish Biology, 71: 933–937.

Ellis, J. R., Armstrong, M. J., Rogers, S. I., and Service, M. 2002. The distribution, structure and diversity of fish assemblages in the Irish Sea. *In* Marine Biodiversity in Ireland and Adjacent Waters, pp. 93–114. Ed. by J. D. Nunn. Ulster Museum, Belfast.

Ellis, T., and Nash, R. D. M. 1997. Predation by sprat and herring on pelagic fish eggs in a plaice spawning area in the Irish Sea. Journal of Fish Biology, 50: 1195–1202.

Eltink, A. T. G. W. 1987. Changes in age-size distribution and sex ratio during spawning and migration of Western mackerel (*Scomber scombrus* L.). ICES Journal of Marine Science, 44: 10–22.

Emeis, K. C., Finney, B. P., Ganeshram, R., Gutiérrez, D., Poulsen, B., and Struck, U. 2010. Impacts of past climate variability on marine ecosystems: lessons from sediment records. Journal of Marine Systems, 79: 333–342.

Engelhard, G. H. 2005. Catalogue of Defra historical catch and effort charts: six decades of detailed spatial statistics for British fisheries. Science Series Technical Report, Cefas Lowestoft, 128. 42 pp.

Engelhard, G. H., and Heino, M. 2004a. Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. Fisheries Research, 66: 299–310.

Engelhard, G. H., and Heino, M. 2004b. Maturity changes in Norwegian spring-spawning herring (*Clupea harengus*): compensatory or evolutionary responses? Marine Ecology Progress Series, 272: 245–256.

Engelhard, G. H., and Heino, M. 2005. Scale analysis suggests frequent skipping of the second reproductive season in Atlantic herring. Biology Letters, 1: 172–175.

Engelhard, G. H., and Heino, M. 2006. Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction. Oecologia, 149: 593–603.

Engelhard, G. H., and Toresen, R. In press. Case study on fisheries-induced adaptive change in Norwegian spring-spawning herring. *In* Fisheries-Induced Adaptive Change. Ed. by U. Dieckmann, O. R. Godø, M. Heino, and J. Mork. Cambridge University Press, Cambridge, UK.

Engelhard, G. H., Dieckmann, U., and Godø, O. R. 2003. Age at maturation predicted from routine scale measurements in Norwegian spring-spawning herring (*Clupea harengus*) using discriminant and neural network analyses. ICES Journal of Marine Science, 60: 304–313.

Engelhard, G. H., South, A. B., and Pinnegar, J. K. 2008. Climate and North Sea cod distribution: a long-term approach. *In* Report of the Workshop on Cod and Future Climate Change (WKCFCC), pp. 81–85. ICES Document CM 2008/OCC:09.

Enghoff, I. B. 2000. Fishing in the southern North Sea region from the 1st to the 16th Century AD: evidence from fish bones. Archaeofauna, 9: 59–132.

Enghoff, I. B., MacKenzie, B. R., and Nielsen, E. E. 2007. The Danish fish fauna during the warm Atlantic period (ca. 7000–3900 BC): Forerunner of future changes? Fisheries Research, 87: 167–180.

Eno, N. C., Clark, R. A., and Sanderson, W. G. 1997. Non-native Marine Species in British Waters: A Review and Directory. Joint Nature Conservation Committee (JNCC), Peterborough. 136 pp.

EU-IP ECOOP. 2007. Interim status report of the European COastal-shelf sea OPerational observing and forecasting system.

Evans, G. L., Williams, P. J. le B., and Mitchelson-Jacob, E. G. 2003. Physical and anthropogenic effects on observed long-term nutrient changes in the Irish Sea. Estuarine, Coastal and Shelf Science, 57: 1159–1168.

Exadactylos, A., and Geffen, A. J. 1995. Population structure of Dover sole *Solea solea*: RAPD and allozyme data divergence in European stocks. Marine Ecology Progress Series, 246: 253–264.

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

Fage, L. 1911. Recherches sur la biologie de l'anchois *Engraulis encrasicolus* (Linné): races–âge-migration. Annales de l'Institut Océanographique, Paris, II: 1–40.

FAO. 2001. Fishery information, data and statistics service (FIDS), FAO Fisheries Department. Available online at http://www.fao.org/fi/struct/fidi.asp#FIDS.

FAO. 2007. The State of World Fisheries and Aquaculture 2006. FAO Fisheries and Aquaculture Department, FAO, Rome, Italy.

Farina, A. C., Freire, J., and Gonzalez-Gurriaran, E. 1997. Demersal fish assemblages in the Galician continental shelf and upper slope (NW Spain): spatial structure and long-term changes. Estuarine, Coastal and Shelf Science, 44: 435–454.

Farmer, A. S. D. 1975. Synopsis of biological data on Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). FAO Fisheries Synopsis, 112. 97 pp.

Fashchuk, D. Ya. 1995. Hydrogen sulphide zone of the northwestern Black Sea shelf: nature, origin, dynamics. Vodnye resursy, Moscow, 22: 568–584 (in Russian).

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J. 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science, 305: 362–366.

Fernö, A., Pitcher, T. J., Melle, W., Nøttestad, L., Mackinson, S., Hollingworth, C., and Misund, O. A. 1998. The challenge of the herring in the Norwegian Sea: making optimal spatial decisions. Sarsia, 83: 149–167.

Finney, B. P., Alheit, J., Emeis, K. C., Field, D. B., Gutiérrez, D., and Struck, U. 2010. Paleoecological studies on variability in marine fish populations: a long-term perspective on the impacts of climatic change on marine ecosystems. Journal of Marine Systems, 79: 316–326.

FishBase. 2007. *Scomber scombrus*. Available online at http://www.fishbase.org/Summary/speciesSummary.php?ID=118andgenusname=Scomberandspeciesname=scombrus.

Fives, J. M., Bez, N., Rivoirard, J., and King, P. 1996. Analysis of the early life history stages of mackerel. 1989 North East Atlantic. ICES Document CM 1996/S:32.

Fock, H., Uiblein, F., Köster, F., and von Westernhagen, H. 2002. Biodiversity and species environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic), sampled by different trawls. Marine Biology, 141: 185–199.

Folke, C. 2006. Resilience: the emergence of a perspective for social–ecological systems analyses. Global Environmental Change, 16: 253–267.

Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C. S., and Walker, B. 2002. Resilience and sustainable development: building adaptive capacity in a world of transformations. Ambio, 31: 437–440.

Folkvord, A. 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1037–1052.

Follesa, M. C., Mulas, A., Porcu, C., and Cau, A. 2009. First record of *Chilomycterus reticulatus* (Osteichthyes: Diodontidae) in the Mediterranean Sea. Journal of Fish Biology, 74: 1677–1681.

Fonds, M. 1979. Laboratory observations on the influence of temperature and salinity on the development of the eggs and growth of the larvae of *Solea solea* (Pisces). Marine Ecology Progress Series, 1: 91–99.

Fonds, M., and Saksena, V. P. 1977. The daily food intake of young soles (*Solea solea* L.) in relation to their size and the water temperature. Actes de Colloques du CNEXO, 4: 51–58.

Fonds, M., Cronie, R., Vethaak, A. D., and van der Puyl, P. 1992. Metabolism, food-consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature. Netherlands Journal of Sea Research, 29: 127–143.

Fortier, L., Ponton, D., and Gilbert, M. 1995. The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. Marine Ecology Progress Series, 120: 11–27.

Fossheim, M., Nilssen, E. M., and Aschan, M. 2006. Fish assemblages in the Barents Sea. Marine Biology Research, 2: 260–269.

Foster-Smith, J. (Ed). 2000. The Marine Fauna and Flora of the Cullercoats District: Marine Species Records for the North East Coast of England. Vol. 1 and 2. Penshaw Press, Sunderland.

Fox, C. J. 2001. Recent trends in stock–recruitment of Blackwater herring (*Clupea harengus* L.) in relation to larval production. ICES Journal of Marine Science, 58: 750–762.

Fox, C. J., O'Brien, C. M., Dickey-Collas, M., and Nash, R. D. M. 2000a. Patterns in the spawning of cod (*Gadus morhua* L.), sole (*Solea solea* L.) and plaice (*Pleuronectes platessa* L.) in the Irish Sea as determined by generalized additive modelling. Fisheries Oceanography, 9: 33–49.

Fox, C. J., Planque, B. P., and Darby, C. D. 2000b. Synchrony in the recruitment time-series of plaice (*Pleuronectes platessa* L.) around the UK and the influence of sea temperature. Journal of Sea Research, 44: 159–168.

Fox, C. J., Geffen, A. J., Blyth, R., and Nash, R. D. M. 2003. Temperature-dependent development rates of plaice (*Pleuronectes platessa* L.) eggs from the Irish Sea. Journal of Plankton Research, 25: 1319–1329.

Fox, C. J., Taylor, M., Dickey-Collas, M., van Damme, C. J. G., Bolle, L., Daan, N., Rohlf, N., *et al.* 2005. Initial results from the 2004 ichthyoplankton survey of the North Sea. ICES Document CM 2005/AA: 04.

Francis, R. C., Hare, S. R., Hollowed, A. B., and Wooster, W. S. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the N. E. Pacific. Fisheries Oceanography, 7: 1–21.

Francour, P., Boudouresque, C. F., Harmelin, J. G., Harmelin-Vivien, M. L., and Quignard, J. P. 1994. Are the Mediterranean waters becoming warmer? Information from biological indicators. Marine Pollution Bulletin, 9: 523–526.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science, 308: 1621–1623.

Frank, K. T., Petrie, B., Shackell, N. L., and Choi, J. S. 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. Ecology Letters, 9: 1096–1105.

Frank, K. T., Petrie, B., and Shackell, N. L. 2007. The ups and downs of trophic control in continental shelf ecosystems. Trends in Ecology and Evolution, 22: 236–242.

Franks, P. J. S. 2001. Turbulence avoidance: an alternate explanation of turbulence-enhanced ingestion rates in the field. Limnology and Oceanography, 46: 959–963.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., and Wanless, S. 2006. From plankton to top predators: bottom–up control of a marine food web across four trophic levels. Journal of Animal Ecology, 75: 1259–1268.

Frederiksen, M., Furness, R. W., and Wanless, S. 2007. Regional variation in the role of bottom–up and top–down processes in controlling sandeel abundance in the North Sea. Marine Ecology Progress Series, 337: 279–286.

Frederiksen, M., Jensen, H., Daunt, F., Mavor, R. A., and Wanless, S. 2008. Differential effects of a local industrial sand lance fishery on seabird breeding performance. Ecological Applications, 18(3): 701–710.

Frei, C., Scholl, R., Fukutome, S., Jurg Schmidli, J., and Vidale, P. L. 2006. Future change of precipitation extremes in Europe: intercomparison of scenarios from regional climate models. Journal of Geophysical Research, 111, D06105, doi: 10.1029/2005JD005965.

Freitas, V., Campos, J., Fonds, M., and van der Veer, H. W. 2007. Potential impact of temperature change on epibenthic predator–bivalve prey interactions in temperate estuaries. Journal of Thermal Biology, 32: 328–340.

Fricke, R. 1999. Annotated checklist of the marine and estuarine fish of Germany, with remarks on their taxonomic identity. Stuttgarter Beiträge zur Naturkunde, (A), 587: 1–67.

Frimodt, C. 1995. Multilingual Illustrated Guide to the World's Commercial Coldwater Fish. Osney Mead, Oxford, UK.

Frisk, M. G., Miller, T. J., Martell, S. J. D., and Sosebee, K. 2008. New hypothesis helps explain elasmobranch "outburst" on Georges Bank in the 1980s. Ecological Applications, 18: 234–245.

Froese, R., and Pauly, D. (Eds). 2007. FishBase. World Wide Web electronic publication. Available online at http://www.fishbase.org, version (08/2007).

Fromentin, J-M., and Planque, B. 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series, 134: 111–118.

Fry, F. E. J. 1957. The aquatic respiration of fish. *In* The Physiology of Fish, Vol. 1, pp 1–63. Ed. by M. E. Brown. Academic Press, New York.

Fry, F. E. J. 1971. The effect of environmental factors on animal activity. *In* Fish Physiology, Vol. 6, pp. 1–98. Ed. by W. S. Hoar and D. J. Randall. Academic Press, New York.

FSBI. 2007. Climate change and the fish of Britain and Ireland: Briefing Paper 4. Fisheries Society of the British Isles. Available online at www.fsbi.org.uk/docs/brief-climate-change-refs.pdf.

Fu, C., Mohn, R., and Fanning, L. P. 2001. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1613–1623.

Fulton, E. A., Smith, A. D. R., and Johnson, C. R. 2003. Effect of complexity on marine ecosystem models. Marine Ecology Progress Series, 253: 1–16.

Furevik, T., Drange, H., and Sorteberg, A. 2002. Anticipated changes in the Nordic Seas marine climate: scenarios for 2020, 2050 and 2080. Fisken og Havet, 4: 1–13.

Furness, R. W., and Tasker, M. L. 1997. Seabird consumption in sand lance MSVPA models for the North Sea, and the impact of industrial fishing on seabird population dynamics. *In* Forage Fish in Marine Ecosystems. Lowell Wakefield Fisheries Symposium Series No. 14: 147–169.

Gallego, A., North, E. W., and Petitgas, P. 2007. Introduction: status and future of modelling physical–biological interactions during the early life of fishes. Marine Ecology Progress Series, 347: 122–126.

Garcia, A., and Palomera, I. 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Scientia Marina, 60(Suppl. 2): 155–166.

Garcia-Soto, C., Pingree, R. D., and Valdés, L. 2002. Navidad development in the southern Bay of Biscay: climate change and swoddy structure from remote sensing and *in situ* measurements. Journal of Geophysical Research, 107, C8, 3118, doi: 10.1029/2001JC001012.

Garrison, L. P., and Link, J. S. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series, 202: 231–240.

Garstang, W. 1905. Report on the trawling investigations 1902–03, with especial reference to the distribution of the plaice. First Report on Fishery and Hydrographic investigations in the North Sea and adjacent waters (southern area). International Fisheries Investigations, Marine Biological Association of the UK, 67–198.

Gaston, K. J. 2003. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford.

Gauld, A. 1990. Movements of lesser sandeels (*Ammodytes marinus* Raitt) tagged in the northwestern North Sea. Journal du Conseil International pour l'Exploration de la Mer, 46: 229–231.

Gauld, J. A., and Hutcheon, J. R. 1990. Spawning and fecundity in the lesser sandeel, *Ammodytes marinus* Raitt, in the north-western North Sea. Journal of Fish Biology, 36: 611–613.

Geffen, A. J. 2009. Advances in herring biology: from simple to complex, coping with plasticity and adaptability. ICES Journal of Marine Science, 66: 1688–1695.

Geffen, A. J., Fox, C. J., and Nash, R. D. M. 2006. Temperature-dependent development rates of cod *Gadus morhua* eggs. Journal of Fish Biology, 69: 1060–1080.

Gelin, A., Crivelli, A. J., Rosecchi, E., and Kerambrun, P. 2001. Can salinity changes affect reproductive success in the brown shrimp *Crangon crangon*? Journal of Crustacean Biology, 21: 905–911.

Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A., and Hawkins, S. J. 2004. Regional climate warming drives long-term community changes of British marine fish. Proceedings of the Royal Society of London, Series B, 271: 655–661.

Gentsch, J. 2001. Nutzung von Wasserinhaltsstoffen zur Parametrisierung der solaren Energieabsorption in einem hydrodynamischen Schelfmeermodell. Das Potential von Fernerkundungsdaten. Diplomarbeit im Fach Ozeanographie, Universität Hamburg.

George, M. R. 1987. Ovarian maturation cycle of sprat, *Sprattus sprattus*. ICES Document CM 1987/H:47.

Gibson, R. N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Netherlands Journal of Sea Research, 32: 191–206.

Gilchrist, A. 1978. Cod Wars and How to Lose them. Q Press, Edinburgh.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., and Charnov, E. L. 2001. Effects of size and temperature on metabolic rate. Science, 293: 2248–2251.

Girsa, I. I., and Danilov, A. N. 1976. Defensive behaviour in sand lance, *Ammodytes hexapterus*, of the White Sea. Journal of Ichthyology, 16: 862–865.

Gislason, H. 2001. The effects of fishing on non-target species and ecosystem structure and function. Conference on Responsible Fisheries in the Marine Ecosystem, 1–4 October 2001, Reykjavik, Iceland. 21 pp.

Gislason, H., and Rice, J. 1998. Modelling the response of size and diversity spectra of fish assemblages to changes in exploitation. ICES Journal of Marine Science, 55: 362–370.

Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia, 83: 453–496.

Goarant, A., Petitgas, P., and Bourriau, P. 2007. Anchovy (*Engraulis encrasicolus*) egg density measurements in the Bay of Biscay: evidence for the spatial variation in egg density with sea surface salinity. Marine Biology, 151: 1907–1915.

Godø, O. R. 2003. Fluctuation in stock properties of north-east Arctic cod related to long-term environmental changes. Fish and Fisheries, 4: 121–137.

Gokoglu, M., Guven, O., Balci, A., Colak, H., and Golani, D. 2008. First records of *Nemichthys scolopaceus* and *Nemipterus randalli* and second record of *Apterichthus caecus* from Antalya Bay, southern Turkey. Journal of the Marine Biological Association 2 – Biodiversity Records. Available online at http://www.mba.ac.uk/jmba/pdf/5122pdf.

Golani, D. 2000. First record of the bluespotted cornetfish from the Mediterranean Sea. Journal of Fish Biology, 56: 1545–1547.

Golani, D. 2004. First record of the muzzled blenny (Osteichthyes: Blenniidae: *Omobranchus punctatus*) from the Mediterranean, with remarks on ship-mediated fish introduction. Journal of the Marine Biological Association of the UK, 84: 851–852.

Golani, D. 2006. The Indian scad (*Decapterus russelli*), (Osteichthyes: Carangidae), a new Indo-Pacific fish invader of the eastern Mediterranean. Scientia Marina, 70: 603–605.

Golani, D., and Capape, C. 2004. First records of the blue stingray, *Dasyatis chrysonota* (Smith, 1828) (Chondrichthyes: Dasyatidae), off the coast of Israel (eastern Mediterranean). Acta Adriatica, 45: 107–113.

Golani, D., and Fine, M. 2002. On the occurrence of *Hippocampus fuscus* in the eastern Mediterranean. Journal of Fish Biology, 60: 764–766.

Golani, D., and Sonin, O. 2006. The Japanese threadfin bream *Nemipterus japonicus*, a new Indo-Pacific fish in the Mediterranean Sea. Journal of Fish Biology, 68: 940–943.

Golani, D., Appelbaum-Golani, B., and Gon, O. 2008. *Apogon smithi* (Kotthaus, 1970) (Teleostei: Apogonidae), a Red Sea cardinalfish colonizing the Mediterranean Sea. Journal of Fish Biology, 72: 1534–1538.

Gómez, F., and Gorsky, G. 2003. Annual microplankton cycles in Villefranche Bay, Ligurian Sea, NW Mediterranean. Journal of Plankton Research, 25: 323–339.

González-Pola, C., Lavín, A., and Vargas-Yáñez, M. 2005. Intense warming and salinity modification of intermediate water masses in the southern corner of the Bay of Biscay for the period 1992–2003. Journal of Geophysical Research, 110: 1–14.

Goren, M., and Galil, B. S. 2005. A review of changes in the fish assemblages of Levantine inland and marine ecosystems following the introduction of non-native fish. Journal of Applied Ichthyology, 21: 364–370.

Graham, L. P., Chen, D., Christensen, O. B., Kjellström, E., Krysanova, V., Meier, H. E. M., Radziewski, M., *et al.* 2006. Projection of future climate change. *In* BALTEX Assessment of Climate Change, pp. 133–219. Ed. by H. von Storch. Springer-Verlag, Berlin.

Granskog, M., Kaartokallio, H., Kuosa, H., Thomas, D. N., and Vainio, J. 2006. Sea ice in the Baltic Sea – a review. Estuarine, Coastal and Shelf Science, 70: 145–160.

Grauman, G. 1974. Investigations on the spawning of Baltic cod in 1968–1970. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 166: 7–9.

Grauman, G. B., and Krenkel, K. 1986. Investigations about the dynamics of spawning processes of the Baltic sprat in 1984. ICES Document CM 1986/J: 17.

Grbec, B., Dulcic, J., and Morovic, M. 2002. Long-term changes in landings of small pelagic fish in the eastern Adriatic – possible influence of climate oscillations over the Northern Hemisphere. Climate Research, 20: 241–252.

Grbec, B., Morovic, M., and Zore-Armanda, M. 2003. Mediterranean oscillation and its relationship to salinity fluctuation in the Adriatic Sea. Acta Adriatica, 44: 61–76.

Greene, C. H., and Pershing, A. J. 2007. Climate drives sea change. Science, 315: 1084–1085.

Greenstreet, S. P. R., and Hall, S. J. 1996. Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. Journal of Animal Ecology, 65: 577–598.

Greenstreet, S. P. R., Spence, F. E., and McMillan, J. A. 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish species assemblage between 1925 and 1996. Fisheries Research, 40: 153–183.

Greenstreet, S., Armstrong, E., Mosegaard, H., Jensen, H., Gibb, I., Fraser, H., Scott, B., *et al.* 2006. Variation in the abundance of sandeels *Ammodyes marinus* off southeast Scotland: an evaluation of area-closure fisheries management and stock abundance assessment methods. ICES Journal of Marine Science, 63: 1530–1550.

Greve, W., Reiners, F., Nast, J., and Hoffmann, S. 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only offshore island of the North Sea. Helgoland Marine Research, 58: 274–288.

Grift, R. E., Tulp, I. Y. M., Clarke, L., Damm, U., McLay, A., Reeves, S., Vigneau, J., *et al.* 2004. Assessment of the ecological effects of the Plaice Box. Report of the European Commission Expert Working Group to Evaluate the Shetland and Plaice Boxes. European Commission, Brussels. 121 pp.

Grimm, S. K., and Herra, T. 1984. Spawning cycles of southern Baltic fish based on surveys of eggs and larvae. ICES Document CM 1984/J:39.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological Modelling, 115: 129–148.

Grishin, A. N., Kovalenko, L. A., and Sorokolit, L. K. 1994. Trophic relations in plankton communities in the Black Sea before and after *Mnemiopsis leidyi* invasion. *In* The Main Results of YugNIRO Complex Researches in the Azov-Black Sea Region and the World Ocean in 1993. Trudi YugNIRO [Proceedings of the Southern Scientific Research Institute of Marine Fisheries and Oceanography], Kerch, 40: 38–44.

Gröger, J. P., Kruse, G. H., and Rohlf, N. 2010. Slave to the rhythm: how large-scale climate cycles trigger herring (*Clupea harengus*) regeneration in the North Sea. ICES Journal of Marine Science, 67: 454–465.

Gucu, A. C. 1997. Role of fishing in the Black Sea ecosystem. *In* Sensitivity to Change: Black Sea, Baltic Sea, and North Sea, pp. 149–162. Ed. by E. Özsoy and A. Mikaelyan. NATO Advanced Science Institutes Series, 2. Environment, Vol. 27. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gucu, A. C. 2002. Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? Estuarine, Coastal and Shelf Science, 54: 439–451.

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

Guidetti, P., Boero, F., and Dulcic, J. 2002. Mass mortality of gilt sardine, *Sardinella aurita* (Clupeidae), in the Adriatic and Ionian seas. Cybium, 26: 317–319.

Gunnarson, B., Ásgeirsson, Þ., and Ingólfsson, A. 2007. The rapid colonization by *Crangon crangon* (Linnaeus, 1758) (Eucarida, Caridea, Crangonidae) of Icelandic coastal waters. Crustaceana, 80: 747–753.

Gutiérrez, D., Sifeddine, A., Field, D. B., Ortlieb, L., Vargas, G., Chavez, F. P., Velazco, F., *et al.* 2009. Rapid reorganization in ocean biogeochemistry off Peru towards the end of the Little Ice Age. Biogeosciences, 6: 835–848.

Haahtela, I. 1974. The marine element in the fauna of the Bothnian Bay. Hydrobiological Bulletin, 8: 232–240.

Haegele, C. W., and Schweigert, J. F. 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Canadian Journal of Fisheries and Aquatic Sciences, 42(Suppl. 1): 39–55.

Hagerman, L., and Vismann, B. 1995. Anaerobic metabolism in the shrimp *Crangon crangon* exposed to hypoxia, anoxia and hydrogen sulfide. Marine Biology, 123: 235–240.

Haidvogel, D., and Beckmann, A. 1999. Numerical Ocean Circulation Modelling. Ocean circulation and mathematical modelling. Series on Environmental Science and Management, Vol. 2. Imperial College Press, London. 319 pp.

Häkkinen, S., and Rhines, P. B. 2004. Decline of subpolar North Atlantic circulation during the 1990s. Science, 304: 555–559.

Halpern, B. S. 2003. The impact of marine reserves. Do reserves work and does reserve size matter? Ecological Applications, 13: S117–S137.

Hannesson, R. 2007. Geographical distribution of fish catches and temperature variations in the northeast Atlantic since 1945. Marine Policy, 31: 32–39.

Hänninen, J., Vuorinen, I., and Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnology and Oceanography, 45: 703–710.

Hansen, B., and Østerhus, S. 2000. North Atlantic-Nordic Seas exchanges. Progress in Oceanography, 45: 109–208.

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

Hansen, F. C., Möllmann, C., Schütz, U., and Neumann, T. 2006. Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. Journal of Plankton Research, 28: 39–54.

Hanson, P., Johnson, T., Kitchell, J., and Schindler, D. E. 1997. Fish bioenergetics 3.0. Report WISCU-T-97-001, University of Wisconsin Sea Grant Institute, Madison, WI.

Harden Jones, F. R. 1968. Fish Migration. Edward Arnold, London. 325 pp.

Harding, D., and Nichols, J. H. 1987. Plankton surveys off the north-east coast of England in 1976: an introductory report and summary of the results. Fisheries Research Technical Report, Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, 86. 56 pp.

Harding, D., Nichols, J. H., and Tungate, D. S. 1978. The spawning of the plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 102–113.

Hardy, A. C. 1924. The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. Fisheries Investigations, Series II, 7: 1–39.

Hare, C. E., Leblanc, K., DiTullio, G. R., Kudela, R. M., Zhang, Y., Lee, P. A., Riseman, S., *et al.* 2007. Consequences of increased temperature and CO_2 for phytoplankton community structure in the Bering Sea. Marine Ecology Progress Series, 352: 9–16.

Hare, S. R., and Mantua, N. J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography, 47: 103–145.

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., *et al.* 2006. The impacts of climate change in coastal marine systems. Ecology Letters, 9: 228–241.

Harms, I., Schrum, C., and Hatten, K., 2005. Numerical sensitivity studies on the variability of climate relevant processes in the Barents Sea. Journal of Geophysical Research, 110: C06002, doi: 10.1029/2004JC002559.

Harris, C. L., Plueddemann, A. J., and Gawarkiewicz, G. C. 1998. Water mass distribution and polar front structure in the western Barents Sea. Journal of Geophysical Research, 103, C2: 2905–2917.

Harris, M. P., Beare, D., Toresen, R., Nøttestad, L., Kloppmann, M., Dörner, H., Peach, K., *et al.* 2007. A major increase in snake pipefish (*Entelurus aequoreus*) in northern European seas since 2003: potential implications for seabird breeding success. Marine Biology, 15: 973–983.

Hart, P. J. B. 1974. The distribution and long-term changes in the abundance of larval *Ammodytes marinus* (Raitt) in the North Sea. *In* The Early Life History of Fish, pp. 171–182. Ed. by J. H. S. Blaxter. Springer-Verlag, Berlin. 765 pp.

Harvey, C. J., Cox, S. P., Essington, T. E., Hansson, S., and Kitchell, J. F. 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. ICES Journal of Marine Science, 60: 939–950.

Harwood, J., and Croxall, J. P. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Marine Mammal Science, 4: 13–33.

Hashimoto, H. 1984. Population structure of the sandeel around Japan. Bulletin of the Japanese Society of Scientific Fisheries (Nissuishi), 50: 1357–1365.

Hasselmann, K. 1976. Stochastic climate models. Part I. Theory. Tellus, 28: 473–485.

Hatfield, E. M. C., Nash, R. D. M., Zimmermann, C., Schön, P-J., Kelly, C., Dickey-Collas, M., MacKenzie, K., *et al.* 2007. The scientific implications of the EU Project WESTHER (Q5RS-2002-01056) to the assessment and management of the herring stocks to the west of the British Isles. ICES Document CM 2007/L:11.

Hátún, H., Sandø, A. B., Drange, H., Hansen, B., and Valdimarsson, H. 2005. Influence of the Atlantic Subpolar Gyre on the thermohaline circulation. Science, 309: 1841–1844.

Hawkins, S. J., Southward, A. J., and Genner, M. J. 2003. Detection of environmental change in a marine ecosystem – evidence from the western English Channel. Science of the Total Environment, 310: 245–246.

Hay, D. E., Toresen, R., Stephenson, R., Thompson, M., Claytor, R., Funk, F., Ivshina, E., *et al.* 2001. Taking stock: an inventory and review of world herring stocks in 2000. *In* Herring: Expectations for a New Millennium, pp. 381–454. Ed. by F. Funk, J. Blackburn, D. Hay, A. J. Paul, R. Stephenson, R. Toresen, and D. Witherell. University of Alaska Sea Grant, AK-SG-01-04, Fairbanks, AK.

Hays, G. C., Richardson, A. J., and Robinson, C. 2005. Climate change and marine plankton. Trends in Ecology and Evolution, 20: 337–344.

Hayward, P., Nelson-Smith, T., and Shields, C. 1996. Sea Shore of Britain and Europe. Harper Collins, London. 352 pp.

Heath, M. R. 2005. Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. ICES Journal of Marine Science, 62: 847–868.

Heath, M. R. 2007a. Responses of fish to climate fluctuations in the Northeast Atlantic. Responses of fish to climate fluctuations in the Northeast Atlantic. *In* The Practicalities of

Climate Change: Adaptation and Mitigation, pp. 102–116. Ed. by L. E. Emery. Proceedings of the 24th Conference of the Institute of Ecology and Environmental Management, Cardiff, 14–16 November 2006.

Heath, M. R. 2007b. Responses of cod to climate change in the North Sea and implications for management. ICES Working Document, 3 April 2007.

Heath, M. R., Henderson, E. W., Slesser, G., and Woodward, E. M. S. 1991. High salinity in the North Sea. Nature, 352: 116.

Heath, M. R., Scott, B., and Bryant, A. D. 1997. Modelling the growth of herring from four different stocks in the North Sea. Journal of Sea Research, 38: 413–436.

Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., *et al.* 1999. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. Fisheries Oceanography, 8: 163–176.

Heath, M. R., MacKenzie, B. R., Ådlandsvik, B., Backhaus, J. O., Begg, G. A., Drysdale, A., Gallego, A., *et al.* 2003. An operational model of the effect of stock structure and spatio-temporal factors on recruitment. Final report of the EU-STEREO project, FAIR-CT98-4122. 1 December 1998–28 February 2002. Contract Report No. 10/03. Fisheries Research Services, Aberdeen. 360 pp.

Heath, M. R., Kunzlik, P. A., Gallego, A., Holmes, S. J., and Wright, P. J. 2008. A model of meta-population dynamics for northern European cod – the dynamic consequences of natal fidelity. Fisheries Research, 93: 92–116.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A., and Bridson, J. 2004. Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using Generalised Additive Models. Fisheries Research, 70: 17–25.

Heessen, H. J. L. 1996. Time-series data for a selection of forty fish species caught during the International Bottom Trawl Survey. ICES Journal of Marine Science, 53: 1079–1084.

Heessen, H. J. L., and Daan, N. 1994. Cod distribution and temperature in the North Sea. ICES Marine Science Symposia, 198: 244–253.

Heessen, H. J. L., and Rijnsdorp, A. D. 1989. Investigations on egg production and mortality of cod (*Gadus morhua* L.) and plaice (*Pleuronectes platessa* L.) in the southern and eastern North Sea in 1987 and 1988. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 15–20.

Heessen, H. J. L., Hislop, J. R. G., and Boon, T. W. 1996. An invasion of the North Sea by blue-mouth, *Helicolenus dactylopterus* (Pisces, Scorpaenidae). ICES Journal of Marine Science, 53: 874–877.

Heil, C. A., Glibert, P. M., Al-Sarawi, M. W., Faraj, M., Behbehani, M., and Husain, M. 2001. First record of a fish-killing *Gymnodinium* sp. bloom in Kuwait Bay, Arabian Sea: chronology and potential causes. Marine Ecology Progress Series, 214: 15–23.

Heincke, F. 1878. Die Varietäten des Herings I. Ber. Kommn Unters. dt. Meere, 3: 37–132.

Heincke, F. 1898. Naturgeschichte des Herrings. Abhandlungen der Deutschen Seefischerei-Vereins, Vol. II. Otto Salle, Berlin. 128 pp.

Heincke, F. 1913. Investigations on the plaice. I. The plaice fishery and protective regulations. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 17: 1–153.

Heino, M., and Engelhard, G. H. 2006. Herring in warming waters: climate change may cause herring to reproduce less often. Options, Winter 2006: 9.

Heino, M., and Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. Bulletin of Marine Science, 70: 639–656.

Heino, M., Dieckmann, U., and Godø, O. R. 2002a. Reaction norm analysis of fisheries-induced adaptive change and the case of the northeast Arctic cod. ICES Document CM 2002/Y:14.

Heino, M., Dieckmann, U., and Godø, O. R. 2002b. Measuring probabilistic reaction norms for age and size at maturation. Evolution, 56: 669–678.

Heino, M., Dieckmann, U., Engelhard, G., and Godø, O. R. 2004. Evolusjonære effekter av fiske. *In* Havets ressurser 2004. Fisken og havet, særnummer 1–2004, pp. 164–166. Ed. by K. Michalsen. Institute of Marine Research, Bergen, Norway.

Helland-Hansen, B., and Nansen, F. 1909. The Norwegian Sea.: its physical oceanography based upon the Norwegian researches 1900–1904. Report on Norwegian Fishery and Marine Investigations, 2. 360 pp..

Helle, K., and Pennington, M. 1999. The relation of the spatial distribution of early juvenile cod (*Gadus morhua* L.) in the Barents Sea to zooplankton density and water flux during the period 1978–1984. ICES Journal of Marine Science, 56: 15–27.

Hemida, F., Diatta, Y., Golani, D., Ben Souisi, J., Guelorget, O., and Capape, C. 2004. On the occurrence of the Monrovian surgeonfish, *Acanthurus monroviae* Steindachner, 1876 (Osteichthyes: Acanthuridae) off the coast of Algeria (southern Mediterranean). Acta Adriatica, 45: 181–185.

Henderson, G. T. D. 1954. Continuous plankton records; the young fish and fish eggs, 1932–39 and 1946–49. Hull Bulletin of Marine Ecology, 3: 215–252.

Henderson, P. A. 2007. Discrete and continuous change in the fish community of the Bristol Channel in response to climate change. Journal of the Marine Biological Association of the UK, 87: 589–598.

Henderson, P. A., and Seaby, R. M. 2005. The role of climate in determining the temporal variation in abundance, recruitment and growth of sole *Solea solea* in the Bristol Channel. Journal of the Marine Biological Association of the UK, 85: 197–204.

Henderson, P. A., Seaby, R. M. H., and Somes, J. R. 2006. A 25-year study of climatic and density-dependent population regulation of common shrimp *Crangon crangon* (Crustacea: Caridea) in the Bristol Channel. Journal of the Marine Biological Association of the UK, 86: 287–298.

Herdman, W. A., and Dawson, R. A. 1902. Fish and Fisheries of the Irish Sea. Lancashire Sea-Fisheries Memoir No. 11. 98 pp.

Heupel, M. R., Simpfendorfer, C. A., and Hueter, R. E. 2003. Running before the storm: blacktip sharks respond to falling barometric pressure associated with Tropical Storm Gabrielle. Journal of Fish Biology, 63: 1357–1363.

Hiddink, J. G., and ter Hofstede, R. 2008. Climate induced increases in species richness of marine fish. Global Change Biology, 14: 453–460.

Hiddink, J. G., Hutton, T., Jennings, S., and Kaiser, M. J. 2006a. Predicting the effects of area closures and fishing effort restrictions on the production, biomass, and species richness of benthic invertebrate communities. ICES Journal of Marine Science, 63: 822–830.

Hiddink, J. G., Jennings, S., Kaiser, M. J., Queirós, A. M., Duplisea, D. E., and Piet, G. J. 2006b. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Canadian Journal of Fisheries and Aquatic Sciences, 63: 721–736.

Hiddink, J. G., MacKenzie, B. R., Rijnsdorp, A., Dulvy, N. K., Nielsen, E. E., Bekkevold, D., Heino, M., *et al.* 2008a. Importance of fish biodiversity for the management of fisheries and ecosystems. Fisheries Research, 90: 6–8.

Hiddink, J. G., Rijnsdorp, A. D., and Piet, G. J. 2008b. Can bottom trawling disturbance increase food production for a commercial fish species? Canadian Journal of Fisheries and Aquatic Sciences, 65: 1393–1401.

Hinrichsen, H-H., Möllmann, C., and Voss, R. 2002. Bio-physical modelling of larval Baltic cod (*Gadus morhua*) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences, 59: 1858–1873.

Hinrichsen, H. H., Schmidt, J. O., Petereit, C., and Möllmann, C. 2005. Survival probability of Baltic larval cod in relation to spatial overlap patterns with its prey obtained from drift model studies. ICES Journal of Marine Science. 62: 878–885.

Hiscock, K. (Ed.) 1998. Benthic marine ecosystems of Great Britain and the north-east Atlantic. Marine Nature Conservation Review. Joint Nature Conservation Committee, Peterborough. 404 pp.

Hiscock, K., Southward, A., Tittley, I., Jory, A., and Hawkins, S. 2001. The impact of climate change on subtidal and intertidal benthic species in Scotland. Report to Scottish Natural Heritage from the Marine Biological Association of the UK – Final Report. Marine Biological Association, Plymouth.

Hiscock, K., Marshall, C., Sewell, J., and Hawkins, S. J. 2006. The structure and functioning of marine ecosystems: an environmental protection and management perspective. English Nature Research Reports, No. 699.

Hislop, J. R. G. 1996. Changes in North Sea gadoid stocks. ICES Journal of Marine Science, 53: 1146–1156.

Hislop, J. R. G., Harris, M. P., and Smith, J. G. M. 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. Journal of Zoology, London, 224: 501 517.

Hjelm, J., Simonsson, J., and Cardinale, M. 2004. Spatial distribution of cod in the Baltic Sea in relation to abiotic factors–a question of fish-age and area. ICES Document CM 2004/L:16. 35 pp.

Hjermann, D. Ø., Stenseth, N. C., and Ottersen, G. 2004a. Indirect climatic forcing of the Barents Sea capelin: a cohort effect. Marine Ecology Progress Series, 273: 229–238.

Hjermann, D. Ø., Ottersen, G., and Stenseth, N. C. 2004b. Competition among fishermen and fish causes the collapse of Barents Sea capelin. Proceedings of the National Academy of Sciences of the USA, 101: 11679–11684.

Hjermann, D. Ø., Bogstad, B., Eikeset, A. M., Ottersen, G., Gjösæter, H., and Stenseth, N. C. 2007. Food web dynamics affect northeast Arctic cod recruitment. Proceedings of the Royal Society of London, Series B, 274: 661–669.

Hjøllo, S. S., Skogen, M. D., and Svendsen, E. 2009. Exploring currents and heat within the North Sea using a numerical model. Journal of Marine Systems, 78: 180–192.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 20: 1–228.

Hoarau, G., Rijnsdorp, A. D., van der Veer, H. W., Stam, W. T., and Olsen, J. L. 2002. Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: microsatellites revealed large-scale spatial and temporal homogeneity. Molecular Ecology, 11: 1165–1176.

Hoarau, G., Piquet, A. M. T., van der Veer, H. W., Rijnsdorp, A. D., Stam, W., and Olsen, J. L. 2004. Population structure of plaice (*Pleuronectes platessa* L.) in northern Europe: a comparison of resolving power between microsatellites and mitochondrial DNA data. Journal of Sea Research, 51: 183–190.

Hobson, E. S. 1986. Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces: Ammodytidae), during the transition between day and night in southeastern Alaska. Copeia, 1: 223–226.

Hodgson, W. C. 1936. The recent state of knowledge concerning the origin and distribution of herring populations in western European waters. The Southern Bight. Rapports et Procès-Verbaux de la Réunion du Conseil International pour l'Exploration de la Mer, 100: 19.

Holden, M. J. 1978. Long-term changes in landings of fish from the North Sea. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 11–26.

Holland, K. N., Brill, R. W., Chang, R. K. C., Sibert, J. R., and Fournier, D. A. 1992. Physiological and behavioural thermoregulation in bigeye tuna. Nature, 358: 410–412.

Holmes, S. J., and Wright, P. J. 2005. Regional variability in cod dynamics in the North Sea and West of Scotland and its implications to management. ICES Document CM 2005/AA:08.

Holst, J. C., Dragesund, O., Hamre, J., Misund, O. A., and Østvedt, O. J. 2002. Fifty years of herring migrations in the Norwegian Sea. ICES Marine Science Symposia, 215: 352–360.

Holst, J. C., Roettingen, I., and Melle, W. 2004. The herring. *In* The Norwegian Sea Ecosystem, pp. 203–226. Ed. by H. R. Skjoldal, R. Sætre, and A. Fernø. Tapir Academic Press, Trondheim.

Holt, J. T., and James, I. D., 2001. An s-coordinate density evolving model of the North West European continental shelf. Part 1. Model description and density structure. Journal of Geophysical Research 106 (C7): 14015–14034.

Holt, J. T., Allen, J. I., Proctor, R., and Gilbert, F. 2005. Error quantification of a high-resolution coupled hydrodynamic–ecosystem coastal–ocean model. Part 1. Model overview and assessment of the hydrodynamics. Journal of Marine Systems, 57: 167–188.

HOMSIR. 2001. Biology of horse mackerel (*Trachurus* spp.) in European Waters. *In* EU-project HOMSIR (Horse mackerel stock identification research). Contract QLRT-PL1999–01438, Available online at http://www.homsir.com/biology/biology.html.

Hopkins, P. J. 1989. Herring predation on fish eggs and larvae in the North Sea. *In* The Early Life History of Fish, p. 459. Ed. by J. H. S. Blaxter, J. C. Gamble, and H. von Westernhagen. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191. 497 pp.

Horwood, J. W. 1993. The Bristol Channel sole [*Solea solea* (L)]: a fisheries case-study. Advances in Marine Biology, 29: 215–367.

Horwood, J. W., and Millner, R. S. 1998. Cold induced abnormal catches of sole. Journal of the Marine Biological Association of the UK, 78: 345–347.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium, 2: 17–29.

Houghton, J. D. R., Doyle, T. K., Davenport, J., and Hays, G. C. 2006. The ocean sunfish *Mola mola*: insights into distribution, abundance and behaviour in the Irish and Celtic Seas. Journal of the Marine Biological Association of the UK, 86: 1237–1243.

Houghton, R. G., and Harding, D. 1976. The plaice of the English Channel: spawning and migration. Journal du Conseil International pour l'Exploration de la Mer, 36: 229–239.

Hubold, G. 1978. Variations in growth rate and maturity of herring in the Northern North Sea in the years 1955–1973. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 154–163.

Huey, R. B., and Kingsolver, J. G. 1993. Evolution of resistance to high temperature in ectotherms. *In* Evolutionary Responses to Environmental Stress. American Naturalist, 142(Suppl.): 21–46.

Hughes, S. L., Holliday, N. P., Colbourne, E., Ozhigin, V., Valdimarsson, H., Østerhus, S., and Wiltshire, K. 2009. Comparison of *in situ* time-series of temperature with gridded sea surface temperature datasets in the North Atlantic. ICES Journal of Marine Science, 66: 1467–1479.

Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S., and, Wilson, J. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution, 20: 380–386.

Hulme, M., Barrow, E., Arnell, N. W., Harrison, P., Downing, T., and Johns, R. 1999. Relative impacts of human-induced climate change and natural variability. Nature, 397: 688–691.

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

Hulme, T. J. 1995. The use of vertebral counts to discriminate between North Sea herring stocks. ICES Journal of Marine Science, 52: 775–779.

Hunt, G. L., and McKinnell, S. 2006. Interplay between top–down, bottom–up, and wasp-waist control in marine ecosystems. Progress in Oceanography, 68: 115–124.

Hunt, G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., and Bond, N. A. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Research II, 49: 5821–5853.

Hunt, G. L., Stabeno, P. J., Strom, S., and Napp, J. M. 2008. Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. Deep Sea Research Part II, 55(16–17): 1919–1944.

Hunter, E., Metcalfe, J. D., and Reynolds, J. D. 2003. Migration route and spawning area fidelity by North Sea plaice. Proceedings of the Royal Society of London, Series B, 270: 2097–2103.

Hunter, E., Metcalfe, J. D., Arnold, G. P., and Reynolds, J. D. 2004. Impacts of migratory behaviour on population structure in North Sea plaice. Journal of Animal Ecology, 73: 377–385.

Hunter, J., and Leong, R. 1981. The spawning energetics of female northern anchovy, *Engraulis mordax*. Fishery Bulletin US, 79: 215–230.

Huret, M., Gohin, F., Delmas, D., Lunven, M., and Garçon, V. 2007. Use of SeaWiFS data for light availability and parameter estimation of a phytoplankton production model of the Bay of Biscay. Journal of Marine Systems, 65: 509–531.

Huret, M., Petitgas, P., and Léger, F. 2009. Potential responses of anchovy (*Engraulis encrasicolus*) larval dispersal to climate change in the Bay of Biscay. ICES Document CM 2009/E:08.

Huret, M., Petitgas, P., and Woillez, M. In press. Dispersal kernels and their drivers captured with a hydrodynamic model and spatial indices: a case study on anchovy (*Engraulis encrasicolus*) early life stages in the Bay of Biscay. Progress in Oceanography.

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

Hurrell, J. W., Kushnir, Y., Visbeck, M., and Ottersen, G. 2003. An Overview of the North Atlantic Oscillation. *In* The North Atlantic Oscillation: Climate Significance and Environmental Impact, pp. 1–35. Ed. by J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck. American Geophysical Union Geophysical Monograph Series, 134.

Huse, G., and Ellingsen, I. 2008. Capelin migrations and climate change – a modelling analysis. Climate Change, 87: 177–197.

Huse, G., Railsback, S., and Fernö, A. 2002. Modelling changes in migration patterns of herring: collective behaviour and numerical domination. Journal of Fish Biology, 60: 571–582.

Huse, G., Salthaug, A., and Skogen, M. D. 2008. Indications of a negative impact of herring on recruitment of Norway pout. ICES Journal of Marine Science, 65: 906–911.

Huse, G., Fernö, A., and Holst, J. C. 2010. Establishment of new wintering areas in herring co-occur with peaks in the recruit- to repeat-spawner ratio. Marine Ecology Progress Series, doi: 10.3354/meps08620.

Husebø, A., Slotte, A., and Stenevik, E. K. 2007. Growth of juvenile Norwegian spring-spawning herring in relation to latitudinal and interannual differences in temperature and fish density in their coastal and fjord nursery areas. ICES Journal of Marine Science, 64: 1161–1172.

Hutchings, J. A., and Myers, R. A. 1994a. What can be learned from the collapse of a renewable resource—Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2126–2146.

Hutchings, J. A., and Myers, R. A. 1994b. Timing of cod reproduction – interannual variability and the influence of temperature. Marine Ecology Progress Series, 108: 21–31.

Hutchinson, W. F., Carvalho, G. R., and Rogers, S. I. 2001. Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. Marine Ecology Progress Series, 223: 251–260.

ICES. 1949. Contributions to Special Scientific Meetings 1948. Climatic changes in the Arctic in relation to plants and animals. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 125: 5–51.

ICES. 1965a. The North Sea Herring. ICES Cooperative Research Report No. 4. 57 pp.

ICES. 1965b. Report of the Working Group on Sole. ICES Cooperative Research Report No. 5. 126 pp.

ICES. 1986. Report of the *ad hoc* Working Group on 1984 and 1985 Sole (*Solea solea* L.) Egg Surveys. ICES Document CM 1986/G:95.

ICES. 1990a. Report of the Sprat Biology Workshop. ICES Cooperative Research Report No. 169. 16 pp.

ICES. 1990b. Report of the Working Group on the Assessment of the Stocks of Sardine, Horse Mackerel and Anchovy. ICES Document CM 1990/Assess:24.

ICES. 1991. Report of the Working Group on the Assessment of the Stocks of Sardine, Horse Mackerel and Anchovy. ICES Document CM 1991/Assess:22.

ICES. 1996. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. ICES Document CM 1996/Assess:7.

ICES. 1999. Report of the ICES Baltic Fisheries Assessment Working Group. ICES Document CM 1999/ACFM:15.

ICES. 2001. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy. ICES Document C M 2001/ACFM:6.

ICES. 2004a. Report of the Working Group on the Assessment of the Demersal Stocks in the North Sea and Skagerrak. ICES Document CM 2004/ACFM:07.

ICES. 2004b. Report of the Study Group on Closed Spawning Areas of Eastern Baltic Cod. ICES Document CM 2004/ACFM:17.

ICES. 2004c. Report of the Study Group on Regional Scale Ecology of Small Pelagic Fish (SGRESP). ICES Document CM 2004/G:06.

ICES. 2004d. Report of the Working Group on Fish Ecology (WGFE), 2–7 April 2004. ICES Document CM 2004/G:09. 257 pp.

ICES. 2005a. Report of the Working Group on the Assessment of the Demersal Stocks in the North Sea and Skagerrak. ICES Document CM 2005/ACFM:07.

ICES. 2005b. Report of the Baltic Fisheries Assessment Working Group. ICES Document CM 2005/ACFM:19. 589 pp.

ICES. 2005c. Report of the Study Group on Multispecies Assessments in the North Sea (SGMSNS). ICES Document CM 2005/D:06.

ICES. 2005d. Report of the ICES Working Group on Genetics in Aquaculture and Fisheries. ICES Document CM/F:01. 51 pp.

ICES. 2005e. Report of the Working Group on Fish Ecology (WGFE), 21–26 February 2005, Santander, Spain. ICES Document CM 2005/G:05. 220 pp.

ICES. 2006a. Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 2: Iceland and East Greenland. ICES Advice. 94 pp.

ICES. 2006b. Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 3: The Barents and the Norwegian Seas. ICES Advice. 89 pp.

ICES. 2006c. Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 4: The Faroe Plateau Ecosystem. ICES Advice. 51 pp.

ICES. 2006d. Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 6: North Sea. ICES Advice. 310 pp.

ICES. 2006e. Sprat in the North Sea (Subarea IV). *In* Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 6: North Sea, pp. 242–248. ICES Advice. 310 pp.

ICES. 2006f. Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 7: Bay of Biscay and Iberian Seas. ICES Advice. 113 pp.

ICES. 2006g. Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 8: Baltic Sea. ICES Advice. 119 pp.

ICES. 2006h. Western horse mackerel (*Trachurus trachurus*) (Divisions IIa, IVa, Vb, VIa, VIIa–c, e–k, VIIIa–e). *In* Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2006. Book 9: Widely Distributed and Migratory Stocks, pp. 69–77. ICES Advice. 255 pp.

ICES. 2006i. ICES Report on Ocean Climate 2005. ICES Cooperative Research Report No. 280. 47 pp.

ICES. 2006j. Zooplankton monitoring results in the ICES area, summary status report 2004/2005. ICES Cooperative Research Report No. 281. 43 pp.

ICES. 2006k. Report of the Working Group on Assessment of New MoU Species (WGNEW), 13–15 December 2005, ICES Headquarters, Copenhagen. ICES Document CM 2006/ACFM:11.

ICES. 2006l. Report of the Working Group on the Assessment of the Demersal Stocks in the North Sea and Skagerrak. ICES Document CM 2006/ACFM:35. 1160 pp.

ICES. 2006m. Annex 2: Stock annexes. 11. Quality handbook: Sandeel in Sub-Area IV. *In* Report of the Working Group on the Assessment of the Demersal Stocks in the North Sea and Skagerrak. ICES Document CM 2006/ACFM:35. 1160 pp.

ICES. 2006n. Report of the Working Group on Fish Ecology (WGFE), 13–17 March 2006, ICES Headquarters, Copenhagen. ICES Document CM 2006/G:06. 154 pp.

ICES. 2006o. Report of the Study Group on Recruitment Variability in North Sea Planktivorous Fish (SGRECVAP). ICES Document CM 2006/LRC:03. 78 pp.

ICES. 2006p. Report of the ICES Working Group on the Application of Genetics in Fisheries and Aquaculture (WGAGFM). ICES Document CM 2006/MCC:04. 63 pp.

ICES. 2007a. North Sea horse mackerel (*Trachurus trachurus*; Division IIIa (eastern part), Division IVb and c, VIId). *In* Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2007. Book 6: North Sea, pp. 207–211. ICES Advice. 249 pp.

ICES. 2007b. Southern horse mackerel (*Trachurus trachurus*; Division IXa). *In* Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2007. Book 7: Bay of Biscay and Western Iberia, pp. 59–63. ICES Advice. 94 pp.

ICES. 2007c. Northeast Atlantic Mackerel (combined Southern, Western and North Sea spawning components). *In* Report of the ICES Advisory Committee on Fishery Management, Advisory Committee on the Marine Environment and Advisory Committee on Ecosystems, 2007. Book 9: Widely Distributed and Migratory Stocks, pp. 74–87. ICES Advice. 129 pp.

ICES. 2007d. Report of the Working Group on Assessment of New MoU Species (WGNEW), 9–11 January 2007, Lorient, France. ICES Document CM 2007/ACFM: 1.

ICES. 2007e. Report of the Herring Assessment Working Group for the Area South of 62ºN (HAWG). ICES Document CM 2007/ACFM:11. 548 pp.

ICES. 2007f. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). ICES Document CM 2007/ACFM:15. 727 pp.

ICES. 2007g. Report of the Arctic Fisheries Working Group (AFWG), 18–27 April 2006, Vigo, Spain. ICES Document CM 2007/ACFM:16. 651 pp.

ICES. 2007h. Report of the Workshop on the Integration of Environmental Information into Fisheries Management Strategies and Advice (WKEFA). ICES Document CM 2007/ACFM:25. 182 pp.

ICES. 2007i. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (WGMHSA). ICES Document CM 2007/ACFM:31. 712 pp.

ICES. 2007j. Report of the Working Group on the Assessment of the Demersal Stocks in the North Sea and Skagerrak. ICES Document CM 2007/ACFM:35.

ICES. 2007k. Report of the Working Group on Fish Ecology (WGFE). ICES Document CM 2007/LRC:03.

ICES. 2007l. Report of the Study Group on Recruitment Variability in North Sea Planktivorous Fish (SGRECVAP). ICES Document CM 2007/LRC:07. 65 pp.

ICES. 2007m. Report of the Workshop on Testing the Entrainment Hypothesis (WKTEST). ICES Document CM 2007/LRC:10.

ICES. 2009. Report of the Working Group on Crangon Fisheries and Life History (WGCRAN), 10–13 May 2009, Oostende, Belgium. ICES Document CM 2009/LCR:07. 63 pp.

Iles, T. D. 1984. Allocation of resources to gonad and soma in Atlantic herring *Clupea harengus* L. *In* Fish Reproduction, pp. 331–348. Ed. by G. W. Potts and R. J. Wootton. Academic Press, London.

Imsland, A. K., Sunde, L. M., Folkvord, A., and Stefansson, S. O. 1996. The interaction of temperature and fish size on growth of juvenile turbot. Journal of Fish Biology, 49: 926–940.

Imsland, A. K., Foss, A., Folkvord, A., and Jonassen, T. M. 2005. The interrelation between temperature regimes and fish size in juvenile Atlantic cod (*Gadus morhua*): effects on growth and feed conversion efficiency. Fish Physiology and Biochemistry, 31: 347–361.

Imsland, A. K., Foss, A., Sparboe, L. O., and Sigurdsson, S. 2006. The effect of temperature and fish size on growth and feed efficiency ratio of juvenile spotted wolffish *Anarhichas minor*. Journal of Fish Biology, 68: 1107–1122.

Ingvaldsen, R. B. 2005. Width of the North Cape Current and location of the Polar Front in the western Barents Sea. Geophysical Research Letters 32, L16603, doi: 1029/2005GL023440.

Inoue, A., Takamori, S., Kuniyuki, K., Kobayashi, S., and Nishina, S. 1967. Studies on fishery biology of the sand-lance, *Ammodytes personatus* (Girard). Bulletin of the Naikai Regional Fisheries Research Laboratory, 25: 1–335.

IPCC. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Ed. by J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson. Cambridge University Press, Cambridge, UK. 881 pp.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, *et al.* Cambridge University Press, Cambridge, UK. 996 pp.

Irigoien, X., Fiksen, Ø., Cotano, U., Uriarte, A., Alvarez, P., Arrizabalaga, H., Boyra, G., *et al.* 2007. Could Biscay Bay anchovy recruit through a spatial loophole? Progress in Oceanography, 74: 132–148.

Irvin, D. N. 1974. Temperature tolerance of early development stages of Dover sole, *Solea solea* (L.). *In* The Early Life History of Fish: The Proceedings of an International Symposium, 17-23 May 1973, Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association, Oban, Scotland, pp. 449–463. Ed. by J. H. S. Blaxter. Springer-Verlag, Berlin and New York.

Ishimatsu, A., Hayashi, M., Lee, K. S., Kikkawa, T., and Kita, J. 2005. Physiological effects on fish in a high-CO_2 world. Journal of Geophysical Research: Oceans, 110, C09S09, doi: 10.1029/2004JC002564.

Ishimatsu, A., Hayashi, M., and Kikkawa, T. 2008. Fish in high-CO2, acidified oceans. Marine Ecology Progress Series, 373: 295–302.

Ivanov, L. S., and Beverton, R. J. H. 1985. The Fisheries Resources of the Mediterranean. Part 2: Black Sea. FAO Studies and Reviews, 60. 135 pp.

Iversen, S. A., Skogen, M. D., and Svendsen, E. 2002. Availability of horse mackerel (*Trachurus trachurus*) in the north-eastern North Sea, predicted by the transport of Atlantic water. Fisheries Oceanography, 11: 245–250.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., *et al.* 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293: 629–637.

Jacobsen, B. 2006. The influence of climate variability on the migration of two pelagic fish species, garfish (*Belone belone* L. 1761) and Atlantic mackerel (*Scomber scombrus* L. 1758) in Danish waters. Master's thesis, Department of Marine Ecology, Biology Institute, University of Århus, Denmark.

Jager, Z., Kleef, L., and Tydeman, P. 1993. The distribution of 0-group flatfish in relation to abiotic factors on the tidal flats in the brackish Dollard (Ems Estuary, Wadden Sea). Journal of Fish Biology, 43: 31– 43.

Jahncke, J., Checkley, D. M., and Hunt, G. L. 2004. Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. Fisheries Oceanography, 13: 208–223.

Jakobsson, J., and Stefansson, G. 1999. Management of summer-spawning herring off Iceland. ICES Journal of Marine Science, 56: 827–833.

Jákupsstovu, S. H. I., and Røttingen, I. 1975. Investigations on capelin (*Mallotus vilosus*) and sand eel (*Ammodytes* sp.) at West Greenland in June–July 1974. ICNAF Research Document 75/53, Serial No. 3552.

Janssen, F. 2002. Statistical analysis of multi-year hydrographic variability in the North Sea and Baltic Sea. Validation and correction of systematic errors in a regional ocean model (in German). PhD thesis, Fachbereich Geowissenschaften, Universität Hamburg, Germany. Available online at http://deposit.ddb.de/cgi-bin/dokserv?idn=967121566

Janssen, F., Schrum, C., Hübner, U., and Backhaus, J. 2001. Validation of a decadal simulation with a regional model for North Sea and Baltic Sea. Climate Research, 18: 55–62.

Janssen, G. M., and Kuipers, B. R. 1980. On tidal migration in the shrimp *Crangon crangon*. Netherlands Journal of Sea Research, 14: 339–348.

Jenkins, J. T. 1925. The Fishes of the British Isles. Frederik Warne and Co. Ltd., London. 408 pp.

Jennings, S., and Beverton, R. J. H. 1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.). ICES Journal of Marine Science, 48: 117–125.

Jennings, S., and Blanchard, J. L. 2004. Fish abundance with no fishing: predictions based on macroecological theory. Journal of Animal Ecology, 73: 632–642.

Jennings, S., and Brander, K. 2010. Predicting the effects of climate change on marine communities and the consequences for fisheries. Journal of Marine Systems, 79: 418–426, doi: 10.1016/j.jmarsys.2008.12.016.

Jennings, S., Greenstreet, S. P. R., and Reynolds, J. 1999a. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology, 68: 617–627.

Jennings, S., Alvsvåg, J., Cotter, A. J. R., Ehrich, S., Greenstreet, S. P. R., Jarre-Teichmann, A., Mergardt, N., *et al.* 1999b. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. Fisheries Research, 40: 125–134.

Jennings, S., Dinmore, T. A., Duplisea, D. E., Warr, K. J., and Lancaster, J. E. 2001a. Trawling disturbance can modify benthic production processes. Journal of Animal Ecology, 70: 459–475.

Jennings, S., Pinnegar, J. K., Polunin, N. V. C., and Boon, T. W. 2001b. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. Journal of Animal Ecology, 70: 934–944.

Jennings, S., Greenstreet, S. P. R., Hill, L., Piet, G. J., Pinnegar, J. K., and Warr, K. J. 2002a. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. Marine Biology, 141: 1085–1097.

Jennings, S., Nicholson, M. D., Dinmore, T. A., and Lancaster, J. E. 2002b. Effects of chronic trawling disturbance on the production of infaunal communities. Marine Ecology Progress Series, 243: 251–260.

Jennings, S., Mélin, F., Blanchard, J. L., Forster R. M., Dulvy, N. K., and Wilson, E. W. 2008. Global-scale predictions of community and ecosystem properties from simple ecological theory. Proceedings of the Royal Society of London, Series B, 275: 1375–1383.

Jensen, Ad. S. 1939. Concerning a change of climate during recent decades in the Arctic and Subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. Det Kongelige Danske Videnskabernes Selskab, Biologiske Meddelelser, 14(8). 75 pp.

Jensen, Ad. S. 1949. Studies on the biology of the cod in Greenland waters. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 123: 1–77.

Jensen, H. 2001. Settlement dynamics in the lesser sandeel *Ammodytes marinus* in the North Sea. PhD thesis, University of Aberdeen, UK.

Jensen, H., and Rolev, A. M. 2004. The sandeel fishing grounds in the North Sea. Information about the foraging areas of the lesser sandeel *Ammodytes marinus* in the North Sea. Working document prepared for the BECAUSE project, November 2004.

Jensen, H., Wright, P. J., and Munk, P. 2003. Vertical distribution of pre-settled sandeel (*Ammodytes marinus*) in the North Sea in relation to size and environmental variables. ICES Journal of Marine Science, 60: 1342–1351.

Jobling, M. 1981. Temperature tolerance and the final preferendum – rapid methods for the assessment of optimum growth temperatures. Journal of Fish Biology, 19: 439–455.

Johannessen, A., Slotte, A., Bergstad, O. A., Dragesund, O., and Røttingen, I. 1995. Reappearance of Norwegian spring spawning herring (*Clupea harengus* L.) at spawning grounds off southwestern Norway. *In* Ecology of Fjords and Coastal Waters, pp. 347–363. Ed. by H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas. Elsevier Science B. V., Amsterdam.

Johannessen, O. M., Bengtsson, L., Miles, M. W., Kuzmina, S. I., Semenov, V. A., Alekseev, G. V., Nagurnyi, A. P., *et al.* 2004. Arctic climate change: observed and modelled temperature and sea-ice variability. Tellus, 56A: 328–341.

Johansen, A. C., and Krogh, A. 1914. The influence of temperature and certain other factors upon the rate of development of the eggs of fish. Publications de Circonstance, Conseil Permanent International pour l'Exploration de la Mer, 68: 1–44.

Jones, J. B., and Campana, S. E. 2009. Stable oxygen isotope reconstruction of ambient temperature during the collapse of a cod (*Gadus morhua*) fishery. Ecological Applications, 19: 1500–1514.

Jones, P. D., Jónsson, T., and Wheeler, D. 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and south-west Iceland. International Journal of Climatology, 17: 1433–1450.

Jones, R. 1977. Some inter-relations between North Sea fish species. ICES Document CM 1977/F:36.

Jones, R., and Hislop, J. R. G. 1978. Changes in North Sea haddock and whiting. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 58–71.

Jónsson, H. 1982. Friends in Conflict: The Anglo-Icelandic Cod Wars and the Law of the Sea. Hurst and Co., London.

Jónsson, S., and Valdimarsson, H. 2005. Flow of Atlantic water to the North Icelandic Shelf and its relation to drift of cod larvae. ICES Journal of Marine Science, 62: 1350–59.

Jordan, D. S. 1907. Fishes. Henry Holt and Co., New York. 647 pp.

Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., *et al.* 2007. Managing evolving fish stocks. Science, 318: 1247–1248.

Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). Journal du Conseil International pour l'Exploration de la Mer, 46: 235–248.

Jung, T., Hilmer, M., Ruprecht, E., and Kleppek, S. 2003. Characteristics of the recent eastward shift of interannual NAO variability. Journal of Climate, 16: 3371–3382.

Junquera, S. 1984. Pêche de l'anchois (*Engraulis encrasicolus*) dans le Golfe de Gascogne et sur le littoral atlantique de Galice depuis 1920. Revue des Travaux de l'Institut des Pêches Maritimes, 48: 133–142.

Junquera, S. 1988. Changes in the anchovy fishery of the Bay of Biscay in relation to climatic and oceanographic variations in the North Atlantic. *In* Proceedings of the International

Symposium on Long Term Changes in Marine Fish Populations, 18–12 November 1986, Vigo, Spain. Instituto Español de Oceanografia, Vigo: 543–554.

Juravleva, L. A., and Grubrina, N. A. 1993. Phosphorus regime in low stream of the Danube River and its discharge in the Black Sea. Gidrobiologicheskiy Zhournal, 29: 81–88. (in Russian)

Kacic, I. 1980. Pelagic fish in the Adriatic: distribution and stock assessment. FAO Fisheries Report, 239: 21–31.

Kamburska, L., and Fonda-Umani, S. 2006. Long-term copepod dynamics in the Gulf of Trieste (northern Adriatic Sea): recent changes and trends. Climatic Research, 31: 195–203.

Karasiova, E. 2002. Variability of sprat peak spawning and larvae appearance timing in the southeastern Baltic Sea during the past six decades. Bulletin of the Sea Fisheries Institute, Gdynia, 156: 57–67.

Karlson, A. M. L., Almqvist, G., Skora, K. E., and Appelberg, M. 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES Journal of Marine Science, 64: 479–486.

Karrer, C., and Post, A. 1990. Zeidae. *In* Check-list of the Fish of the Eastern Tropical Atlantic (CLOFETA), Vol. 2, pp. 631–633. Ed. by J. C. Quéro, J. C. Hureau, C. Karrer, A. Post, and L. Saldanha. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

Kattsov, V., Vavulin, S., and Govorkova, V. 2001. Performance of current GCMs in high latitudes in the context of global climate change and variability studies. *In* Proceedings of the First Korea–Russia Joint Workshop on Climate Change and Variability, 18–20 December 2001, Jeju, Korea, pp. 15–20.

Kell, L. T., Pilling, G. M., and O'Brien, C. M. 2005. Implications of climate change for the management of North Sea cod (*Gadus morhua*). ICES Journal of Marine Science, 62: 1483–1491.

Kell, L. T., Nash, R. D. M., Dickey-Collas, M., Pilling, G. M., Hintzen, N. H., and Roel, B. A. 2009. Lumpers or splitters? Evaluating recovery and management plans for metapopulations of herring. ICES Journal of Marine Science, 66: 1776–1783.

Kerr, R. A. 2000. A North Atlantic climate pacemaker for the centuries. Science, 288: 1984–1986.

Kideys, A. E. 2002. Fall and rise of the Black Sea ecosystem. Science, 297: 1482–1484.

Kideys, A. E., Gordina, A. D., Bingel, F., and Niermann, U. 1999. The effect of environmental conditions on the distribution of eggs and larvae of anchovy (*Engraulis encrasicolus* L.) in the Black Sea. ICES Journal of Marine Science, 56(Suppl.): 58–64.

Kimmel, D. G., Miller, W. D., Harding, L., Houde, E. D., and Roman, M. R. 2009. Estuarine ecosystem response captured using a synoptic climatology. Estuaries and Coasts, 32: 403–409.

Kimura, S., Kishi, M. J., Nakata, H., and Yamashita, Y. 1992. A numerical analysis of population dynamics of the sand lance (*Ammodytes personatus*) in the eastern Seto Inland Sea, Japan. Fisheries Oceanography, 1: 321–332.

King, D. P. F. 1985. Morphological and meristic differences among spawning aggregations of Northeast Atlantic herring, *Clupea harengus* L. Journal of Fish Biology, 26: 591–607.

Kinne, O. 1962. Irreversible nongenetic adaptation. Comparative Biochemistry and Physiology, 5: 265–282.

Kirby, R. R., Johns, D. G., and Lindley, J. A. 2006. Fathers in hot water: rising sea temperatures and a Northeastern Atlantic pipefish baby boom. Biology Letters, 2: 597–600.

Kishi, M. J., Kimura, S., Nakata, H., and Yamashita, Y. 1991. A biomass-based model for the sand lance (*Ammodytes personatus*) in Seto Inland Sea, Japan. Ecological Modelling. 54: 247–263.

Kishi, M. J., Kashiwai, M., Ware, D. M., Megrey, B. A., Eslinger, D. L., Werner, F. E., Aita, N. M., *et al.* 2007a. NEMURO—a lower trophic level model for the North Pacific marine ecosystem. *In* Special Issue on NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) and NEMURO.FISH (NEMURO for Including Saury and Herring) – Modeling of North Pacific Marine Ecosystems. Ecological Modelling, 202 (1–2): 12–25.

Kishi, M. J., Megrey, B. A., Ito, S-I., and Werner, F. E. 2007b. Preface. *In* Special Issue on NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) and NEMURO.FISH (NEMURO for Including Saury and Herring) – Modeling of North Pacific Marine Ecosystems. Ecological Modelling, 202 (1–2): 3–6.

Kita, J., Tsuchida, S., and Setoguma, T. 1996. Temperature preference and tolerance, and oxygen consumption of the marbled rockfish, *Sebastiscus marmoratus*. Marine Biology, 125: 467–471.

Kjesbu, O. S., Klungsøyr, J., Kryvi, H., Witthames, P. R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Canadian Journal of Fisheries and Aquatic Sciences, 48: 2333–2343.

Kloppmann, M. H. F., and Ulleweit, J. 2007. Off-shelf distribution of pelagic snake pipefish, *Entelurus aequoreus* (Linnaeus, 1758), west of the British Isles. Marine Biology, 151: 271–275.

Knight, J. R., Folland, C. K., and Scaife, A. A. 2006. Climate impacts of the Atlantic multidecadal oscillation. Geophysical Research Letters, 33, L17706.

Knijn, R. J., Boon, T. W., Heessen, H. J. L., and Hislop, J. R. G. 1993. Atlas of North Sea Fish. ICES Cooperative Research Report No. 194. 368 pp.

Konsulov, A. S., and Kamburska, L. A. 1998. New ctenophore *Beroe ovata* invasion in the Black Sea. Triode na Institut po Oceanologiya BAN, Varna: 195–197.

Kooijman, S. A. L. M. 1993. Dynamic Energy Budgets in Biological Systems. Theory and Applications in Ecotoxicology. Cambridge University Press, UK. 350 pp.

Kooijman, S. A. L. M. 2000. Dynamic energy and mass budgets in biological systems. Cambridge University Press, UK. 424 pp.

Köster, F. W., and Möllmann, C. 2000a. Egg cannibalism in Baltic sprat *Sprattus sprattus*. Marine Ecology Progress Series, 196: 269–277.

Köster, F. W., and Möllmann, C. 2000b. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science, 57: 310–323.

Köster, F. W., Möllmann, C., Neuenfeldt, S., St John, M. A., Plikshs, M., and Voss, R. 2001a. Developing Baltic cod recruitment models. I. Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring, and sprat. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1516–1533.

Köster, F. W., Hinrichsen, H-H., St John, M. A., Schnack, D., MacKenzie, B. R., Tomkiewicz, J., and Plikshs, M. 2001b. Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1534–1556.

Köster, F. W., Hinrichsen, H-H., Schnack, D., St John, M. A., MacKenzie, B. R., Tomkiewicz, J., Möllmann, C., *et al.* 2003a. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock–recruitment relationships. Scientia Marina, 67(Suppl. 1): 129–154.

Köster, F. W., Möllmann, C., Neuenfeldt, S., Vinther, M., St John, M. A., Tomkiewicz, J., Voss, R., *et al.* 2003b. Fish stock development in the central Baltic Sea (1976–2000) in relation to variability in the environment. ICES Marine Science Symposia, 219: 294–306.

Köster, F. W., Möllmann, C., Hinrichsen, H-H., Tomkiewicz, J., Wieland, K., Kraus, G., Voss, R., *et al.* 2005. Baltic cod recruitment – the impact of climate variability on key processes. ICES Journal of Marine Science, 62: 1408–1425.

Kotoulas, G., Bonhomme, F., and Borsa, P. 1995. Genetic structure of the common sole *Solea vulgaris* at different geographic scales. Marine Biology, 122: 361–375.

Koutsikopoulos, C., and Lacroix, N. 1992. Distribution and abundance of sole (*Solea solea* L.) eggs and larvae in the Bay of Biscay between 1986 and 1989. Netherlands Journal of Sea Research, 29: 81–91.

Koutsikopoulos, C., and Le Cann, B. 1996. Physical processes and hydrological structures related to the Bay of Biscay anchovy. Scientia Marina, 60: 9–19.

Koutsikopoulos, C., Desaunay, Y., Dorel, D., and Marchand, J. 1989. The role of coastal areas in the life history of sole (*Solea solea* L.) in the Bay of Biscay. Scientia Marina, 53: 567–575.

Koutsikopoulos, C., Fortier, L., and Gagne, J. A. 1991. Cross-shelf dispersion of Dover sole eggs and larvae (*Solea solea*) in Biscay Bay and recruitment to inshore nurseries. Journal of Plankton Research, 13: 923–945.

Koutsikopoulos, C., Beillois, P., Leroy, C., and Taillefer, F. 1998. Temporal trends and spatial structures of the sea surface temperature in the Bay of Biscay. Oceanologica Acta, 21: 335–344.

Kovacic, M., and Golani, D. 2007. First record of *Papillogobius melanobranchus* in the Mediterranean Sea and new data on geographic distributions, bathymetric ranges and morphology of several small benthic fish in the Levant. Cybium, 31: 417–425.

Krichak, S. O., and Alpert, P. 2005. Signatures of the NAO in the atmospheric circulation during wet winter months over the Mediterranean region. Theoretical and Applied Climatology, 82: 27–39.

Kristiansen, T., Lough, R. G., Werner, F. E., Broughton, E., and Buckley, L. J. 2009. Individual-based modeling of feeding ecology and prey selection of larval cod in Georges Bank. Marine Ecology Progress Series, 376: 227–243.

Krohn, M., Reidy, S., and Kerr, S. 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 54(Suppl. 1): 113–121.

Kroiss, H., Zessner, M., and Lampert, C. 2005. Nutrient Management in the Danube Basin and its Impact on the Black Sea. Technical Report EVK-1CT-2000–00051, Vienna University of Technology, Vienna, Section 6: 69.

Kühn, W., Peck, M. A., Hinrichsen, H-H., Daewel, U. A., Pohlmann, T., Stegert, C., and Tamm, S. 2008. Defining habitats suitable for larval fish in the German Bight (southern North Sea): an IBM approach using spatially and temporally resolved, size-structured prey fields. Journal of Marine Systems, 74: 329–342.

Kuipers, B. R., and Dapper, R. 1984. Nursery function of Wadden Sea tidal flats for the brown shrimp *Crangon crangon*. Marine Ecology Progress Series, 17: 171–181.

Kuipers, B. R., and Fonds, M. 1978. Consumption and utilization of food by juvenile plaice in the Wadden Sea. *In* Physiology and Behaviour of Marine Organisms, Proceedings of the 12th European Marine Biology Symposium, 5–12 September 1997, Stirling, p. 47. Ed. by D. S. McLusky, and A. J. Berry, Pergamon Press, Oxford.

Kullenberg, G. 1981. Physical oceanography. *In* The Baltic Sea, pp. 135–145. Ed. by A. Volpio. Elsevier Oceanography Series, 30. 418 pp.

Kunzlik, P. A., Gauld, J. A., and Hutcheon, J. R. 1986. Preliminary results of the Scottish sandeel tagging project. ICES Document CM 1986/G:7.

Kurlansky, M. 1997. Cod: A Biography of the Fish that Changed the World. Walker Publishing, New York.

Kushmaro, A., Rosenberg, E., Fine, M., Ben Haim, Y., and Loya, Y. 1998. Effects of temperature on the bleaching of the coral *Oculina patagonica* by the Vibrio AK-1. Marine Ecology Progress Series, 171: 131–137.

La Mesa, M., Donato, F., Giannetti, G., and Arneri, E. 2009. Growth and mortality rates of European anchovy (*Engraulis encrasicolus*) in the Adriatic Sea during the transition from larval to juvenile stages. Fisheries Research, 96: 275–280.

Lafrance, P., Castonguay, M., Chabot, D., and Audet, C. 2005. Ontogenetic changes in temperature preference of Atlantic cod. Journal of Fish Biology, 66: 553–567.

Lajus, D. L., Lajus, J. A., Dmitrieva, Z. V., Kraikovski, A. V., and Alexandrov, D. A. 2005. The use of historical catch data to trace the influence of climate on fish populations: examples from the White and Barents Sea fisheries in the 17th and 18th centuries. ICES Journal of Marine Science, 62: 1426–1435.

Lamb, H. H., and Johnson, A. I. 1959. Climatic variation and observed changes in the general circulation. Parts I and II. Geographical Annals of Stockholm, 41: 94–134.

Langham, N. P. E. 1971. The distribution and abundance of larval sand-eels (Ammodytidae) in Scottish waters. Journal of the Marine Biological Association of the UK, 51: 697–707.

Lankford, T. E., , and Targett, T. E. 2001. Low-temperature tolerance of age-0 Atlantic croakers: recruitment implications for US Mid-Atlantic estuaries. Transactions of the American Fisheries Society, 130: 236–249.

Lankin, K., Peck, M. A., Buckley, L. J., and Bengtson, D. A. 2008. The effects of temperature, body size and growth rate on energy losses due to metabolism in early life stages of haddock (*Melanogrammus aeglefinus*). Marine Biology, 155: 461–472.

Lapinska, E., and Szaniawska, A. 2006. Environmental preferences of *Crangon crangon* (Linnaeus, 1758), *Palaemon adspersus* Rathke, 1837, and *Palaemon elegans* Rathke, 1837 in the littoral zone of the Gulf of Gdańsk. Crustaceana, 79: 649–662.

Larrañeta, M. G. 1981. La pesquería de sardina, *Sardina pilchardus* (Walb.) de Castellón. Investigacion Pesque, 45: 47–91.

Last, J. M. 1989. The food of herring, *Clupea harengus*, in the North Sea, 1983–1986. Journal of Fish Biology, 34: 489–501.

Launiainen, J., Seinä, A., Johansson, M., Lahtinen, M., Alenius, P., and Bareiss, J. 2001. Northern Atlantic forcing reflections to sea ice and hydrological conditions in the northern seas. *In* Third Study Conference on BALTEX. 2–6 July 2001, Mariehamn, Finland. International BALTEX Secretariat Report, 20: 137–139.

Laverack, M. S., and Blackler, M. 1974. Fauna and Flora of St Andrews Bay. Scottish Academic Press, Edinburgh. 310 pp.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659–668.

Lazure, P., and Dumas, F. 2008. An external-internal mode coupling for a 3D hydrodynamical Model for Applications at Regional Scale (MARS). Advances in Water Resources, 31: 233–250.

Le Cann, B. 1982. Evolution annuelle de la structure hydrologique du plateau continental au sud de la Bretagne: modélisation numérique. Thèse de 3ème cycle, Université de Bretagne Occidentale.

Le Pape, O., Chauvet, F., Desaunay, Y., and Guerault, D. 2003. Relationship between interannual variations of the river plume and the extent of nursery grounds for the common sole (*Solea solea*, L.) in Vilaine Bay. Effects on recruitment variability. Journal of Sea Research, 50: 177–185.

Le Quéré, C., Aumont, O., Monfray, P., and Orr, J. 2003. Propagation of climatic events on ocean stratification, marine biology, and CO_2: case studies over the 1979–1999 period. Journal of Geophysical Research, 108: 3375.

Lea, E. 1911. A study on the growth of herrings. Publications de Circonstance, Conseil Permanent International pour l'Exploration de la Mer, 61: 35–57.

Lebreiro, S. M., Francés, G., Abrantes, F. F. G., Diz, P., Bartels-Jónsdóttir, H. B., Stroynowski, Z. N., Gil, I. M., *et al.* 2006. Climate change and coastal hydrographic response along the Atlantic Iberian margin (Tagus Prodelta and Muros Ría) during the last two millennia. The Holocene, 16: 1003–1015.

Lees, K., Pitois, S., Scott, C., Frid, C., and Mackinson, S. 2006. Characterizing regime shifts in the marine environment. Fish and Fisheries, 7: 104–127.

Leggett, W. C., and Frank, K. T. 2008. Paradigms in fisheries oceanography. Oceanography and Marine Biology: an Annual Review, 46: 331.

Lehmann, A., Lorenz, P., and Jacob, D. 2004. Modelling the exceptional Baltic Sea inflow events in 2002–2003. Geophysical Research Letters, 31, L21308, doi: 10.1029/2004GL020830.

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J. M., *et al.* 2006. Climate variability, fish, and fisheries. Journal of Climate, 19: 5009–5030.

Leis, J. M. 2006. Are larvae of demersal fish plankton or nekton? Advances in Marine Biology, 51: 57–141.

Leterme, S. C., Edwards, M., Seuront, L., Attrill, M. J., Reid, P. C., and John, A. W. G. 2005. Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic. Limnology and Oceanography, 50: 1244–1253.

Leterme, S. C., Seuront, L., and Edwards, M. 2006. Differential contribution of diatoms and dinoflagellates to phytoplankton biomass in the NE Atlantic Ocean and the North Sea. Marine Ecology Progress Series. 312: 57–65.

Levins, R. 1969. Thermal acclimation and heat resistance in *Drosophila* species. American Naturalist, 103: 483–499.

Levitus, S., Antonov, J. I., Boyer, T. P., and Stephens, C. 2000. Warming of the World Ocean. Science, 287: 2225–2229.

Lewis, K., Allen, J. I., Richardson, A. J., and Holt, J. T. 2006. Error quantification of a high resolution coupled hydrodynamic ecosystem coastal-ocean model. Part 3. Validation with Continuous Plankton Recorder data. Journal of Marine Systems, 63: 209–224.

Lewy, P., Nielsen, N., and Gislason, H. 2004. Stock dynamics of sandeel in the North Sea and sub-regions including uncertainties. Fisheries Research, 68: 237–248.

Licandro, P., and Ibanez, F. 2000. Changes of zooplankton communities in the Gulf of Tigulio (Ligurian Sea, western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. Journal of Plankton Research, 22: 2225–2253.

Lien, V., Ingvaldsen, R., Loeng, H., and Skagseth, Ø. 2006. Climate variability in the Barents Sea 2000–2005. ICES Document CM 2006/C:36. (Poster)

Lima, F. P., Queiroz, N., Ribeiro, P. A., Hawkins, S. J., and Santos, A. M. 2006. Geographic expansion of a marine gastropod, *Patella rustica* Linnaeus, 1758, and its relation with unusual climatic events. Journal of Biogeography, 33: 812–822.

Lindley, J. A., Kirby, R. R., Johns, D. G., and Reid, P. C. 2006. Exceptional abundance of the snake pipefish (*Entelurus aequoreus*) in the northeastern Atlantic Ocean. ICES Document CM 2006/C:06.

Link, J. S. 2002. Does food web theory work for marine ecosystems? Marine Ecology Progress Series, 230: 1–9.

Litzow, M. A., and Ciannelli, L. 2007. Oscillating trophic control induces community reorganisation in a marine ecosystem. Ecology Letters, 10: 1124–1134.

Llope, M., Anadón, R., Viesca, L., Quevedo, M., González-Quirós, R., and Stenseth, N. C. 2006. Hydrographic dynamics in the southern Bay of Biscay: integrating multi-scale physical variability over the last decade (1993–2003). Journal of Geophysical Research, 111, C0921.

Llope, M., Chan, K-S., Ciannelli, L., Reid, P. C., Stige, L. C., and Stenseth, N. C. 2009. Effects of environmental conditions on the seasonal distribution of phytoplankton biomass in the North Sea. Limnology and Oceanography, 54: 512–524.

Llope, M., Daskalov, G. M., Rouyer, T. A., Mihneva, V., Chan, K-S., Alexander, N., Grishin, A. N., *et al.* In press. Fishing, agriculture and urban sewage, together with climate variation have triggered regime shifts in the Black Sea. Global Change Biology.

Lloret, J., Lleonart, J., Solé, I., and Fromentin, J. M. 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fisheries Oceanography, 10: 33–50.

Lloret, J., Palomera, I., Salet, J., and Solé, I. 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). Fisheries Oceanography, 13: 102–110.

Lluch-Belda, D., Crawford, R. J. M., Kawasaki, T., MacCall, A. D., Parrish, R. H., Schwartzlose, R. A., and Smith, P. E. 1989. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. South African Journal of Marine Science, 8: 195–205.

Lo, N. 1985. A model for temperature-dependent northern anchovy egg development and an automated procedure for the assignment of age to staged eggs. *In* An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, *Engraulis mordax*, pp. 43–50. Ed. by R. Lasker. NOAA Technical Report. NMFS, 36. 99 pp.

Lo, N. C. H., Smith, P. E., and Butler, J. L. 1995. Population growth of northern anchovy and Pacific sardine using stage-specific matrix models. Marine Ecology Progress Series, 127: 15–26.

Loeng, H. 1979. A review of the sea ice conditions of the Barents Sea and the area west of Spitsbergen. Fisken og Havet, 1979(2): 29–75. (in Norwegian with English abstract)

Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. Polar Research, 10: 5–18.

Logemann, K., and Harms, I. H. 2006. High resolution modelling of the North Icelandic Irminger Current (NIIC). Ocean Science Discussion, 3: 1149–1189.

Longhurst, A. 1998. Ecological Geography of the Sea. Academic Press, San Diego.

Lønning, S., Kjørsvik, E., and Petersen, I. B. F. 1988. A comparative study of pelagic and demersal eggs from common marine fish in northern Norway. Sarsia, 73:49–60.

Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London, Series B, 269: 49–54.

Lotze, H. K., and Worm, B. 2009. Historical baselines for large marine animals. Trends in Ecology and Evolution, 24: 254–262.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., *et al.* 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science, 312: 1806–1809.

Lough, R. G., Buckley, L. J., Werner, F. E., Quinlan, J. A., and Edwards, K. P. 2005. A general biophysical model of larval cod (*Gadus morhua*) growth applied to populations on Georges Bank. Fisheries Oceanography, 14: 241–262.

Louisy, P. 2006. Peces marinos de Europa y del Mediterráneo. Ediciones Omega, Barcelona. 458 pp.

Lozano Rey, L. 1928. Fauna Ibérica: Peces. Museo Nacional de Ciencias Naturals, Madrid. 692 pp.

Lozano Rey, L. 1947. Peces Ganoideos y Fisóstomos. Memorias de la Real Academia de Ciencias, Madrid. 839 pp.

Lozano Rey, L. 1952a. Peces Fisoclistos, Subserie Toracicos, Primera Parte (Ordenes Bericiformes, Zeiformes, Perciformes, Escorpeniformes y Balistiformes). Memorias de la Real Academia de Ciencias, Madrid. 378 pp.

Lozano Rey, L. 1952b. Peces Fisoclistos, Subserie Toracicos, Segunda Parte (Ordenes Labriformes y Escombriformes). Memorias de la Real Academia de Ciencias, Madrid. 703 pp.

Lozano Rey, L. 1960. Peces Fisoclistos, Subserie Toracicos (Ordenes Equeniformes y Gobiformes, Pediculados y Asimetricos. Ictiologia Iberica, Madrid. 613 pp.

Lu, J., and Greatbatch, R. J. 2002. The changing relationship between the NAO and northern hemisphere climate variability. Geophysical Research Letters, 29, 1148, doi: 10.1029/2001GL014052.

Ludwig, W., Dumont, E., Meybeck, M., and Heussner, S. 2009. River discharges of water and nutrients to the Mediterranean and Black Sea: major drivers for ecosystem changes during past and future decades? Progress in Oceanography, 80: 199–217.

Lumberg, A., and Ojaveer, E. 1991. On the environment and zooplankton dynamics in the Gulf of Finland in 1961–1990. Proceedings of the Estonian Academy of Sciences, Ecology, 1: 131–140.

Ly, B., Diop, M., and Girardin, M. 1996. Guide et nomenclature nationale commerciale des especes marines (poissons, crustaces et mollusques) pechees en Mauritanie. Centre National de Recherches Océanographiques et des Pêches, Ministère des Pêches et de l'Economie Maritime.

Lythgoe, J., and Lythgoe, G. 1991. Fish of the Sea. The North Atlantic and Mediterranean. Blandford Press, London. 256 pp.

Macer, C. T. 1965. The distribution of larval sand eels (Ammodytidae) in the southern North Sea. Journal of the Marine Biological Association of the UK, 45: 187–207.

Macer, C. T. 1966. Sand eels (Ammodytidae) in the south -western North Sea; their biology and fishery. Fishery Investigations, Series 2, 24: 1–55. Ministry of Agriculture, Fisheries and Food, UK.

Mackay, K. T. 1973. Aspects of the biology of Atlantic mackerel in ICNAF Subarea 4. ICNAF Research Document 73/70, Ser. No. 3019. 11 pp.

MacKenzie, B. R., and Köster, F. W. 2004. Fish production and climate. Sprat in the Baltic Sea. Ecology, 85: 784–794.

MacKenzie, B. R., Hinrichsen, H. H., Plikshs, M., Wieland, K., and Zezera, A. S. 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. Marine Ecology Progress Series, 193: 143–156.

MacKenzie, B. R., Alheit, J., Conley, D. J., Holm, P., and Kinze, C. C. 2002. Ecological hypotheses for a historical reconstruction of upper trophic level biomass in the Baltic Sea and Skagerrak. Canadian Journal of Fisheries and Aquatic Sciences, 59: 173–190.

MacKenzie, B. R., Gislason, H., Möllmann, C., and Köster, F. W. 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Global Change Biology, 13: 1–20.

MacLeod, C. D., Santos, M. B., Reid, R. J., Scott, B. E., and Pierce, G. J. 2007. Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? Biological Letters, 3(2): 185–188.

Macpherson, E. 2003. Species range size distribution for some marine taxa in the Atlantic Ocean. Effects of latitude and depth. Biological Journal of the Linnean Society, 80: 437–455.

Macpherson, E., and Duarte, C. M. 1994. Patterns of species richness, size and latitudinal range of Eastern Atlantic fish. Ecography, 17: 242–248.

Maes, J., Taillieu, A., van Damme, P. A., Cottenie, K., and Ollevier, F. 1998. Seasonal patterns in the fish and crustacean community of a turbid temperate estuary (Zeeschelde Estuary, Belgium). Estuarine, Coastal and Shelf Science, 47: 143–151.

Magee, A., Myrick, C. A., and Cech, J. J. 1999. Thermal preference of female threespine sticklebacks under fed and food-deprived conditions. California Fish and Game, 85: 102–112.

Mahé, K., Destombes, A., Coppin, F., Koubbi, P., Vaz, S., Le Roy, D., and Carpentier, A. 2005. Le rouget barbet de roche *Mullus surmuletus* (L. 1758) en Manche orientale et mer du Nord. Rapport de Contrat Ifremer/CRPMEM, Nord-Pas-de-Calais. 187 pp.

Malmberg, S. A., and Valdimarsson, H. 2003. Hydrographic conditions in Icelandic waters 1990–1999. ICES Marine Science Symposia, 219: 50–60.

Malzahn, A. M., Clemmesen, C., Wiltshire, K. H., Laakmann, S., and Boersma, M. 2007. Comparative nutritional condition of larval dab *Limanda limanda* and lesser sandeel *Ammodytes marinus* in a highly variable environment. Marine Ecology Progress Series, 334: 205–212.

Mamie, J. C. J., Beare, D. J., Jones, E. G., Kienzle, M., Dobby, H., Heath, M. R., and Reid, D. G. 2007. Aspects of the distribution and growth of bluemouth (*Helicolenus dactylopterus*, Delaroche 1809) since its invasion of the northern North Sea in 1991. Fisheries Oceanography, 16: 85–94.

Mantzouni, I., Sørensen, H., O'Hara, R. B., and MacKenzie, B. R. 2010. Hierarchical modeling of temperature and habitat effects on population dynamics of North Atlantic cod. ICES Journal of Marine Science, doi:10.1093/icesjms/fsp291.

Marancik, K. E., and Hare, J. A. 2007. Large-scale patterns in fish trophodynamics of estuarine and shelf habitats of the Southeast United States. Bulletin of Marine Science, 80: 67–91.

Maravelias, C. D. 2001. Habitat associations of Atlantic herring in the Shetland area: influence of spatial scales and geographic segmentation. Fisheries Oceanography, 10: 259–267.

Maravelias, C. D., and Reid, D. G. 1997. Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Marine Ecology Progress Series, 147: 1–9.

Maravelias, C. D., Reid, D. G., Simmonds, E. J., and Haralabous, J. 1996. Spatial analysis and mapping of acoustic survey data in the presence of high local variability: geostatistical application to North Sea herring. Canadian Journal of Fisheries and Aquatic Sciences, 53: 1497–1505.

Maravelias, C. D., Tsitsika, E. V., and Papaconstantinou, C. 2007. Seasonal dynamics, environmental preferences and habitat selection of John Dory (*Zeus faber*). Estuarine, Coastal and Shelf Science, 72: 703–710.

Marchand, J. 1991. The influence of environmental conditions on the settlement, distribution and growth of 0-group sole (*Solea solea* (L.)) in a macro-tidal estuary (Vilaine, France). Netherlands Journal of Sea Research, 27: 307–316.

Marchand, J., and Masson, G. 1989. Process of estuarine colonization by 0-group sole (*Solea solea*): hydrological conditions, behaviour, and feeding activity in the Vilaine estuary.

Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 267–295.

Marcos, M., Gomis, D., Monserrat, S., Álvarez, E., Pérez, B., and García-Lafuente, J. 2005. Consistency of long sea-level time-series in the northern coast of Spain. Journal of Geophysical Research, 110: 1–13.

Marine Institute. 2009. The Stock Book – Leabhar na Stoc: Annual Review of Fish Stocks in 2009 with Management Advice for 2010. Marine Institute, Fisheries Science Services. Galway, Ireland. 446 pp.

Marshall, C. T., O'Brien, L., Tomkiewicz, J., Köster, F. W., Kraus, G., Marteinsdottir, G., Morgan, M. J., *et al.* 2003. Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. Journal of Northwest Atlantic Fisheries Science, 33: 161–190.

Massé, J. 1996. Acoustic observations in the Bay of Biscay: schooling, vertical distribution, species assemblages and behaviour. Scientia Marina, 60(Suppl. 2): 227–234.

Massutí, E., Moranta, J., Gordon, J. D. M., Morales-Nin, B., and Oliver, P. 2008a. The wrapping up of the IDEA project: International Workshop on Environment, Demersal Resources and Fisheries. Journal of Marine Systems, 71: 221–222.

Massutí, E., Monserrat, S., Oliver, P., Moranta, J., López-Jurado, J. L., Marcos, M., Hidalgo, M., *et al.* 2008b. The influence of oceanographic scenarios on the population dynamics of demersal resources in the western Mediterranean: hypothesis for hake and red shrimps off Balearic Islands. Journal of Marine Systems, 71: 421–438.

Mastrototaro, F., Carlucci, R., Capezzuto, F., and Sion, L. 2007. First record of dwarf flathead *Elates ransonnetii* (Platycephalidae) in the Mediterranean Sea (north-western Ionian Sea). Cybium, 31: 393–394.

Masuda, H., Amaoka, K., Araga, C., Uyeno, T., and Yoshino, T. 1984. The Fishes of the Japanese Archipelago, Vol. 1. Tokai University Press, Tokyo. 437 pp.

Matthäus, W., and Schinke, H. 1994. Mean atmospheric circulation patterns associated with major Baltic inflows. Deutsche Hydrographie Zeitschrift, 46: 321–338.

Matthäus, W., and Nausch, G. 2003. Hydrographic–hydrochemical variability in the Baltic Sea during the 1990s in relation to changes during the 20th century. ICES Marine Science Symposia, 219: 132–143.

Mavruk, S., and Avsar, D. 2007. Non-native fish in the Mediterranean from the Red Sea, by way of the Suez Canal. Reviews in Fish Biology and Fisheries, 18: 251–262.

Maynou, F. 2008. Environmental causes of the fluctuations of red shrimp (*Aristeus antennatus*) landings in the Catalan Sea. Journal of Marine Systems, 71: 294–302.

McCauley, R. W., and Huggins, N. W. 1979. Ontogenetic and nonthermal seasonal effects on thermal preferenda of fish. American Zoologist, 19: 267–271.

McPherson, A. A., Stephenson, R. L., and Taggart, C. T. 2003. Genetically different Atlantic herring *Clupea harengus* spawning waves. Marine Ecology Progress Series, 247: 303–309.

McQuatters-Gollop, A., Raitsos, D. E., Edwards, M., and Attrill, M. J. 2007. A long-term chlorophyll data set reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient trends. Limnology and Oceanography, 52: 635–648.

McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. Reviews in Fish Biology and Fisheries, 7: 297–329.

Megrey, B. A., Link, J. S., Hunt, G. L., and Moksness, E. 2009. Comparative marine ecosystem analysis: applications, opportunities, and lessons learned. Progress in Oceanography, 81: 2–9.

Meier, H. E. M., Doescher, R., and Faxen, T. 2003. A multiprocessor coupled ice-ocean model for the Baltic Sea: Application to salt inflow. Journal of Geophysical Research 108(C8), 3273, doi: 10.1029/2000JC000521.

Melvin, G. D., and Stephenson, R. L. 2007. The dynamics of a recovering fish stock: Georges Bank herring. ICES Journal of Marine Science, 64: 69–82.

Melvin, G. D., Stephenson, R. L., and Power, M. J. 2009. Oscillating reproductive strategies of herring in the western Atlantic in response to changing environmental conditions. ICES Journal of Marine Science, 66: 1784–1792.

Menard, F., Dallot, S., Thomas, G., and Braconnot, J. C. 1994. Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. Marine Ecology Progress Series, 104: 139–152.

Mikhailov, K., and Prodanov, K. 2002. Early sex maturation of the anchovy *Engraulis encrasicolus* (L.) in the northwestern part of the Black Sea. *In* Proceedings of the 3rd International Conference on EuroGOOS: Building the European Capacity in Operational Oceanography, 3–6 December 2002, Athens, p. 34.

Millán, M. 1999. Reproductive characteristics and condition status of anchovy *Engraulis encrasicolus* L. from the Bay of Cadiz (SW Spain). Fisheries Research, 41: 73–86.

Miller, J. M., Burke, J. S., and Fitzhugh, G. R. 1991. Early life history patterns of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. Netherlands Journal of Sea Research, 27: 261–275.

Miller, P. J., and Loates, M. J. 1997. Fish of Britain and Europe. HarperCollins Publishers, London.

Millner, R. S., and Whiting, C. L. 1996. Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. ICES Journal of Marine Science, 53: 1185–1195.

Millner, R. S., Flatman, S., Rijnsdorp, A. D., van Beek, F. A., de Clerck, R., Damm, U., Tetard, A., *et al.* 1996. Comparison of long-term trends in growth of sole and plaice populations. ICES Journal of Marine Science, 53: 1196–1198.

Mitchell, J. M. 1864. The Herring: Its Natural History and National Importance. Edmonston and Douglas, Edinburgh. 372 pp.

Moksness, E., and Torstensen, E. 1985. The buoyancy of sprat (*Sprattus sprattus*) eggs and larvae in the Skagerrak area. ICES Document CM 1985/L:6.

Molinero, J. C., Ibanez, F., Nival, P., Buecher, I., and Souissi, S. 2005. North Atlantic climate and northwestern Mediterranean plankton variability. Limnology and Oceanography, 50: 1213–1220.

Mollet, F. M., Kraak, S. B. M., and Rijnsdorp, A. D. 2007. Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*. Marine Ecology Progress Series, 351: 189–199.

Möllmann, C., and Köster, F. W. 2002. Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. Journal of Plankton Research, 24: 959–977.

Möllmann, C., Kornilovs, G., and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. Journal of Plankton Research, 22: 2015–2038.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F. W., and Hinrichsen, H-H. 2003a. The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fisheries Oceanography, 12: 360–368.

Möllmann, C., Köster, F. W., Kornilovs, G., and Sidrevics, L. 2003b. Interannual variability in population dynamics of calanoid copepods in the Central Baltic Sea. ICES Marine Science Symposia, 219: 294–306.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2004. Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology, 65: 1563–1581.

Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2005. Climate, zooplankton and pelagic fish growth in the Central Baltic Sea. ICES Journal of Marine Science, 62: 1270–1280.

Möllmann, C., Müller-Karulis, B., Diekmann, R., Flinkman, J., Kornilovs, G., Lysiak-Pastuszak, E., *et al.* 2006. An integrated ecosystem assessment of the central Baltic Sea and the Gulf of Riga. ICES Document CM 2006/P:03.

Möllmann, C., Müller-Karulis, B., Kornilovs, G., and St John, M. A. 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade and feedback loops in a simple ecosystem. ICES Journal of Marine Science, 65: 302–310.

Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15: 1377–1393.

Monserrat, S., López-Jurado, J. L., and Marcos, M. 2008. A mesoscale index to describe the regional ocean circulation around the Balearic Islands. Journal of Marine Systems, 71: 413–420.

Monteleone, D. M., and Peterson, W. T. 1986. Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound. Marine Ecology Progress Series, 30: 133–143.

Moreau, E. 1881–1891. Histoire Naturelle des Poissons de la France, Vol. I–II. G. Masson, Paris.

Morel, A., and Antoine, D. 1994. Heating rate within the upper ocean in relation to its bio-optical state. American Meteorological Society, 24: 1652–1665.

Morri, C., and Bianchi, C. N. 2001. Recent changes in biodiversity in the Ligurian Sea (NW Mediterranean): is there a climatic forcing? *In* Structure and Processes in the Mediterranean Ecosystems, pp. 375–384. Ed. by F. M. Faranda, L. Guglielmo, and G. Spezie. Springer Verlag, Milan.

Motos, L. 1996. Reproductive biology and fecundity of the Bay of Biscay anchovy population (*Engraulis encrasicolus*, L.). Scientia Marina, 60(Suppl. 2): 195–207.

Motos, L., Uriarte, A., and Valencia, V. 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus*, L.). Scientia Marina, 60(Suppl. 2): 117–140.

Moura, T., Figueiredo, I., Neves, A., Farias, I., Serra-Pereira, B., and Gordo, L. 2008. First occurrence of the deepwater shark *Centroscymnus owstoni* on the Portuguese continental slope. Cybium, 32: 271–272.

MRAG and UNEP-WCMC. 2007. How can we use concepts of structure and function to integrate the ecosystem approach into marine monitoring? Conservation Challenge No. 2, Joint Nature Conservation Committee, Peterborough. 32 pp.

Munday, P. L., Dixson, D. L., Donelson, J. M., Jones, G. P., Pratchett, M. S., Devitsina, G. V., and Døving, K. B. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. Proceedings of the National Academy of Sciences of the USA, 106: 1848–1852.

Munk, P. 1991. Changes in mean size and distribution of juvenile North Sea sprat (*Sprattus sprattus* L.) in the period 1976 –90. ICES Document CM 1991/H:41.

Munk, P. 1993. Differential growth of larval sprat *Sprattus sprattus* across a tidal front in the eastern North Sea. Marine Ecology Progress Series, 99: 17–29.

Munk, P., Wright, P. J., and Pihl, N. J. 2001. Distribution of the early stages of cod, plaice and lesser sandeel across haline fronts in the North Sea. Estuarine, Coastal and Shelf Science, 56: 139–149.

Murawski, S. A. 1993. Climate-change and marine fish distributions – forecasting from historical analogy. Transactions of the American Fisheries Society, 122: 647–658.

Murta, A., and Borges, M. F. 1996. Factors affecting the abundance of distribution of horse mackerel *Trachurus trachurus* (Linnaeus, 1758) in the Portuguese waters. ICES Document CM 1996/S:17.

Muus, B. J., and Nielsen, J. G. 1999. Seafish. Blackwell Science, Oxford. 340 pp.

Muus, B. J., Nielsen, J. G., Dahlstrøm, P., and Nyström, B. O. 1997. Zeevissen van Noord- en West-Europa. Schuyt and Co Uitgevers en Importeurs BV, Haarlem.

Muus, B. J., Nielsen, J. G., Dahlstrøm, P., and Nyström, B. O. 1998. Peces de Mar del Atlántico y del Mediterráneo. Ediciones Omega, Barcelona. 337 pp.

Myers, R. A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence and variability using meta-analytic approaches. ICES Journal of Marine Science, 58: 937–951.

Myers, R. A., and Mertz, G. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. Fishery Bulletin US, 95: 762–772.

Myers, R. A., MacKenzie, B. R., Bowen, K. G., and Barrowman, N. J. 2001. What is the carrying capacity of fish in the ocean? A meta-analysis of population dynamics data from the North Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1464–1476.

Naeem, S., Loreau, M., and Inchausti, P. 2002. Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. *In* Biodiversity and Ecosystem Functioning, pp. 3–11. Ed. by M. Loreau, S. Naeem, and P. Inchausti. Oxford University Press, Oxford. 312 pp.

Nagoshi, M., and Sano, M. 1979. Population studies of sand eel, *Ammodytes personatus*, in Ise Bay. I. Growth and its relation to population density. Japanese Journal of Ecology, 29: 1–10.

Nash, R. D. M. 1990. Fish assemblages in the Irish Sea. *In* Irish Sea Study Group Report. Part 1. Nature Conservation, pp. 325–333. Liverpool University Press, Liverpool.

Nash, R. D. M., and Dickey-Collas, M. 2005. The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (*Clupea harengus* L.). Fisheries Oceanography, 14: 279–291.

Nash, R. D. M., Dickey-Collas, M., and Kell, L. T. 2009. Stock and recruitment in North Sea herring (*Clupea harengus*); compensation and depensation in the population dynamics. Fisheries Research, 95: 88–97.

Neat, F., and Righton, D. 2007. Warm water occupancy by North Sea cod. Proceedings of the Royal Society of London, Series B, 274: 789–798.

Neja, Z. 1995. The stock size and changes in the growth rate of the northwest Atlantic mackerel (*Scomber scombrus* L.) in 1971–1983. Acta Ichthyologica et Piscatoria, 25: 114–121.

Neudecker, T., and Damm, U. 1992. Seasonality of egg-bearing shrimp (*Crangon crangon* L.) in coastal waters of the German Bight. ICES Document CM 1992/K:28.

Neumann, T. X. 2000. Towards a 3D-ecosystem model of the Baltic Sea. Journal of Marine Systems, 25: 405–419.

Nicholls, R. J., and Mimura, N. 1998. Regional issues raised by sea-level rise and their policy implications. Climate Research, 11: 5–18.

Nichols, J. H. 2001. Management of North Sea herring and prospects for the new millennium. *In* Herring: Expectations for a New Millennium. Lowell Wakefield Fisheries Symposium Series, No. 18: 645-665.

Nielsen, E. E., Bagge, O., and MacKenzie, B. R. 1998. Wind-induced transport of plaice (*Pleuronectes platessa*) early life-history stages in the Skagerrak–Kattegat. Journal of Sea Research, 39: 11–28.

Nielsen, E. E., Hansen, M. M., Ruzzante, D. E., Meldrup, D., and Grønkjær, P. 2003. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. Molecular Ecology, 12: 1497–1508.

Nielsen, E. E., Nielsen, P. H., Meldrup, D., and Hansen, M. M. 2004. Genetic population structure of turbot (*Scophthalmus maximus* L.) supports the presence of multiple hybrid zones for marine fish in the transition zone between the Baltic Sea and the North Sea. Molecular Ecology, 13: 585–595.

Nielsen, E. E., MacKenzie, B. R., Magnussen, E., and Meldrup, D. 2007. Historical analysis of Pan I in Atlantic cod (*Gadus morhua*): temporal stability of allele frequencies in the southeastern part of the species distribution. Canadian Journal of Fisheries and Aquatic Sciences, 64: 1448–1455.

Nielsen, J. G., and Casey, J. 2008. *Poecilopsetta beanii* (Pleuronectidae): a new record for the East Atlantic. Cybium, 32: 181–182.

Niermann, U., Bingel, F., Gorban, A., Gordina, A. D., Gucu, A. C., Kideys, A. E., Konsulov, A., *et al.* 1994. Distribution of anchovy eggs and larvae (*Engraulis encrasicolus* Cuv.) in the Black Sea in 1991–1992. ICES Journal of Marine Science, 51: 395–406.

Nisbet, R. M., Muller, E. B., Lika, K., and Kooijman, S. A. L. M. 2000. From molecules to ecosystems through dynamic energy budget models. Journal of Animal Ecology, 69: 913–926.

Nissling, A. 2004. Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea – implications for stock development. Hydrobiologia, 514: 115–123.

Nissling, A., Kryvi, H., and Vallin, L. 1994. Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. Marine Ecology Progress Series, 110: 67–74.

Nissling, A., Westin, L., and Hjerne, O. 2002. Reproductive success in relation to salinity for three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), and flounder (*Pleuronectes flesus*), in the brackish water Baltic Sea. ICES Journal of Marine Science, 59: 93–108.

Nobre, A. 1935. Fauna Marinha de Portugal. 1. Vertebrados (Mammiferos, Reptis e Peixes). 574 pp.

Norcross, J. J., Massmann, W. H., and Joseph, E. B. 1961. Investigations of inner continental shelf waters off Lower Chesapeake Bay. Part II. Sand lance larvae, *Ammodytes americanus*. Science, 11: 49–59.

North, E. W., Gallego, A., and Petitgas, P. (Eds). 2009. Manual of recommended practices for modelling physical–biological interactions during fish early life. ICES Cooperative Research Report No. 295. 111 pp.

Nøttestad, L., Misund, O. A., and Melle, W. 2007. Herring at the Arctic front: influence of temperature and prey on their spatio-temporal distribution and migration. Marine Ecology, 28(Suppl. 1): 123–133.

O'Brien, C. M., Fox, C. J., Planque, B., and Casey, J. 2000. Climate variability and North Sea cod. Nature, 404: 142.

O'Brien, L. 1999. Factors influencing the rate of sexual maturity and the effect on spawning stock for Georges Bank and Gulf of Maine Atlantic cod *Gadus morhua* stocks. Journal of Northwest Atlantic Fishery Science, 25: 179–203.

Oeberst, R., Klenz, B., Gröhsler, T., Dickey-Collas, M., Nash, R. D. M., and Zimmermann, C. 2009. When is year-class strength determined in western Baltic herring? ICES Journal of Marine Science, 66: 1667–1672.

Oguz, T., and Gilbert, D. 2007. Abrupt transitions of the top–down controlled Black Sea pelagic ecosystem during 1960–2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. Deep-Sea Research I, 54: 220–242.

Oguz, T., Malanotte-Rizzoli, P., and Aubrey, D. 1995. Wind and thermohaline circulation of the Black Sea driven by yearly mean climatological forcing. Journal of Geophysical Research, 100: 6845–6863.

Oguz, T., Dippner, J. W., and Kaymaz, Z. 2006. Climatic regulation of the Black Sea hydrometeorological and ecological properties at interannual-to-decadal time scales. Journal of Marine Systems, 60: 235–254.

Ohlmann, J. C., Siegel, D. A., and Mobley, C. D. 2000a. Ocean radiant heating. Part I. Optical influences. Journal of Physical Oceanography, 30: 1833–1848.

Ohlmann, J. C., Siegel, D. A., and Mobley, C. D. 2000b. Ocean radiant heating. Part II. Parameterizing solar radiation transmission through the upper ocean. Journal of Physical Oceanography, 30: 1849–1865.

Ojaveer, E., and Kalejs, M. 2005. The impact of climate change on the adaptation of marine fish in the Baltic Sea. ICES Journal of Marine Science, 62: 1492–1500.

Olaso, I., Gutiérrez, J. L., Villamor, B., Carrera, P., Valdés, L., and Abaunza, P. 2005. Seasonal changes in the north-eastern Atlantic mackerel diet (*Scomber scombrus*) in the north of Spain (ICES Division VIIIc). Journal of the Marine Biological Association of the UK, 85: 415–418.

Olsen, E. M., Heino, M., Lilly, G. R., Morgan, M. J., Brattey, J., Ernande, B., and Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature, 428: 932–935.

Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., *et al.* 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature, 437: 681–686.

Osborn, T. J., and Briffa, K. R. 2006. The spatial extent of 20th-century warmth in the context of the past 1200 years. Science, 311: 841–844.

Otterlei, E., Nyhammer, G., Folkvord, A., and Stefansson, S. O. 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2099–2111.

Ottersen, G., and Stenseth, N. C. 2001. Atlantic climate governs oceanographic and ecological variability in the Barents Sea. Limnology and Oceanography, 46: 1774–1780.

Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography, 4: 278–292.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., and Stenseth, N. C. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia, 128: 1–14.

Ottersen, G., Loeng, H., Ådlandsvik, B., and Ingvaldsen, R. 2003. Temperature variability in the Northeast Atlantic. ICES Marine Science Symposia, 219: 86–94.

Ottersen, G., Stenseth, N. C., and Hurrell, J. W. 2004. Climatic fluctuations and marine systems: a general introduction to the ecological effects. *In* Marine Ecosystems and Climate

Variation: the North Atlantic, pp. 3–14. Ed. by N. C. Stenseth, G. Ottersen, J. Hurrell, and A. Belgrano. Oxford University Press, Oxford.

Ottersen, G., Hjermann, D. Ø., and Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fisheries Oceanography, 15: 230–243.

Ovchinnikov, I. M., and Osadchiy, I. 1991. Secular variability of winter climatic conditions influencing peculiarities of hydrological conditions in the Black Sea. *In* The Variability of the Black Sea Ecosystem: Natural and Anthropogenic Factors, pp. 85–89. Ed. by M. E. Vinogradov. Nauka, Moscow. (in Russian)

Ovchinnikov, I. M., and Popov, Yu. I. 1987. Cold intermediate layer formation in the Black Sea. Oceanology, Moscow, 27: 739–748. (in Russian)

Overholtz, W. J. 1989. Density-dependent growth in the northwest Atlantic stock of Atlantic mackerel (*Scomber scombrus*). Journal of Northwest Atlantic Fisheries Science, 9: 115–121.

Overland, J. E., Spillane, M. C., Percival, D. B., Wang, M., and Mofjeld, H. O. 2004. Seasonal and regional variation of pan-Arctic surface air temperature over the instrumental record. Journal of Climate, 17: 3263–3282.

Ozhigin, V. K., and Luka, G. I. 1985. Some peculiarities of capelin migrations depending on thermal conditions in the Barents Sea. *In* The Proceedings of the Soviet-Norwegian Symposium on the Barents Sea Capelin, 14–17 August 1984, Bergen, pp. 135–147. Ed. by H. Gjøsæter. Institute of Marine Research, Bergen, Norway.

Özsoy, E. 1999. Sensitivity to global change in temperate Euro-Asian seas (the Mediterranean, Black Sea and Caspian Sea). *In* The Eastern Mediterranean as a Laboratory Basin for the Assessment of Contrasting Ecosystems, pp. 281–300. Ed. by P. Malanotte-Rizolli, and V. N. Eremeev. Kluwer, Dordrecht.

Pain, C. C., Piggott, M. D., Goddard, A. J. H., Fang, F., Gorman, G. J., Marshall, D. P., Eaton, M. D., *et al.* 2005. Three-dimensional unstructured mesh ocean modelling. Ocean Modelling, 10: 5–33.

Pais, A., Merella, P., Garippa, G., and Follesa, M. C. 2007. Westward range expansion of the Lessepsian migrant *Fistularia commersonii* (Fistulariidae) in the Mediterranean Sea, with notes on its parasites. Journal of Fish Biology, 70: 269–277.

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., García, A., and Morales-Nin, B. 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. Progress in Oceanography, 74: 377–396.

Parker-Humphreys, M. 2004. Distribution and relative abundance of demersal fishes from beam trawl surveys in the Bristol Channel (ICES division VIIf) 1993–2001. Science Series Technical Report, Cefas, Lowestoft, 123. 67 pp.

Parmanne, R., Rechlin, O., and Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana, 10: 29–59.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics, 37: 637–669.

Parra, G., and Yúfera, M. 2002. Tolerance response to water pH in larvae of two marine fish species, gilthead seabream, *Sparus aurata* (L.) and Senegal sole, *Solea senegalensis* (Kaup), during development. Aquaculture Research, 33: 747–752.

Parrish, B. B., Saville, A., Craig, R. E., Baxter, I. G., and Priestley, R. 1959. Observations on herring spawning and larval distribution in the Firth of Clyde in 1958. Journal of the Marine Biological Association of the UK, 38: 445–453.

Parsons, A. R., Bourke, R. H., Muench, R. D., Chiu, C-S., Lynch, J. F., Miller, J. H., Plueddemann, A. J., *et al.* 1996. The Barents Sea Polar Front in summer. Journal of Geophysical Research, 101, C6: 14201–14221.

Pastoors, M. A., Rijnsdorp, A. D., and van Beek, F. A. 2000. Effects of a partially closed area in the North Sea ("plaice box") on stock development of plaice. ICES Journal of Marine Science, 57: 1014–1022.

Pätsch, J., and Kühn, W. 2008. Nitrogen and carbon cycling in the North Sea and exchange with the North Atlantic—a model study. Part I. Nitrogen budget and fluxes. Continental Shelf Research, 28: 767–787.

Patterson, K. R. 1983. Some observations on the ecology of the fish of the muddy sand ground in the Irish Sea. PhD thesis, University of Liverpool, UK.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. Science, 279: 860–863.

Pauly, D., Christensen, V., Guenette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R., *et al.* 2002. Towards sustainability in world fisheries. Nature, 418: 689–695.

Pawson, M. G., Pickett, G. D., and Walker, P. 2002. The coastal fisheries of England and Wales, Part IV: a review of their status, 1999–2001. Science Series Technical Report, Cefas, Lowestoft, 116. 83 pp.

Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaug, T., Gallego, A., Gröger, J., Licandro, P., *et al.* 2009. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. ICES Journal of Marine Science, 66: 272–277.

Pearson, R. G., and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12: 361–371.

Pearson, W. H., Woodruff, D. L., and Sugarman, P. C. 1984. The burrowing behavior of sand lance, *Ammodytes hexapterus*: Effects of oil-contaminated sediment. Marine Environmental Research, 11: 17–32.

Peck, M. A., and Daewel, U. 2007. Physiologically based limits to food consumption, and individual-based modeling of foraging and growth of larval fish. Marine Ecology Progress Series, 347: 171–183.

Peck, M. A., Buckley, L. J., and Bengtson, D. A. 2004. Inter-individual differences in rates of routine energy loss and growth in young-of-year juvenile Atlantic cod (*Gadus morhua*). Journal of Fish Biology, 64: 984–995.

Peck, M. A., Buckley, L. J., and Bengtson, D. A. 2006. Effects of temperature and body size on the swimming velocity of larval and juvenile Atlantic cod (*Gadus morhua*): implications for individual-based modeling. Environmental Biology of Fish, 75: 419–429.

Pecquerie, L. 2007. Modélisation bio-énergétique de la croissance, du développement et de la reproduction d'un petit pélagique: l'anchois du Golfe de Gascogne. PhD thesis, Ifremer, France.

Pedersen, S. A., Lewy, P., and Wright, P. 1999. Assessments of the lesser sandeels (*Ammodytes marinus*) in the North Sea based on revised stock divisions. Fisheries Research, 41: 221–241.

Perez, T., Garrabou, J., Sartoretto, S., Harmelin, J. G., Francour, P., and Vacelet, J. 2000. Mortalité massive d'invertébrés marins: unévénement sans précédent en Méditerranée nord-occidentale. Comptes Rendus de l'Académie des Sciences Paris, Sciences et Vie, 323: 853–865.

Perlmutter, A. 1956. Sea fisheries. Report to the government of Israel, Technical Assistance Program USOM Agricultural Report: 58.

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. Science, 308: 1912–1915.

Perry, R. I., Batchelder, H. P., Mackas, D. L., Chiba, S., Durbin, E., Greve, W., and Verheye, H. M. 2004. Identifying global synchronies in marine zooplankton populations: issues and opportunities. ICES Journal of Marine Science, 61: 445–456.

Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. Journal of Marine Systems, 79: 427–435.

Petersen, G. H. 1977. The occurrence of the sand eel (*Ammodytes dubius*) in 0.1 m^2 van Veen grab samples taken during winter in Godhavn Havn, Disko Bugt. Journal du Conseil International pour l'Exploration de la Mer, 37: 309–310.

Petitgas, P., and Grellier, P. 2003. Size selective processes for anchovy in Biscay, 2000–2002: recruitment, adult survival and spawning. ICES Document CM 2003/N:07.

Petitgas, P., Massé, J., Grellier, P., and Beillois, P. 2003. Variation in the spatial distribution of fish length: a multi-annual geostatistics approach on anchovy in Biscay, 1983–2002. ICES Document CM 2003/Q:15.

Petitgas, P., Beillois, P, Massé, J., and Grellier, P. 2004. On the importance of adults in maintaining population habitat occupation of recruits as deduced from observed schooling behaviour of age-0 anchovy in the Bay of Biscay. ICES Document CM 2004/J:13.

Petitgas, P., Huret, M., Léger, F., Peck, M. A., Dickey-Collas, M., and Rijnsdorp, A. D. 2009. Patterns and schedules in hindcasted environments and fish life cycles. ICES Document CM 2009/E:25.

Philippart, C. J. M., Henderson, P. A., Johannessen, T., Rijnsdorp, A. D., and Rogers, S. I. 1998. Latitudinal variation in fish recruits in northwest Europe. Journal of Sea Research, 39: 69–78.

Philippart, C. J. M., Cadée, G. C., van Raaphorst, W., and Riegman, R. 2000. Long-term phytoplankton–nutrient interactions in a shallow coastal sea: algal community structure, nutrient budgets, and denitrification potential. Limnology and Oceanography, 45: 131–144.

Philippart, C. J. M., Anadón, R., Danovaro, R., Dippner, J. W., Drinkwater, K. F., Hawkins, S. J., O'Sullivan, J., *et al.* 2007a. Climate Change Impacts on the European Marine and Coastal Environment. Marine Board–European Science Foundation Position Paper 9. 82 pp. Available online at www.esf.org/marineboard.

Philippart, C. J. M., Beukema, J. J., Cadée, G. C., Dekker, R., Goedhart, P. W., van Iperen, J. M., Leopold, M. F., *et al.* 2007b. Impacts of nutrient reduction on coastal communities. Ecosystems, 10: 95–110.

Pihl, L. 1990. Year-class strength regulation in plaice (*Pleuronectes platessa* L.) on the Swedish west coast. Hydrobiologia, 195: 79–88.

Pihl, L., and Rosenberg, R. 1984. Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. Marine Ecology Progress Series, 15: 159–168.

Pilchavant, K., Person-Le-Ruyet, J., Le Bayon, N., Severe, A., Le Roux, A., and Boeuf, G. 2001. Comparative effects of long-term hypoxia on growth, feeding and oxygen consumption in juvenile turbot and European sea bass. Journal of Fish Biology, 59: 875–883.

Pilling, G. M., Millner, R. S., Easey, M. W., Maxwell, D. A., and Tidd, A. N. 2007. Phenology and North Sea cod *Gadus morhua* L.: has climate change affected otolith annulus formation and growth? Journal of Fish Biology, 70: 584–599.

Pingree, R. D. 2002. Ocean structure and climate (eastern North Atlantic): *in situ* measurement and remote sensing (altimeter). Journal of the Marine Biological Association of the UK, 82: 681–707.

Pingree, R. D. 2005. North Atlantic and North Sea climate change: curl up, shut down, NAO and ocean colour. Journal of the Marine Biological Association of the UK, 85: 1301–1315.

Pingree, R. D., and Griffiths, D. K. 1978. Tidal fronts on the shelf seas around the British Isles. Journal of Geophysical Research, 83: 4615–4622.

Pingree, R. D., and Le Cann, B. 1989. Celtic and Armorican shelf and slope residual currents. Progress in Oceanography, 23: 303–338.

Pinnegar, J. K., and Engelhard, G. H. 2008. The 'shifting baseline' phenomenon: a global perspective. Reviews in Fish Biology and Fisheries, 18: 1–16.

Pinnegar, J. K., Polunin, N. V. C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M-L., Hereu, B., *et al.* 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation, 27: 179–200.

Pinnegar, J. K., Jennings, S., O'Brien, C. M., and Polunin, N. V. C. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. Journal of Applied Ecology, 39: 377–390.

Pinnegar, J. K., Polunin, N. V. C., and Badalamenti, F. 2003. Long-term changes in the trophic level of western Mediterranean fishery and aquaculture landings. Canadian Journal of Fisheries and Aquatic Sciences, 60: 222–235.

Pinnegar, J. K., Stelzenmüller, V., van der Kooij, J., Engelhard, G. H., Garrick-Maidment, N., and Righton, D. A. 2008. Occurrence of the short-snouted seahorse *Hippocampus hippocampus* in the central North Sea. Cybium, 32: 343–346.

Pinto, J. G., Spangehl, T., Ulbrich, U., and Speth, P. 2006. Assessment of winter cyclone activity in a transient ECHAM4-OPYC3 GHG experiment. Meteorologische Zeitschrift, 15: 279–291.

Pinto, J. M., Pearson, W. H., and Anderson, J. W. 1984. Sediment preferences and oil contamination in the Pacific sand lance *Ammodytes hexapterus*. Marine Biology, 83: 193–204.

Pitcher, T. J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. Ecological Applications, 11: 601–617.

Pitois, S. G., and Fox, C. J. 2008. Empirically modelling the potential effects of changes in temperature and prey availability on the growth of cod larvae in UK shelf seas. ICES Journal of Marine Science, 65: 1559–1572.

Plagmann, J. 1939. Ernährungsbiologie der Garnele (*Crangon vulgaris* Fabr.). Helgoländer Wissenschaftlichen Meeresuntersuchungen, 2: 113–162.

Planque, B., and Frédou, T. 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 56: 2069–2077.

Planque, B., Beillois, P., Jégou, A. M., Lazure, P., Petitgas, P., and Puillat, I. 2003a. Large-scale hydroclimatic variability in the Bay of Biscay: the 1990s in the context of interdecadal changes. ICES Marine Science Symposia, 219: 61–70.

Planque, B., Fox, C. J., Saunders, M. A., and Rockett, P. 2003b. On the prediction of short term changes in the recruitment of North Sea cod (*Gadus morhua*) using statistical temperature forecasts. Scientia Marina, 67 (Suppl. 1): 211–218.

Planque, B., Bellier, E., and Lazure, P. 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. Fisheries Oceanography, 16: 16–30.

Planque, B., Fromentin, J-M., Cury, P., Drinkwater, K., Jennings, S., Kifani, S., and Perry, R. I. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? Journal of Marine Systems, 79: 403–417.

Platt, T., Fuentes-Yaco, C., and Frank, K. T. 2003. Spring algal bloom and larval fish survival. Nature, 423: 398–399.

Plikshs, M., Kalejs, M., and Graumann, G. 1993. The influence of environmental conditions and spawning stock size on the year-class strength of the Eastern Baltic cod. ICES Document CM 1993/J:22.

Plounevez, S., and Champalbert, G. 1999. Feeding behaviour and trophic environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. Estuarine, Coastal and Shelf Science, 49: 177–191.

Poll, M. 1947. Faune de Belgique. Poissons Marine. Musée Royal d'Histoire Naturelle de Belgique. 452 pp.

Polonsky, A., Voskresenskaya, E., and Belokopitov, V. 1997. Variability of northwestern Black Sea hydrography and river discharges as part of the global ocean-atmosphere fluctuations. *In* Sensitivity to Change: Black Sea, Baltic Sea and North Sea, pp. 11–24. Ed. by E. Özsoy and A. Mikaelyan. NATO Advanced Science Institutes Series, 2. Environment, Vol. 27. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Polovina, J. J., Mitchum, G. T., and Evans, G. T. 1995. Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the central and north Pacific, 1960–88. Deep-Sea Research I, 42: 1701–1716.

Polunin, N. V. C., Morales-Nin, B., Pawsey, W. E., Cartes, J. E, Pinnegar, J. K., and Moranta, J. 2001. Feeding relationships in Mediterranean bathyal assemblages elucidated by carbon and nitrogen stable-isotope data. Marine Ecology Progress Series, 220: 13–23.

Pope, J. G., Shepherd, J. G., Webb, J., Stebbing, A. R. D., and Mangel, M. 1994. Successful surf-riding on size spectra: the secret of survival in the sea. Philosophical Transactions of the Royal Society of London, Series B, 343: 41–49.

Pope, J. G., Rice, J. C., Daan, N., Jennings, S., and Gislason, H. 2006. Modelling an exploited marine fish community with 15 parameters–results from a simple size-based model. ICES Journal of Marine Science, 63: 1029–1044.

Popp-Madsen, K. 1994. Tobis or not tobis. Et vigtigt spørgsmål for dansk fiskeri. (Sandeels or not sandeels? An important question for the Danish fishery). Fisken og Havet, 45: 27–34.

Pörtner, H. O., and Farrell, A. P. 2008. Physiology and climate change. Science, 322: 690–692.

Pörtner, H. O., and Knust, R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science, 315: 95–97.

Pörtner H. O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A., *et al.* 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). Continental Shelf Research, 21: 1975–1997.

Pörtner, H. O., Storch, D., and Heilmayer, O. 2005. Constraints and trade-offs in climate-dependent adaptation: energy budgets and growth in a latitudinal cline. Scientia Marina, 69: 271–285.

Pörtner, H. O., Bennett, A. F., Bozinovic, F., Clarke, A., Lardies, M. A., Lucassen, M., Pelster, B., *et al.* 2006. Trade-offs in thermal adaptation: the need for a molecular to ecological integration. Physiological and Biochemical Zoology, 79: 295–313.

Pörtner, H. O., Bock, C., Knust, R., Lannig, G., Lucassen, M., Mark, F., and Sartoris, F. J. 2008. Cod and climate in a latitudinal cline: physiological analyses of climate effects in marine fish. Climate Research, 37: 253–270.

Post, J. R., and Evans, D. O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*) – laboratory, *in situ* enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences, 46: 1958–1968.

Postuma, K. H. 1972. On the abundance of mackerel (*Scomber scombrus* L.) in the northern and north-eastern North Sea in the period 1959–1969. ICES Journal of Marine Science, 34: 455–465.

Poulard, J-C., and Blanchard, F. 2005. The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. ICES Journal of Marine Science, 62: 1436–1443.

Poulsen, B. 2010. The variability of fisheries and fish populations prior to industrialized fishing: an appraisal of the historical evidence. Journal of Marine Systems, 79: 327–332.

Poulsen, B., Holm, P., and MacKenzie, B. R. 2007. A long-term (1667–1860) perspective on impacts of fishing and environmental variability on fisheries for herring, eel, and whitefish in the Limfjord, Denmark. Fisheries Research, 87: 181–195.

Pouvreau, S., Bourles, Y., Lefebvre, S., Gangnery, A., and Alunno-Bruscia, M. 2006. Application of a dynamic energy budget model to the Pacific oyster, *Crassostrea gigas*, reared under various environmental conditions. Journal of Sea Research, 56: 156–167.

Proctor, R., Wright, P. J., and Everitt, A. 1998. Modelling the transport of larval sandeels on the north-west European shelf. Fisheries Oceanography, 7: 347–354.

Prodanov, K., Mikhaylov, K., Daskalov, G., Maxim, K., Ozdamar, E., Shlyakhov, V., Chashchin, A., *et al.* 1997. Environmental management of fish resources in the Black Sea and their rational exploitation. General Fisheries Commission of the Mediterranean, Studies and Reviews, 68.

Pulgar, J. M., Aldana, M., Bozinovic, F., and Ojeda, F. P. 2003. Does food quality influence thermoregulatory behavior in the intertidal fish *Girella laevifrons*? Journal of Thermal Biology, 28: 539–544.

Quéro, J. C. 1998. Changes in the Euro-Atlantic fish species composition resulting from fishing and ocean warming. Italian Journal of Zoology, 65 (Suppl.): 493–499.

Quéro, J. C., Du Buit, M. H., and Vayne, J. J. 1998. Les observations de poissons tropicaux et le rechauffement des eaux de l'Atlantique européen. Oceanologica Acta, 21: 345–351.

Quéro, J. C., Porche, P., and Vayne, J. J. 2003. Guide les poissons de l'Atlantique européen. Delachaux and Niestle, Paris. 465 pp.

Quigley, D. T. G., and Flannery, K. 1995. Sailfin dory *Zenopsis conchifer* (Lowe 1852): further records from Irish waters and a review of north-west European records. Irish Naturalists' Journal, 25: 71–76.

Rachor, E. 1990. Changes in sublittoral zoobenthos in the German Bight with regard to eutrophication. Netherlands Journal of Sea Research, 25: 209–214.

Rapoport, E. H. 1975. Areografía. Estrategias Geográficas de las Especies. Fondo de Cultura Económica, México [in Spanish].

Rapoport, E. H. 1982. Areography. Geographical Strategies of Species. Pergamon Press, Oxford and New York.

Rauck, G., and Zijlstra, J. J. 1978. On the nursery-aspects of the Waddensea for some commercial fish species and possible long-term changes. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 172: 266–275.

Ré, P. 1996. Anchovy spawning in the Mira estuary. Scientia Marina, 60(Suppl. 2): 141–153.

Reay, P. J. 1970. Synopsis of biological data on North Atlantic sandeels of the genus *Ammodytes*. FAO Fisheries Synopsis No. 82.

Reay, P. J. 1972. The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. Journal du Conseil, Conseil International pour l'Exploration de la Mer, 34: 485–504.

Redeke, H. C. 1941. Fauna van Nederland. X. Pisces (Cyclostomi-Euichthyes). A. W. Sijthoff's Uitgeversmaatschappij, Leiden. 331 pp.

Redeke, H. C., and van Breemen, P. J. 1907. Die Verbreitung der planktonischen Eier und Larven einiger Nutzfische in der südlichen Nordsee. Verhandelingen van het Rijksinstituut voor Onderzoek der Zee, 2: 3–37.

Reeves, S. A. 1994. Seasonal and annual variation in catchability of sandeels at Shetland. ICES Document CM 1994/D:19.

Regner, S. 1996. Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. Scientia Marina, 60(Suppl. 2): 167–177.

Regner, S., and Gacic, M. 1974. The fluctuations of sardine catch along the eastern coast and solar activity. Acta Adriatica, 15: 1–15.

Reid, D. G. 2001. SEFOS – Shelf Edge Fisheries and Oceanography Studies: an overview. Fisheries Research, 50: 1–15.

Reid, D. G., Turrell, W. R., Walsh, M., and Corten, A. 1997. Cross-shelf processes north of Scotland in relation to the southerly migration of western mackerel. ICES Journal of Marine Science, 54: 168–178.

Reid, D. G., Walsh, M., and Turrell, W. R. 2001a. Hydrography and mackerel distribution on the shelf edge west of the Norwegian deeps. Fisheries Research, 50: 141–150.

Reid, P. C., Planque, B., and Edwards, M. 1998a. Is observed variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? Fisheries Oceanography, 7: 282–288.

Reid, P. C., Edwards, M., Hunt, H. G., and Warner, J. W. 1998b. Phytoplankton change in the North Atlantic. Nature, 391: 546.

Reid, P. C., Borges, M. F., and Svendsen, E. 2001b. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. Fisheries Research, 50: 163–171.

Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M., and Stevens, D. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fisheries Oceanography, 12: 260–269.

Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. G. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. Fish and Fisheries, doi: 10.1111/j.1467–2979.2008.00324.x

Renz, J., and Hirche, H. J. 2006. Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the central Baltic Sea. I. Seasonal and spatial distribution. Marine Biology, 148: 567–580.

Revelante, N., and Gilmartin, M. 1976. The effect of Po river discharge on phytoplankton dynamics in the northern Adriatic Sea. Marine Biology, 34: 259–271.

Rhein, M. 1991. Ventilation rates of the Greenland and Norwegian Seas derived from distributions of chlorofluoromethanes F11 and F12. Deep Sea Research Part A, 38: 484–503.

Rhein, M. 1996. Convection in the Greenland Sea, 1982–1993. Journal of Geophysical Research, 101: 18183–18192.

Rice, A. L., and Chapman, C. J. 1971. Observations on the burrows and burrowing behaviour of two mud-dwelling decapod crustaceans, *Nephrops norvegicus* and *Goneplax rhomboides*. Marine Biology, 10: 330–342.

Rice, J. 1995. Food web theory, marine food webs, and what climate change may do to northern fish populations. *In* Climate Change and Northern Fish Populations, pp. 561–568. Ed. by R. J. Beamish. Canadian Special Publication in Fisheries and Aquatic Science, 121.

Rice, J., and Gislason, H. 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. ICES Journal of Marine Science, 53: 1214–1225.

Richards, S. W., and Kendall, A. W. 1973. Distribution of sand lance, *Ammodytes* sp., larvae on the continental shelf from Cape Cod to Cape Hatteras from R/V Dolphin surveys in 1966. Fishery Bulletin US, 71: 371–386.

Richards, S. W., Perlmutter, A., and McAneny, D. C. 1963. A taxonomic study of the genus *Ammodytes* from the east coast of the North America (Teleostei: Ammodytes). Copeia, 2: 358–377.

Richardson, A. J., and Gibbons, M. J. 2008. Are jellyfish increasing in response to ocean acidification? Limnology and Oceanography, 53: 2040–2045.

Richardson, A. J., and Schoeman, D. S. 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science, 305: 1609–1612.

Richardson, A. J., Bakun, A, Hays, G. C., and Gibbons, M. J. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology and Evolution, 24: 312–322.

Riebesell, U., Zondervan, I., Rost, B., Tortell, P. D., Zeebe, R. E., and Morel, F. M. M. 2000. Reduced calcification of marine plankton in response to increased atmospheric CO_2. Nature, 407: 634–637.

Rijnsdorp, A. D. 1993a. The relation between juvenile growth and the onset of sexual maturation of female North Sea plaice, *Pleuronectes platessa* L. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1617–1631.

Rijnsdorp, A. D. 1993b. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. Oecologia, 96: 391–401.

Rijnsdorp, A. D., and Millner, R. S. 1996. Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s. ICES Journal of Marine Science, 53: 1170–1184.

Rijnsdorp, A. D., and Pastoors, M. A. 1995. Modelling the spatial dynamics and fisheries of North Sea plaice (*Pleuronectes platessa* L.) based on tagging data. ICES Journal of Marine Science, 52: 963–980.

Rijnsdorp, A. D., and van Beek, F. A. 1991. Changes in growth of North Sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.). Netherlands Journal of Sea Research, 27: 441–457.

Rijnsdorp, A. D., and van Leeuwen, P. I. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. ICES Journal of Marine Science, 53: 1199–1213.

Rijnsdorp, A. D., and Vingerhoed, B. 1994. The ecological significance of geographical and seasonal differences in egg size in sole *Solea solea* (L). Netherlands Journal of Sea Research, 32: 255–270.

Rijnsdorp, A. D., and Witthames, P. R. 2005. Ecology of reproduction. *In* Flatfish Biology and Exploitation, pp. 68–93. Ed. by R. N. Gibson. Academic Press, London.

Rijnsdorp, A. D., van Stralen, M., and van der Veer, H. W. 1985. Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. Transactions of the American Fisheries Society, 114: 461–470.

Rijnsdorp, A. D., van Beek, F. A., Flatman, S., Miller, J. M., Riley, J. D., Giret, M., and de Clerk, R. 1992. Recruitment of sole, *Solea solea* (L.), in the Northeast Atlantic. Netherlands Journal of Sea Research, 29: 173–192.

Rijnsdorp, A. D., van Keeken, O. A., and Bolle, L. J. 2004. Changes in productivity of the southeastern North Sea as reflected in the growth of plaice and sole. ICES Document CM 2004/K: 13.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. ICES Journal of Marine Science, 66: 1570–1583.

Riley, J. D. 1974. The distribution and mortality of sole eggs [*Solea solea* (L.)] in inshore areas. *In* The Early Life History of Fish, pp. 39–52. Ed. by J. H. S. Blaxter. Springer Verlag, Berlin.

Riley, J. D. 1986. Determination of the distribution of the planktonic and small demersal stages of fish in the coastal waters of England, Wales and adjacent areas between 1970 and 1984. Fisheries Research Technical Report, MAFF Directorate of Fisheries Research, Lowestoft, 84. 23 pp.

Riley, J. D., Symonds, D. J., and Woolner, L. E. 1981. On the factors influencing the distribution of 0-group demersal fish in coastal waters. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 178: 223–228.

Rindorf, A., and Lewy, P. 2006. Warm, windy winters drive cod north and homing of spawners keeps them there. Journal of Applied Ecology, 43: 445–453.

Ringuette, M., Castonguay, M., Runge, J. A., and Gregoire, F. 2002. Atlantic mackerel (*Scomber scombrus*) recruitment fluctuations in relation to copepod production and juvenile growth. Canadian Journal of Fisheries and Aquatic Sciences, 59: 646–656.

Rixen, M., Beckers, J-M., Levitus, S., Antonov, J., Boyer, T., Maillard, C., Fichaut, M. , *et al.* 2005. The Western Mediterranean Deep Water: a proxy for climate change. Geophysical Research Letters, 32, L12608, doi: 10.1029/2005GL022702.

Robichaud, D., and Rose, G. A. 2004. Migratory behaviour and range in the Atlantic cod: inference from a century of tagging. Fish and Fisheries, 5: 185–214.

Robins, C. R., and Bohlke, J. E. 1970. The first Atlantic species of the Ammodytid fish genus *Embolichthys*. Notulae Naturae, 430: 1–11.

Robinson, A. R., Leslie, W. G., Theocharis, A., and Lascaratos, A. 2001. Mediterranean Sea circulation. *In* Encyclopedia of Ocean Sciences, pp. 1689–1706. Ed. by J. H. Steele, S. A. Thorpe, and K. K. Turekian. Academic Press, San Diego. 3000 pp.

Robinson, L., and Frid, C. 2003. Dynamic ecosystem models and the evaluation of ecosystem effects of fishing: can we make meaningful predictions? Aquatic Conservation: Marine and Freshwater Ecosystems, 13: 5–20.

Röckmann, C., St John, M. A., Schneider, U. A., and Tol, R. S. J. 2007a. Testing the implications of a permanent or seasonal marine reserve on the population dynamics of Eastern Baltic cod under varying environmental conditions. Fisheries Research, 85: 1–13.

Röckmann, C., Schneider, U. A., St John, M. A., and Tol, R. S. J. 2007b. Rebuilding the eastern Baltic cod stock under environmental change—a preliminary approach using stock, environmental, and management constraints. Natural Resource Modeling, 20: 223–262.

Roff, D. A. 2002. Life History Evolution. Sinauer Associates, Sunderland, MA.

Rogers, J. 1985. Atmospheric circulation changes associated with the warming over the northern North Atlantic in the 1920s. Journal of Climate and Applied Meteorology, 24: 1303–1310.

Rogers, S. I. 1989. The ecology of juvenile Dover sole *Solea solea* L.: a review of literature. Progress in Underwater Science, 14: 53–66.

Rogers, S. I. 1992. Environmental factors affecting the distribution of sole (*Solea solea* (L.) within a nursery area. Netherlands Journal of Sea Research, 29: 153–161.

Rogers, S. I., Millner, R. S., and Mead, T. A. 1998a. The distribution and abundance of young fish on the east and south coast of England (1981 to 1997). Science Series Technical Report, Cefas, Lowestoft, 108. 130 pp.

Rogers, S. I., Rijnsdorp, A. D., Damm, U., and Vanhee, W. 1998b. Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990 to 1995. Journal of Sea Research, 39: 79–102.

Romano, J. C., Bensoussan, N., Younes, W. A. N., and Arlhac, D. 2000. Anomalie thermique dans les eaux du golfe de Marseille durand l'été 1999. Une explication partielle de la mortalité d'invertébrés fixés? Comptes Rendus de l'Académie des Sciences Paris, Sciences et Vie, 323: 415–427.

Rönkkönen, S., Ojaveer, E., Raid, T., and Viitasalo, M. 2004. Long-term changes in Baltic herring (*Clupea harengus membras*) growth in the Gulf of Finland. Canadian Journal of Fisheries and Aquatic Sciences, 61: 219–229.

Rose, G. A. 2005. On distributional responses of North Atlantic fish to climate change. ICES Journal of Marine Science, 62: 1360–1374.

Rose, G. A., and Leggett, W. C. 1988. Atmosphere–ocean coupling and Atlantic cod migrations: effects of wind-forced variations in sea temperatures and currents on nearshore distributions and catch rates of *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Sciences, 45: 1234–1243.

Rose, G. A., de Young, B., Kulka, D. W., Goddard, S. V., and Fletcher, G. L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences, 57: 644–663.

Rothschild, B. J. 1986. Dynamics of Marine Fish Populations. Harvard University Press, Cambridge, MA.

Rothstein, L. M., Cullen, J. J., Abbott, M., Chassignet, E. P., Denman, K., Doney, S. C., Ducklow, H., *et al.* 2006. Modeling Ocean Ecosystems: The Paradigm Program. Oceanography, 19: 22–51.

Rudstam, L. G., Aneer, G., and Hilden, M. 1994. Top–down control in the pelagic Baltic ecosystem. Dana, 10: 105–129.

Runge, J. A., Castonguay, M., De LaFontaine, Y., Ringuette, M., and Beaulieu, J. L. 1999. Covariation in climate, zooplankton biomass and mackerel recruitment in the southern Gulf of St Lawrence. Fisheries Oceanography, 8: 139–149.

Russell, F. S. 1953. The English Channel. Transactions of the Devonshire Association for the Advancement of Science, Literature and Art, 85. 17 pp.

Russell, F. S. 1976. The Eggs and Planktonic Stages of British Marine Fish. Academic Press, London. 524 pp.

Russo, A., and Artegiani, A. 1996. Adriatic Sea hydrography. Scientia Marina, 60(Suppl. 2): 33–43.

Russo, A., Rabitti, S., and Bastianini, M. 2002. Decadal climatic anomalies in the northern Adriatic Sea inferred from a new oceanographic data set. PSZNI Marine Ecology, 23: 340–351.

Ruzzante, D. E., Taggart, C. T., Doyle, R. W., and Cook, D. 2001. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. Conservation Genetics, 2: 257–269.

Ruzzante, D. E., Mariani, S., Bekkevold, D., Andre, C., Mosegaard, H., Clausen, L. A. W., Dahlgren, T. G., *et al.* 2006. Biocomplexity in a highly migratory marine fish, Atlantic herring. Proceedings of the Royal Society of London, Series B, 273: 1459–1464.

Rykaczewski, R. R., and Checkley, D. M. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. Proceedings of the National Academy of Sciences of the USA, 105: 1965–1970.

Ryland, J. S. 1964. The feeding of plaice and sand-eel larvae in the southern North Sea. Journal of the Marine Biological Association of the UK, 44: 343–364.

Ryland, J. S., Nichols, J. H., and Sykes, A. M. 1975. Effect of temperature on the embryonic development of the plaice *Pleuronectes platessa* L. (Teleostei). Journal of Experimental Marine Biology and Ecology, 18: 121–137.

Sabatés, A., Martín, P., Lloret, J., and Raya, V. 2006. Sea warming and fish distribution: the case of the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. Global Change Biology, 12: 2209–2219.

Sabatés, A., Olivar, M. P., Salat, J., Palomera, I., and Alemany, F. 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Progress in Oceanography, 74: 355–376.

Sæmundsson, B. 1934. Probable influence of changes in temperature on the marine fauna of Iceland. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 86 (I): 1–6.

Sætersdal, G., and Loeng, H. 1987. Ecological adaption of reproduction in Northeast Arctic cod. Fisheries Research, 5: 253–270.

Sætre, R. (Ed.) 2007. The Norwegian Coastal Current – Oceanography and Climate. Tapir Academic Press, Trondheim, Norway. 159 pp.

Salen-Picard, C., Darnaude, A. M., Arlhac, D., and Harmelin-Vivien, M. L. 2002. Fluctuations of macrobenthic populations: a link between climate-driven river run-off and sole fishery yields in the Gulf of Lions. Oecologia, 133: 380–388.

Sánchez, I., Fernández, C., and Arrontes, J. 2005. Long-term changes in the structure of intertidal assemblages following invasion by *Sargassum muticum* (Phaeophyta). Journal of Phycology, 41: 942–949.

Santojanni, A., Arneri, E., Bernardini, V., Cingolani, N., Di Marco, M., and Russo, A. 2006a. Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. Climate Research, 31: 181–193.

Santojanni, A., Cingolani, N., Arneri, E., Belardinelli, A., Giannetti, G., Colella, S., Donato, F., *et al.* 2006b. Recruitment of sardine (*Sardina pilchardus* Walbaum, 1792) in the Adriatic Sea and environmental factors. Biologia Marina Mediterranea, 13: 158–166.

Sapota, M. R. 2004. The round goby (*Neogobius melanostomus*) in the Gulf of Gdańsk–a species introduction into the Baltic Sea. Hydrobiologia, 514: 219–224.

Sarmiento, J. L., Slater, R., Barber, R., Bopp, L., Doney, S. C., Hirst, A. C., Kelypas, J., *et al.* 2004. Response of ocean ecosystems to climate warming. Global Biogeochemical Cycles, 18: 1–23.

Savage, R. E. 1937. The food of North Sea herring 1930–1934. Fisheries Investigations, Series II. 15(5). 60 pp.

Savage, R. E., and Wimpenny, R. S. 1936. Phytoplankton and the herring. Fisheries Investigations, Series II, 15(1). 88 pp.

Savenkoff, C., Castonguay, M., Chabot, D., Hammill, M. O., Bourdages, H., and Morissette, L. 2007. Changes in the northern Gulf of St Lawrence ecosystem estimated by inverse modelling: evidence of a fishery-induced regime shift? Estuarine, Coastal and Shelf Science, 73: 711–724.

Schauer, U., Muench, R. D., Rudels, B., and Timokhov, L. 1997. The impact of eastern Arctic shelf waters on the Nansen Basin intermediate layers. Journal of Geophysical Research, 102: 3371–3382.

Schauer, U., Loeng, H., Rudels, B., Ozhigin, V. K., and Dieck, W. 2002. Atlantic water flow through the Barents and Kara Seas. Deep-Sea Research I, 49: 2281–2298.

Scheffer, M., and Carpenter, S. 2003. Catastrophic regime shifts in ecosystems: liking theory to observation. Trends in Ecology and Evolution, 18: 648–656.

Scheffer, M., and van Nes, E. H. 2004. Mechanisms for regime shifts: can we use lakes as microcosms for oceans? Progress in Oceanography, 60: 303–319.

Scheffer, M., Carpenter, J., Foley, J. A., and Walker, B. 2001. Catastrophic shifts in ecosystems. Nature, 413: 591–596.

Schell, I. I. 1961. The ice off Iceland and the climates during the last 1200 years approximately. Geographical Annals of Stockholm, 43: 354–362.

Schipper, P., Lurling, M., and Scheffer, M. 2004. Increase of atmospheric CO_2 promotes phytoplankton productivity. Ecology Letters, 7: 446–451.

Schmidt, J. O., van Damme, C., Röckmann, C., and Dickey-Collas, M. 2009. Recolonisation of spawning grounds in a recovering fish stock: recent changes in North Sea herring. Scientia Marina, 73: S1.

Schrum, C., and Backhaus, J. O. 1999. Sensitivity of atmosphere–ocean heat exchange and heat content in North Sea and Baltic Sea. A comparative assessment. Tellus, 51A: 526–549.

Schrum, C., Siegismund, F., and St John, M. 2003. Decadal variations in the circulation and stratification pattern of the North Sea. Are the 1990s unusual? ICES Marine Science Symposia, 219: 121–131.

Schrum, C., Alekseeva, I., and St John, M. 2006a. Development of a coupled physical–biological ecosystem model ECOSMO. Part I. Model description and validation for the North Sea. Journal of Marine Systems, 61: 79–99.

Schrum, C., St John, M., and Alekseeva, I. 2006b. ECOSMO, a coupled ecosystem model of the North Sea and Baltic Sea. Part II. Spatial–seasonal characteristics in the North Sea as revealed by EOF analysis. Journal of Marine Systems, 61: 100–113.

Schulz, J., Möllmann, C., and Hirche, H. J. 2007. Vertical zonation of the zooplankton community in the Central Baltic Sea in relation to hydrographic stratification as revealed by multivariate discriminant function and canonical analysis. Journal of Marine Systems, 67: 47–58.

Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J., *et al.* 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science, 21: 289–347.

Scott, J. S. 1982. Depth, temperature and salinity preferences of common fish of the Scotian Shelf. Journal of Northwest Atlantic Fishery Science, 3: 29–39.

Scott, W. B., and Scott, M. G. 1988. Atlantic Fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences, 219. 731 pp.

SEFOS. 1997. Distribution, dispersal and migration in relation to oceanography. *In* Shelf Edge Fisheries and Oceanography Study, Final Report, May 1997, Ch. 4. Supported by the European Union AIR programme.

Segers, F., Dickey-Collas, M., and Rijnsdorp, A. D. 2007. Prey selection by North Sea herring (*Clupea harengus* L.), with special regard to fish eggs. ICES Journal of Marine Science, 64: 60–68.

Shaw, P. W., Turan, C., Wright, J. M., O'Connell, M., and Carvalho, G. R. 1999. Microsatellite DNA analysis of population structure in Atlantic herring (*Clupea harengus*), with direct comparison to allozyme and mtDNA RFLP analyses. Heredity, 83: 490–499.

Shchepetkin, A. F., and McWilliams, J. C. 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Modelling, 9: 347–404.

Shell, K. M., Frouin, R., Nakamoto, S., and Somerville, R. C. J. 2003. Atmospheric response to solar radiation absorbed by phytoplankton. Journal of Geophysical Research 18, D15, 4445, doi: 10.1029/2003JD003440.

Sherman, K., Jones, C., Sullivan, L., Smith, W., Berrien, P., and Ejsymont, L. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. Nature, 291: 486–489.

Sherman, K., Smith, W., Morse, W., Berman, M., Green, J., and Ejsymont, L. 1984. Spawning strategies of fish in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Marine Ecology Progress Series, 18: 1–19.

Shiganova, T. A. 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fisheries Oceanography, 7: 305–310.

Silva, A. 1999. Feeding habits of John Dory, *Zeus faber*, off the Portuguese continental coast. Journal of the Marine Biological Association of the UK, 79: 333–340.

Simmonds, E. J. 2007. Comparison of two periods of North Sea herring stock management: success, failure, and monetary value. ICES Journal of Marine Science, 64: 686–692.

Simonov, A. I., and Altman, E. N. (Eds.) 1991. Project "The USSR seas". Hydrometeorology and hydrochemistry of the USSR seas. Vol. 4: Black Sea, No. 1: Hydrometeorological conditions. Hydrometeoizdat, St Petersburg. (in Russian)

Simonov, A. I., Ryabinin, A. I., and Gershanovitch, D. E. (Eds.) 1992. Project "The USSR seas". Hydrometeorology and hydrochemistry of the USSR seas. Vol. 4: Black Sea, No. 1: Hydrometeorological conditions and oceanological bases of the biological productivity. Hydrometeoizdat, St Petersburg. (in Russian)

Simonsen, C. S., Munk, P., Folkvord, A., and Pedersen, S. A. 2006. Feeding ecology of Greenland halibut and sandeel larvae off West Greenland. Marine Biology, 149: 937–952.

Simpson, A. C. 1959. The spawning of the plaice (*Pleuronectes platessa* L.) in the Irish Sea. ICES Document CM 1957:54. 6 pp.

Sims, D. W. 1999. Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? Proceedings of the Royal Society of London, Series B, 266: 1437–1443.

Sims, D. W. 2003. Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free ranging sharks. Journal of Fish Biology, 63: 53–73.

Sims, D. W., and Merrett, D. A. 1997. Determination of zooplankton characteristics in the presence of surface feeding basking sharks *Cetorhinus maximus*. Marine Ecology Progress Series, 158: 297–302.

Sims, D. W., and Quayle, V. A. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature, 393: 460–464.

Sims, D. W., Southall, E. J., Quayle, V. A., and Fox, A. M. 2000. Annual social behaviour of basking sharks associated with coastal front areas. Proceedings of the Royal Society of London, Series B, 267: 1897–1904.

Sims, D. W., Southall, E. J., Richardson, A. J., Reid, P. C., and Metcalfe, J. D. 2003. Seasonal movement and behavior of basking sharks from archived tagging: no evidence of winter hibernation. Marine Ecology Progress Series, 248: 187–196.

Sims, D. W., Wearmouth, V. J., Genner, M. J., Southward, A. J., and Hawkins, S. J. 2004. Low-temperature-driven early spawning migration of a temperate marine fish. Journal of Animal Ecology, 73: 333–341.

Sinclair, M. 1988. Marine Populations: An Essay on Population Regulation and Speciation. University of Washington Press, Seattle.

Sinclair, M. 2009. Herring and ICES: a historical sketch of a few ideas and their linkages. ICES Journal of Marine Science, 66: 1652–1661.

Sinclair, M., and Iles, T. D. 1989. Population regulation and speciation in the oceans. Journal du Conseil International pour l'Exploration de la Mer, 45: 165–175.

Sinovic, G., and Alegria, V. 1997. Variations in abundance and size of sardine, *Sardina pilchardus* (Walb.) in the eastern Adriatic. Oceanologica Acta, 20: 201–206.

Skagseth, Ø., Orvik, K. A., and Furevik, T. 2004. Coherent variability of the Norwegian Atlantic Slope Current derived from TOPEX/ERS altimeter data. Geophysical Research Letters, 31, L14304, doi: 1029/2004GL020057.

Skogen, M. D., and Moll, A. 2005. Importance of ocean circulation in biophysical ocean models: Advances in Marine Ecosystem Modelling Research Symposium, Plymouth Marine Laboratory, 27–29 June 2005. (Poster presentation)

Skogen, M. D., Svendsen, E., Berntsen, D. A., Aksne, D., and Ulvestad, K. B. 1995. Modelling the primary production in the North Sea using a coupled three-dimensional physical-chemical–biological model. Estuarine, Coastal and Shelf Science, 41: 545–565.

Skogen, M. D., Walsh, M., Reid, D. G., Skegen, D., and Svendsen, E. 1996. Modelling studies on the feeding migration of western mackerel. ICES Document CM 1996/S:38.

Skogen, M. D., Søiland, H., and Svendsen, E. 2004. Effects of changing nutrient loads to the North Sea. Journal of Marine Systems, 46: 23–38.

Skogen, M. D., Budgell, W. P., and Rey, F. 2007. Interannual variability of the Nordic Seas primary production. ICES Journal of Marine Science, 64: 889–898.

Skud, B. E. 1982. Dominance in fish: the relation between environment and abundance. Science, 216: 144–149.

Slagstad, D., and McClimans, T. A. 2005. Modeling the ecosystem dynamics of the Barents Sea including the marginal ice zone. I. Physical and chemical oceanography. Journal of Marine Systems, 58: 1–18.

Slotte, A. 1999. Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. Journal of Fish Biology, 54: 338–355.

Slotte, A., and Fiksen, Ø. 2000. State-dependent spawning migration in Norwegian spring-spawning herring. Journal of Fish Biology, 56: 138–162.

Smed, J. 1947. Monthly anomalies of the surface temperature in the sea round South Greenland during the years 1876–1939. Conseil International pour l'Exploration de la Mer, Annales Biologiques, 2 (1945–1947): 16–22.

Smed, J. 1949. The increase in the sea temperature in northern waters during recent years. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 125: 21–25.

Smith, M. M., and Heemstra, P. C. 1986. Smith's Sea Fish. Springer Verlag, South Africa.

Smith, W. G., and Morse, W. W. 1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. Marine Ecology Progress Series, 24: 1–13.

Smith-Vaniz, W. F. 1986. Carangidae. *In* Fishes of the North-eastern Atlantic and the Mediterranean, Vol. 2, pp. 815–844. UNESCO, Paris.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fish: a review. Bulletin of Marine Science, 60: 1129–1157.

Solhaug, T. 1976. De norske fiskeriers historie 1815–1880. Universitetsforlaget, Bergen.

Solic, M., Krstulovic, N., Marasovic, I., Baranovic, A., Pucher-Petkovic, T., and Vucetic, T. 1997. Analysis of time-series of planktonic communities in the Adriatic Sea: distinguishing between natural and man-induced changes. Oceanologica Acta, 20: 131–143.

Solmundsson, J., Karlsson, H., and Palsson, J. 2003. Sexual differences in spawning behaviour and catchability of plaice (*Pleuronectes platessa*) west of Iceland. Fisheries Research, 61: 57–71.

Solow, A. R. 2002. Fisheries recruitment and the North Atlantic Oscillation. Fisheries Research, 54: 295–297.

Somarakis, S., Palomera, I., Garcia, A., Quintanilla, L., Koutsikopoulos, C., Uriarte, A., and Motos, L. 2004. Daily egg production of anchovy in European waters. ICES Journal of Marine Science, 61: 944–958.

Somot, S., Sevault, F., and Deque, M. 2006. Transient climate change scenario simulation of the Mediterranean Sea of the twenty-first century using a high resolution ocean circulation model. Climate Dynamics, 27: 851–879.

Sorokin, Y. I. 2002. The Black Sea: Ecology and Oceanography. Backhuys, Leiden.

Sorteberg, A., and Kvingedal, B. 2006. Atmospheric forcing on the Barents Sea winter ice extent. Journal of Climate, 19: 4772–4784.

Southward, A. J. 1980. The western English Channel – an inconstant ecosystem? Nature, 285: 361–366.

Southward, A. J., Boalch, G. T., and Maddock, L. 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. Journal of the Marine Biological Association of the UK, 68: 423–445.

Southward, A. J., Langmead, O., Hardman-Mountford, N. J., Aiken, J., Boalch, G. T., Dando, P. R., Genner, M. J., *et al.* 2005. Long-term oceanographic and ecological research in the western English Channel. Advances in Marine Biology, 47: 1–105.

Sparholt, H. 1990. An estimate of the total biomass of fish in the North Sea. Journal du Conseil, Conseil International pour l'Exploration de la Mer, 46: 200–210.

Sparholt, H. 1996. Causal correlation between recruitment and spawning stock size of central Baltic cod? ICES Journal of Marine Science, 53: 771–779.

Stafford, R., Whittaker, C., Velterop, R., Wade, O., and Pinnegar, J. 2006. Final Report, Programme 13: North Sea Whiting Stomach Contents. Fisheries Science Partnership: 2006/07. Cefas, Lowestoft. 25 pp.

Stebbing, A. R. D., Turk, S. M. T., Wheeler, A., and Clarke, K. R. 2002. Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960–2001). Journal of the Marine Biological Association of the UK, 82: 177–180.

STECF. 2005a. Report of the STECF–SGRST Working Group on anchovy in the Bay of Biscay. Brussels, 11–14 July, 2005. European Commission, DG-Fish, Brussels.

STECF. 2005b. *Ad hoc* scientific working group on management measures for sandeel, Norway pout, anglerfish and horse mackerel in the North Sea and Skagerrak. Charlottenlund, May 2005.

Steele, J. H. 2004. Regime shifts in the ocean: reconciling observations and theory. Progress in Oceanography, 60: 135–141.

Stefánsson, U. 1954. Temperature variations in the North Icelandic coastal area. Rit Fiskideildar, 1: 1–27.

Stehmann, M. F. W., Seret, B., Costa, E. M., and Baro, J. 2008. *Neoraja iberica* n. sp., a new species of pygmy skate (Elasmobranchii, Rajidae) from the southern upper slope of the Iberian peninsula (eastern North Atlantic). Cybium, 32: 51–71.

Stenevik, E. K., and Osland, H. 2001. Timing of hatching in lesser sandeel *Ammodytes marinus* from Norwegian coastal waters based on otolith microstructure analysis. Journal of Ichthyology, 41: 313–316.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K-S., and Lima, M. 2002. Ecological effects of climate fluctuations. Science, 297: 1292–1296.

Stepputtis, D. 2006. Distribution patterns of Baltic sprat (*Sprattus sprattus* L.) – causes and consequences. PhD thesis, Leibniz Institute for Marine Research, Kiel, Germany. 198 pp.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. American Naturalist, 133: 240–256.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in species ecosystems. Ecology, 73: 747–754.

Struski, C., Petitgas, P., and Huret, M. 2009. Long-term hindcast and climate change forecast of habitat unsuitability using bioenergetics and physical-biogeochemical models: anchovy in the Bay of Biscay and the North Sea. ICES Document CM 2009/E:22.

Suding, K. N., Gross, K. L., and Houseman, G. R. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution, 19: 46–53.

Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. Sarsia, 85: 277–298.

Sundby, S., and Nakken, O. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. ICES Journal of Marine Science, 65: 953–962.

Suryan, R. M., Saba, V. S., Wallace, B. P., Hatch, S. A., Frederiksen, M., and Wanless, S. 2009. Environmental forcing on life history strategies: evidence for multi-trophic level responses at ocean basin scales. Progress in Oceanography, 81: 214–222.

Sutton, R. T., and Hodson, D. L. R. 2005. Atlantic Ocean forcing of North American and European summer climate. Science, 309: 115–118.

Svåsand, T., Jørstad, K. E., Otterå, H., and Kjesbu, O. S. 1996. Differences in growth performance between Arcto-Norwegian and Norwegian coastal cod reared under identical conditions. Journal of Fish Biology, 49: 108–119.

Svendsen, E., Skogen, M., Budgell, P., Huse, G., Stiansen, J. E., Ådlandsvik, B., Vikebø, F., *et al.* 2007. An ecosystem modelling approach to predicting cod recruitment. Deep-Sea Research II, 54: 2810–2821.

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. Journal du Conseil Permanent International pour l'Exploration de la Mer, 18: 287–295.

Svetovidov, A. N. 1948. Gadiformes. *In* Fauna of the USSR: Fishes, Vol. IX(4). Ed. by E. N. Pavlovskii and A. A. Shtakel'berg. Zoological Institute, Academy of Sciences of the USSR (in Russian). English translation (1962) by W. J. Walters and V. W. Walters. Israel Program for Scientific Translations. 304 pp.

Swaby, S. E., and Potts, G. W. 1999. The sailfin dory, a first British record. Journal of Fish Biology, 54: 1338–1340.

Swain, D. P., Sinclair, A. F., Castonguay, M., Chouinard, G. A., Drinkwater, K. F., Fanning, L. P., and Clark, D. S. 2003. Density- vs. temperature-dependent growth of Atlantic cod (*Gadus morhua*) in the Gulf of St Lawrence and on the Scotian Shelf. Fisheries Research, 59: 327–341.

Symonds, D. J., and Rogers, S. I. 1995. The influence of spawning and nursery grounds on the distribution of sole *Solea solea* (L) in the Irish Sea, Bristol Channel and adjacent areas. Journal of Experimental Marine Biology and Ecology, 190: 243–261.

Talbot, J. W. 1977. The dispersal of plaice eggs and larvae in the southern bight of the North Sea. Journal du Conseil International pour l'Exploration de la Mer, 37: 221–248.

Talbot, J. W. 1978. Changes in plaice larval dispersal in the last fifteen years. Rapports et Procès-Verbaux des Réunions du Conseil Internationale pour l'Exploration de la Mer, 172: 114–123.

Tåning, Å. V. 1953. Long term change in hydrography and fluctuations in fish stocks. Annual Proceedings of the International Commission for the Northwest Atlantic Fisheries, 3: 69–77.

Tasker, M. (Ed.) 2008. The effects of climate change on the distribution and abundance of marine species in the OSPAR Maritime Area. ICES Cooperative Research Report No. 293. 45 pp.

Taylor, A. H., Allen, J. I., and Clark, P. A. 2002. Extraction of a weak climatic signal by an ecosystem. Nature, 416: 629–632.

Teal, L. R., de Leeuw, J. J., van der Veer, H. W., and Rijnsdorp, A. D. 2008. Effects of climate change on growth of 0-group sole and plaice. Marine Ecology Progress Series, 358: 219–230.

Temming, A. 1989. Long-term changes in stock abundance of the common dab (*Limanda limanda* L.) in the Baltic Proper. Rapports et Procès-Verbaux des Réunions du Conseil Internationale pour l'Exploration de la Mer, 190: 39–50.

Temming, A., and Damm, U. 2002. Life cycle of *Crangon crangon* in the North Sea: a simulation of the timing of recruitment as a function of the seasonal temperature signal. Fisheries Oceanography, 11: 45–58.

Temming, A., Floeter, J., and Ehrich, S. 2007. Predation hot spots: large scale impact of local aggregations. Ecosystems, 10: 865–876.

Teng, H., Washington, W. M., Meehl, G. A., Buja, L. E., and Strand, G. W. 2006. Twenty-first century Arctic climate change in the CCSM3 IPCC scenario simulations. Climate Dynamics, 26: 601–616.

Thetmeyer, H., Waller, U., Kenneth, D., Black, K. D., Inselmann, S., and Rosenthal, H. 1999. Growth of European sea bass *Dicentrarchus labrax* L. under hypoxic and oscillating oxygen conditions. Aquaculture, 174: 355–367.

Thomsen, H. 1937. Variations of the surface temperature at Selvogsbanki, Iceland, during the years 1895–1936. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 105: 51–55.

Thygesen, U. H., Nilsson, F. L. A., and Andersen, K. H. 2007. Eulerian techniques for individual-based models with additive components. Journal of Marine Systems, 67: 179–188.

Tičina, V. 2000. Biology and commercial importance of sprat, *Sprattus sprattus phalericus* (L. 1758), in the Adriatic Sea. PhD thesis, University of Zagreb, Croatia. 133 pp. (in Croatian)

Tirelli, V., Borne, D., Tullis, F., Cigar, M., Fonda-Unmani, S., and Brandt, S. 2006. Energy density of anchovy *Engraulis encrasicolus* L. in the Adriatic Sea. Journal of Fish Biology, 68: 982–989.

Tomkiewicz, J., Lehman, K. M., and St John, M. A. 1998. Oceanographic influences on the distribution of Baltic cod, *Gadus morhua*, during spawning in the Bornholm Basin of the Baltic Sea. Fisheries Oceanography, 7: 48–62.

Toresen, R. 1990. Long-term changes in growth of Norwegian spring-spawning herring. Journal du Conseil International pour l'Exploration de la Mer, 47: 48–56.

Toresen, R. 2001. Spawning stock fluctuations and recruitment variability related to temperature for selected herring (*Clupea harengus*) stocks in the North Atlantic. *In* Herring:

Expectations for a New Millennium. Lowell Wakefield Fisheries Symposium Series No. 18: 315–334.

Toresen, R., and Jakobsson, J. 2002. Exploitation and management of Norwegian spring-spawning herring in the 20th century. ICES Marine Science Symposia, 215: 558–571.

Toresen, R., and Østvedt, O. J. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries, 1: 231–256.

Torstensen, E., and Gjøsæter, J. 1995. Occurrence of 0-group sprat (*Sprattus sprattus*) in the littoral zone along the Norwegian Skagerrak coast 1945–1992, compared with the occurrence of 0-group herring (*Clupea harengus*). Fisheries Research, 21: 409–421.

Tortonese, E. 1956. Leptocardia, Cyclostoma, Selachii. Fauna d'Italia 2. Calderini, Bologna. 334 pp.

Tortonese, E. 1970. Osteichthyes. Pesci ossei (parte 1). Fauna d'Italia 10. Calderini, Bologna. 565 pp.

Tortonese, E. 1975. Osteichthyes. Pesci ossei (parte 2). Fauna d'Italia 11. Calderini, Bologna. 636 pp.

Townsend, C. R., Begon, M. and Harper, J. L. 2003. Essentials of Ecology, 2nd edn. Blackwell Publishing, Malden, MA, USA. 544 pp.

Trippel, E. A. 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Transactions of the American Fisheries Society, 127: 339–359.

Tsikhon-Lukanina, E. A., Reznichenko, O. G., and Lukasheva, T. A. 1992. What ctenophore *Mnemiopsis* eats in the Black Sea inshore waters? Oceanology, Moscow, 32: 724–729.

Tsikliras, A. C. 2008. Climate-related geographic shift and sudden population increase of a small pelagic fish (*Sardinella aurita*) in the eastern Mediterranean Sea. Marine Biology Research, 4: 477–481.

Tsuchida, S. 1995. The relationship between upper temperature tolerance and final preferendum of Japanese marine fish. Journal of Thermal Biology, 20: 35–41.

Turley, C. M., Bianchi, A., Christaki, U., Harris, J. R. W., Psarra, S., Ruddy, G., Stutt, E. D., *et al.* 2000. Relationship between primary producers and bacteria in an oligotrophic sea: the Mediterranean and biogeochemical implications. Marine Ecology Progress Series, 193: 11–18.

Ueyama, R., and Monger, B. C. 2005. Wind-induced modulation of seasonal phytoplankton blooms in the North Atlantic derived from satellite observations. Limnology and Oceanography, 50: 1820–1829.

Uriarte, A., and Lucio, P. 2001. Migration of adult mackerel along the Atlantic European shelf edge from a tagging experiment in the south of the Bay of Biscay in 1994. Fisheries Research, 50: 129–139.

Uriarte, A., Prouzet, P., and Villamor, B. 1996. Bay of Biscay and Ibero Atlantic anchovy populations and their fisheries. Scientia Marina, 60(Suppl. 2): 237–255.

Valdés, L., and Lavín, A. 2002. Dynamics and human impact in the Bay of Biscay: An ecological perspective. *In* Large Marine Ecosystems of the North Atlantic, pp. 293–320. Ed. by K. Sherman and H. R. Skjoldal. Elsevier Science, Amsterdam.

Valdés, L., and Moral, M. 1998. Time-series analysis of copepod diversity and species richness in the southern Bay of Biscay off Santander, Spain, in relation to environmental conditions. ICES Journal of Marine Science, 55: 783–792.

Valenzuela, G. S., and Vargas, C. A. 2002. Comparative larval growth rate of *Sprattus sprattus* in relation to physical and biological oceanographic features in the North Sea. Archive of Fishery and Marine Research, 49: 213–230.

Valenzuela, G., Alheit, J., Coombs, S. H., and Knust, R. 1991. Spawning patterns of sprat and survival changes of sprat larvae in relation to frontal systems in the German Bight. ICES Document CM 1991/L:45.

Vallin, L., Nissling, A., and Westin, L. 1999. Potential factors influencing reproductive success of Baltic cod, *Gadus morhua*: a review. Ambio, 28: 92–99.

van Beek, F. A., Rijnsdorp, A. D., and de Clerck, R. 1989. Monitoring juvenile stocks of flatfish in the Wadden Sea and the coastal areas of the southeastern North Sea. Helgoländer Wissenschaftlichen Meeresuntersuchungen, 43: 461–477.

van Beek, F. A., van Leeuwen, P. I., and Rijnsdorp, A. D. 1990. On the survival of plaice and sole discards in the otter trawl and beam trawl fisheries in the North Sea. Netherlands Journal of Sea Research, 26: 151–160.

van Damme, C. J. G., and Couperus, A. S. 2008. Mass occurrence of snake pipefish: result of a change in climate? Journal of Sea Research, 60: 117–125.

van Damme, C. J. G., Dickey-Collas, M., Rijnsdorp, A. D., and Kjesbu, O. S. 2009. Fecundity, atresia and spawning strategies of Atlantic herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences, 66: 2130–2141.

van den Hurk, B., Klein Tank, A., Lenderink, G., van Ulden, A., van Oldenborgh, G. J., Katsman, C., van den Brink, H., *et al.* 2006. KNMI Climate Change Scenarios 2006 for the Netherlands. KNMI Scientific Report WR 2006–01, KNMI. Utrecht. 82 pp.

van der Land, M. A. 1991. Distribution of flatfish eggs in the 1989 egg surveys in the southeastern North Sea, and mortality of plaice and sole eggs. Netherlands Journal of Sea Research, 27: 277–286.

van der Meeren, T., and Ivannikov, V. P. 2006. Seasonal shift in spawning of Atlantic cod (*Gadus morhua* L.) by photoperiod manipulation: egg quality in relation to temperature and intensive larval rearing. Aquaculture Research, 37: 898–913.

van der Veer, H. W., and Witte, J. I. L. 1999. Year-class strength of plaice *Pleuronectes platessa* in the Southern Bight of the North Sea: a validation and analysis of the inverse relationship with winter seawater temperature. Marine Ecology Progress Series, 184: 245–257.

van der Veer, H. W., Pihl, L., and Bergman, M. J. N. 1990. Recruitment mechanism in North Sea plaice *Pleuronectes platessa*. Marine Ecology Progress Series, 64: 1–12.

van der Veer, H. W., Ruardij, P., van den Berg, A. J., and Ridderinkhof, H. 1998. Impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice *Pleuronectes platessa* L. in the southern North Sea. Journal of Sea Research, 39: 29–40.

van der Veer, H. W., Berghahn, R., Miller, J. M., and Rijnsdorp, A. D. 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the Flatfish Symposia. ICES Journal of Marine Science, 57: 202–215.

van der Veer, H. W., Kooijman, S. A. L. M, and van der Meer, J. 2001. Intra- and interspecies comparison of energy flow in North Atlantic flatfish species by means of dynamic energy budgets. Journal of Sea Research, 45: 303–320.

van der Veer, H. W., Cardoso, J. F. M. F., and van der Meer, J. 2006. Estimation of DEB parameters for various North Atlantic bivalve species. Journal of Sea Research, 56: 107–124.

van der Veer, H. W., Bolle, L. J., Geffen, A. J., and Witte, J. I. L. 2009. Variability in transport of fish eggs and larvae. IV. Interannual variability in larval stage duration of immigrating plaice in the Dutch Wadden Sea. Marine Ecology Progress Series, 390: 213–223.

van der Veer, H. W., Freitas, V., Cardoso, J. F. M. F., Lika, K., Campos, J., Peck, M. A., Kooijman, S. A. L. M. (In press). Temperature tolerance and energetics, a Dynamic Energy Budget-based comparison of North Atlantic marine species. Philosophical Transactions of the Royal Society.

van Haren, R. J. F., and Kooijman, S. A. L. M. 1993. Application of a dynamic energy budget model to *Mytilus edulis* (L.). Netherlands Journal of Sea Research, 31: 119–133.

van Keeken, O. A., van Hoppe, M., Grift, R. E., and Rijnsdorp, A. D. 2007. The implications of changes in the spatial distribution of juveniles for the management of North Sea plaice (*Pleuronectes platessa*). Journal of Sea Research, 57: 187–197.

Vaz, S., and Petitgas, P. 2002. Study of the Bay of Biscay anchovy population dynamics using spatialized age-specific matrix models. ICES Document CM 2002/O:07.

Velasco, F., and Olaso, I. 1998. John Dory *Zeus faber* (Linnaeus, 1758) feeding off Galicia and in the Cantabrian Sea: dietary shifts with size. Boletino del Instituto Espanol de Oceanografia, 14: 69–79.

Vilhjálmsson, H. 1997. Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century. Rit Fiskideildar, 40: 7–29.

Villamor, B., Abaunza, P., and Celso Farina, A. 2004. Growth variability of mackerel (*Scomber scombrus*) off north and northwest Spain and a comparative review of the growth patterns in the Northeast Atlantic. Fisheries Research, 69: 107–121.

Villamor, B., Abaunza, P., Petitgas, P., Massé, J., and Uriarte, A. 2007. Bay of Biscay anchovy: a resource in crisis. ICES Insight, 44: 9–10.

Vinagre, C., Costa, M. J., and Cabral, H. N. 2007. Impact of climate and hydrodynamics on sole larval immigration towards the Tagus estuary, Portugal. Estuarine, Coastal and Shelf Science, 75: 516–524.

Vinje, T. 2001. Anomalies and trends of sea-ice extent and atmospheric circulation in the Nordic Seas during the period 1864–1998. Journal of Climate, 14: 255–267.

Vinje, T., and Kvambekk, Å. 1991. Barents Sea drift ice characteristics. Polar Research, 10: 59–68.

Vinogradov, M. E. (Ed.) 1991. The Variability of the Black Sea Ecosystem: Natural and Anthropogenic Factors. Nauka, Moscow. (in Russian)

Vinogradov, M. E., and Simonov, A. I. 1989. Changes in the Black Sea ecosystem. *In* Basic modern problems of study of the World Ocean. Plenary reports of the 3rd Congress of Soviet Oceanographers, pp. 61–75. Ed. by L. M. Brekhovski. The III Conference of Soviet Oceanographers. Gydrometeoizdat, Leningrad.

Visbeck, M., Chassignet, E., Curry, R., Delworth, T., Dickson, R. R., and Krahmann, G. 2003. The ocean's response to North Atlantic Oscillation variability. *In* The North Atlantic Oscillation. pp. 113–146. Ed. by J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck. American Geophysical Union Geophysical Monograph Series, 134.

von Westernhagen, H., Dethlefsen, V., Bade, T., and Wosniok, W. 2002. Species assemblages of pelagic fish embryos in the southern North Sea between 1984 and 2000. Helgoland Marine Research, 55: 242–251.

Voss, R., Köster, F. W., and Dickmann, M. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research, 1497: 1–15.

Waede, M. 1954. Beobachtungen zur osmotischen, chemischen und thermischen Resistenz von Scholle und Flunder (*Pleuronectes platessa* und *Platichthys flesus*). Kieler Meeresforschung, 10: 58–67.

Wahl, E., and Alheit, J. 1988. Changes in the distribution and abundance of sprat eggs during spawning season. ICES Document CM 1988/H:45.

Walczowski, W., and Piechura, J. 2006. New evidence of warming propagating toward the Arctic Ocean. Geophysical Research Letters, 33, L12601: doi: 10.1029/2006GL025872.

Walker, G. T., and Bliss, E. M. 1932. World Weather V. Memoirs of the Royal Meteorological Society of London, 4 (36): 53–84.

Wallace, J. M., and Gutzler, D. S. 1981. Teleconnections in the geopotential height field during the northern hemisphere winter. Monthly Weather Review, 109: 784–812.

Wallace, W. 1924. First report on the young herring in the southern North Sea and English Channel. Part I. Distribution and growth of larval and post–larval stages. Fisheries Investigations, Series II, 7: 1–73.

Walsh, M., Reid, D. G., and Turrell, W. R. 1995. Understanding mackerel migration off Scotland: tracking with echosounders and commercial data, and including environmental correlates and behaviour. ICES Journal of Marine Science, 52: 925–939.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., *et al.* 2002. Ecological responses to recent climate change. Nature, 416: 389–395.

Wanless, S., Wright, P. J., Harris, M. P., and Elston, D. A. 2004. Evidence for a decrease in the size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-year period. Marine Ecology Progress Series, 279: 237–246.

Ware, D. M., and Thomson, R. E. T. 2005. Bottom–up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science, 308: 1280–1284.

Wasmund, N., and Uhlig, S. 2003. Phytoplankton trends in the Baltic Sea. ICES Journal of Marine Science, 60: 177–186.

Wasmund, N., Nausch, G., and Matthäus, W. 1998. Phytoplankton spring blooms in the southern Baltic Sea – spatio-temporal development and long-term trends. Journal of Plankton Research, 20: 1099–1117.

Wassmann, P., Slagstad, D., Riser, C. W., and Reigstad, M. 2006. Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone: II. Carbon flux and interannual variability. Journal of Marine Systems, 59: 1–24.

Watermeyer, K. E., Shannon, L. J., and Griffiths, C. L. 2008. Changes in the trophic structure of the southern Benguella before and after the onset of industrial fishing. African Journal of Marine Science, 30: 351–382.

Weijerman, M., Lindeboom, H. J., and Zuur, A. F. 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. Marine Ecology Progress Series, 298: 21–39.

Welleman, H. C., and Daan, N. 2001. Is the Dutch shrimp fishery sustainable? Senckenbergiana Maritima, 31: 321–328.

Wetsteijn, B. 1981. Feeding of North Sea turbot and brill. ICES Document CM 1981/G:74. 18 pp.

Wheeler, A. 1969. The Fish of the British Isles and North-west Europe. Michigan State University Press. 613 pp.

Wheeler, A. 1978. Key to the Fish of Northern Europe. Frederick Warne, London. 380 pp.

Wheeler, A. C. 1992. A list of the common and scientific names of fishes of the British Isles. Journal of Fish Biology, 41(Suppl. A): 1–37.

Wheeler, A. C., Merrett, N. R., and Quigley, D. T. G. 2004. Additional records and notes for Wheeler's (1992) List of the common and scientific names of fishes of the British Isles. Journal of Fish Biology, 65(Suppl. B): 1–40.

Whitehead, P. J. P. 1985. FAO species catalogue. Vol. 7 Clupeoid fishes of the world. An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 1 Chirocentridae, Clupeidae and Pristigasteridae. FAO Fisheries Synopsis No. 125, 7(1): 303 pp.

Whitehead, P. J. P., Bauchot, M. L., Hureau, J-C., Nielsen, J., and Tortonese, E. (Eds). 1984–1986. Fishes of the North-eastern Atlantic and the Mediterranean. Vol. I–III. UNESCO, Paris. 1473 pp.

Whittames, E. R., Walker, M. G., Dinis, M. T., and Whiting, C. L., 1995. The geographical variation in the potential annual fecundity of Dover sole *Solea solea* (L.) from European shelf waters during 1991. Netherlands Journal of Sea Research, 34: 45–58.

Wieland, K., and Zuzarte, F. 1991. Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987–1990. ICES Document CM 1991/J:31.

Wieland, K., Waller, U., and Schnack, D. 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana, 10: 163–177.

Wieland, K., Storr-Paulsen, M., and Sünksen, K. 2006. Fishery and environmental aspects relevant for the decline and recovery of the Atlantic cod (*Gadus morhua*) stock in Greenland offshore waters. *In* Report of the Workshop on the Decline and Recovery of Cod Stocks throughout the North Atlantic, Including Tropho-dynamic Effects (WKDRCS), 9–12 May 2006, St John's, Canada. ICES Document CM 2006/OCC: 12. 35 pp.

Wilderbuer, T. K., Hollowed, A. B., Ingraham, W. J., Spencer, P. D., Conners, M. E., Bond, N. A., and Walters, G. E. 2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. Progress in Oceanography, 55: 235–247.

Willmer, P., Stone, G., and Johnston, I. A. 2000. Environmental Physiology of Animals. Blackwell Scientific Publications, Oxford.

Wiltshire, K. H., and Manly, B. F. J. 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. Helgoland Marine Research, 58: 269–273.

Wimpenny, R. S. 1953. The Plaice. Arnold, London. 145 pp.

Winberg, G. G. 1956. Intensivnost obmena I pishchevye potrebnosti ryb. Nauchnye Trudy Belorusskovo Gosudarstvennovo Universiteta imeni V. I. Lenina, Minsk. 243 pp. (Rate of metabolism and food requirements of fish). Fisheries Research Board of Canada Translation Series No. 194(1), 1960.

Winger, P. D. 2005. Effect of environmental conditions on the natural activity rhythms and bottom trawl catchability of Atlantic cod (*Gadus morhua*). Dissertation Abstracts International Part B: Science and Engineering, 66: 153.

Winslade, P. 1971. Behavioural and embryological studies on the lesser sandeel *Ammodytes marinus* (Raitt). PhD thesis. University of East Anglia, UK.

Winslade, P. 1974a. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) I. The effect of food availability on activity and the role of olfaction in food detection. Journal of Fish Biology, 6: 565–576.

Winslade P. 1974b. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) II. The effect of light intensity on activity. Journal of Fish Biology, 6: 577–586.

Winslade, P. 1974c. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) III. The effect of temperature on activity and the environmental control of the annual cycle of activity. Journal of Fish Biology, 6: 587–599.

Winters, G. H., and Wheeler, J. P. 1987. Recruitment dynamics of spring-spawning herring in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 44: 882–900.

Winters, G. H., and Wheeler, J. P. 1996. Environmental and phenotypic factors affecting the reproductive cycle of Atlantic herring. ICES Journal of Marine Science, 53: 73–88.

Winther, N. G., and Johannessen, J. A. 2006. North Sea circulation: Atlantic inflow and its destination. Journal of Geophysical Research, 111, C12018, doi:10.1029/2005JC003310.

Wirszubski, A. 1953. On the biology and biotope of the red mullet, *Mullus barbatus* L. Bulletin of the Sea Fisheries Research Station, Caesarea, 7: 1–20.

Witthames, P. R., Greer Walker, M., Dinis, M. T., and Whiting, C. L. 1995. The geographical variation in the potential annual fecundity of Dover sole *Solea solea* (L.) from European shelf waters during 1991. Netherlands Journal of Sea Research, 34: 45–58.

Woehrling, D., Lefebvre, A., Le Fevre-Lehorff, G., and Delesmont, R. 2005. Seasonal and longer term trends in sea temperature along the French North Sea coast 1975 to 2002. Journal of the Marine Biological Association of the UK, 85: 39–48.

Woillez, M., Petitgas, P., and Huret, M. 2009. Environmental monitoring using biophysical models and statistical detection procedures: application to the Bay of Biscay. Working Document to the ICES Benchmark Workshop on Short-Lived Species (WKSHORT), 31 August–4 September 2009, Institute of Marine Research, Bergen, Norway.

Wollebaek, A. 1908. Remarks on decapod crustaceans of the North Atlantic and Norwegian fjords (I and II). Bergens Museums Aarbok, 12: 1–77.

Woodhead, P. J. M. 1964a. The death of North Sea fish during the winter of 1962/63 particularly with reference to the sole, *Solea vulgaris*. Helgoländer Wissenschaftlichen Meeresuntersuchungen, 10: 283–300.

Woodhead, P. J. M. 1964b. The death of fish and sublittoral fauna in the North Sea and the English Channel during the winter of 1963. Journal of Animal Ecology, 33: 169–173.

Woodhead, P. J. M. 1964c. Changes in the behaviour of the sole, *Solea vulgaris*, during cold winters and the relation between the winter catch and sea temperature. Helgoländer Wissenschaftlichen Meeresuntersuchungen, 10: 328–342.

Worm, B., and Myers, R. A. 2003. Meta-analysis of cod-shrimp interactions reveals top–down control in oceanic food webs. Ecology, 84: 162–173.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., *et al.* 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 314: 787–790.

Wright, P., Verspoor, E., Andersen, C., Donald, L., Kennedy, F., Mitchell, A., Munk, P., *et al.* 1998. Population structure in the lesser sandeel (*Ammodytes marinus*) and its implications for fishery-predator interactions. DG XIV Contract No. 94/071, Final Report October 1998.

Wright, P. J., and Bailey, M. C. 1996. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. Marine Biology, 126: 143–152.

Wright, P. J., and Tasker, M. L. 1996. Analysis of fish consumption by seabirds by age class of prey fish. *In* Seabird/fish interactions, with particular reference to seabirds in the North Sea, pp. 42–44. Ed. by G. L. Hunt and R. W. Furness. ICES Cooperative Research Report No. 216. 87 pp.

Wright, P. J., Jensen, H., and Tuck, I. 2000. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. Journal of Sea Research, 44: 243–256.

Wright, P. J., Neat, F. C., Gibb, F. M., and Gibb, I. M. 2006. Evidence for metapopulation substructuring in cod from the West of Scotland and North Sea. Journal of Fish Biology, 69(Suppl. C): 181–199.

Yamahira, K., and Conover, D. O. 2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality. Ecology, 83: 1252–1262.

Yamahira, K., and Takeshi, K. 2008. Variation in juvenile growth rates among and within latitudinal populations of the medaka. Population Ecology, 50: 3–8.

Yamashita, Y., Tanaka, M., and Miller, J. M. 2001. Ecophysiology of juvenile flatfish in nursery grounds. Journal of Sea Research, 45: 205–218.

Yang, J. 1982a. The dominant fish fauna in the North Sea and its determination. Journal of Fish Biology, 20: 635–643.

Yang, J. 1982b. An estimate of the fish biomass in the North Sea. Journal du Conseil International pour l'Exploration de la Mer, 40: 161–172.

Yang, J. 1982c. A tentative analysis of the trophic levels of North Sea fish. Marine Ecology Progress Series, 7: 247–252.

Yarrell, W. 1836. A History of British Fish. John Van Voorst, London. 472 pp.

Yin, K. D., Harrison, P. J., Chen, J., Huang, W., and Qian, P. Y. 1999. Red tides during spring 1998 in Hong Kong: is *El Niño* responsible? Marine Ecology Progress Series, 187: 289–294.

Young, E. F., and Holt, J. T. 2007. Prediction and analysis of long-term variability of temperature and salinity in the Irish Sea. Journal of Geophysical Research, 112, C01008, doi: 10.1029/2005JC003386.

Yunev, O. A., Vedernikov, V. I., Basturk, O., Yilmaz, A., Kideys, A. E., Moncheva, S., and Konovalov, S. K. 2002. Long-term variations of surface chlorophyll *a* and primary production in the open Black Sea. Marine Ecology Progress Series, 230: 11–28.

Zaitsev, Yu. 1993. Impact of eutrophication on the Black Sea fauna. General Fisheries Commission for the Mediterranean, Studies and Reviews, 64: 63–86.

Zaitsev, Yu., and Mamaev, V. 1997. Marine biological diversity in the Black Sea: a study of change and decline. Black Sea Environmental Publications No. 3, UN Publications, New York. 208 pp.

Zakhartsev, M. V., De Wachter, B., Sartoris, F. J., Pörtner, H. O., and Blust, R. 2003. Thermal physiology of the common eelpout (*Zoarces viviparus*). Journal of Comparative Physiology, 173B: 365–378.

Zeller, D., and Reinert, J. 2004. Modelling spatial closures and fishing effort restrictions in the Faroe Islands marine ecosystem. Ecological Modelling, 172: 403–420.

Zengin, M. 2003. The current status of Turkey's Black Sea fisheries and suggestions on the use of those fisheries. Workshop on Responsible Fisheries in the Black Sea and Azov Sea and Evaluation of Demersal Fish Resources. Black Sea Ecosystem Recovery Project, 15–17/4, Istanbul, Turkey. Available online at http://www.blacksea-environment.org/text/default.htm.

Zenkevich, L. A. 1963. Biology of Seas of the USSR. Academy of Sciences of the USSR, Moscow. 739 pp. (in Russian)

Zheng, J. 1996. Herring stock–recruitment relationship and recruitment patterns in the North Atlantic and Northeast Pacific oceans. Fisheries Research, 26: 257–277.

Zijlstra, J. J. 1958. On the herring races spawning in the southern North Sea and English Channel. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 143: 134–145.

Zupanovic, S. 1968. O uzrocima fluktuacija u lovinama srdele na istocnoj obali jadrana. [The causes of fluctuations in sardine catches along the eastern Adriatic coast.] Anali Jadranskog Instituta, 4: 401–491.

Zuur, A. F., Tuck, I. D., and Bailey, N. 2003. Dynamic common factor analysis to estimate common trends in fisheries time-series. Canadian Journal of Fisheries and Aquatic Sciences, 60: 542–552.

Annex 1. Ecotypes of North Sea fish

Taxonomic list of fish recorded from or about the North Sea, including their biogeographical affinities, reproductive mode, maximum length, trophic guild, trophic level (from FishBase), and habitat type. For references, see Section 25.

Family	**Species**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Petromyzontidae	*Lampetra fluviatilis*	River lamprey	Boreal	Fluvial spawner	45	Ectoparasite	4.5	Coastal	Demersal	Yang (1982a)
Petromyzontidae	*Petromyzon marinus*	Sea lamprey	Boreal	Fluvial spawner	120	Ectoparasite	4.4	Shelf	Demersal	Yang (1982a)
Myxinidae	*Myxine glutinosa*	Hagfish	Atlantic	Demersal eggs	45	Scavenger	3.5	Shelf	Demersal	Yang (1982a)
Hexanchidae	*Hexanchus griseus*	Six-gilled shark	Atlantic	Viviparous	500	Piscivore	4.3	Slope	Bathydemersal	Yang (1982a)
Alopiidae	*Alopias vulpinus*	Thresher shark	Atlantic	Viviparous	560	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Cetorhinidae	*Cetorhinus maximus*	Basking shark	Atlantic	Viviparous	980	Planktivore	3.2	Shelf	Epipelagic	Yang (1982a)
Lamnidae	*Isurus oxyrinchus*	Short-fin mako shark	Atlantic	Viviparous	400	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Lamnidae	*Lamna nasus*	Porbeagle shark	Atlantic	Viviparous	370	Piscivore	4.5	Shelf	Epipelagic	Yang (1982a)
Scyliorhinidae	*Galeus melastomus*	Black-mouthed dogfish	Lusitanian	Demersal eggs	90	Bentho-piscivore	4.2	Slope	Bathydemersal	Yang (1982a)
Scyliorhinidae	*Scyliorhinus canicula*	Lesser spotted dogfish	Lusitanian	Demersal eggs	80	Bentho-piscivore	3.7	Inner shelf	Demersal	Yang (1982a)
Scyliorhinidae	*Scyliorhinus stellaris*	Nurse hound	Lusitanian	Demersal eggs	162	Piscivore	4.0	Inner shelf	Reef-associated	Yang (1982a)
Triakidae	*Galeorhinus galeus*	Tope shark	Lusitanian	Viviparous	200	Piscivore	4.2	Shelf	Benthopelagic	Yang (1982a)
Triakidae	*Mustelus asterias*	Starry smooth hound	Lusitanian	Viviparous	140	Carcinophage	3.7	Shelf	Demersal	Yang (1982a)
Triakidae	*Mustelus mustelus*	Smooth hound	Lusitanian	Viviparous	150	Carcinophage	3.8	Shelf	Demersal	Yang (1982a)
Carcharhinidae	*Carcharhinus longimanus*	Oceanic white-tip shark	Atlantic	Viviparous	350	Piscivore	4.2	Oceanic	Epipelagic	One vagrant [1]
Carcharhinidae	*Prionace glauca*	Blue shark	Atlantic	Viviparous	383	Piscivore	4.2	Oceanic	Epipelagic	Yang (1982a)
Sphyrnidae	*Sphyrna zygaena*	Common hammerhead	Atlantic	Viviparous	400	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Dalatiidae	*Dalatias licha*	Darkie charlie	Atlantic	Viviparous	180	Piscivore	4.2	Slope	Bathydemersal	Yang (1982a)
Dalatiidae	*Etmopterus spinax*	Velvet belly	Atlantic	Viviparous	45	Piscivore	3.8	Slope	Bathydemersal	Yang (1982a)
Dalatiidae	*Somniosus microcephalus*	Greenland shark	Boreal	Viviparous	650	Piscivore	4.2	Slope	Benthopelagic	Yang (1982a)

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[1] One specimen washed ashore in Sweden, 2004.

Family	**Species**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} (cm)	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Squalidae	*Squalus acanthias*	Spurdog	Boreal	Viviparous	105	Piscivore	4.3	Shelf	Benthopelagic	Yang (1982a)
Echinorhinidae	*Echinorhinus brucus*	Bramble shark	Atlantic	Viviparous	250	Piscivore	4.4	Slope	Bathydemersal	Compagno (1984)
Squatinidae	*Squatina squatina*	Angel shark	Lusitanian	Viviparous	250	Piscivore	4.1	Inner shelf	Demersal	Yang (1982a)
Torpedinidae	*Torpedo marmorata*	Marbled electric ray	Lusitanian	Viviparous	60	Piscivore	4.5	Shelf	Demersal	Yang (1982a)
Torpedinidae	*Torpedo nobiliana*	Common electric ray	Lusitanian	Viviparous	180	Piscivore	4.5	Shelf	Demersal	Yang (1982a)
Rajidae	*Amblyraja radiata*	Starry ray	Boreal	Demersal eggs	90	Piscivore	4.0	Shelf	Demersal	Yang (1982a)
Rajidae	*Dipturus batis*	Common skate	Boreal	Demersal eggs	250	Piscivore	4.0	Shelf	Demersal	Yang (1982a)
Rajidae	*Dipturus linteus*	Sail ray	Boreal	Demersal eggs	110	Benthivore	3.5	Slope	Demersal	Laverack and Blackler (1974)
Rajidae	*Dipturus nidarosiensis*	Black skate	Boreal	Demersal eggs	200	Piscivore	3.5	Slope	Bathydemersal	Yang (1982a)
Rajidae	*Dipturus oxyrinchus*	Long-nosed skate	Lusitanian	Demersal eggs	150	Piscivore	3.5	Slope	Bathydemersal	Yang (1982a)
Rajidae	*Leucoraja circularis*	Sandy ray	Lusitanian	Demersal eggs	120	Piscivore	3.5	Outer shelf	Demersal	Yang (1982a)
Rajidae	*Leucoraja fullonica*	Shagreen ray	Boreal	Demersal eggs	100	Piscivore	3.5	Outer shelf	Demersal	Yang (1982a)
Rajidae	*Leucoraja naevus*	Cuckoo ray	Lusitanian	Demersal eggs	70	Piscivore	3.9	Shelf	Demersal	Yang (1982a)
Rajidae	*Raja brachyura*	Blonde ray	Lusitanian	Demersal eggs	120	Piscivore	4.0	Inner shelf	Demersal	Yang (1982a)
Rajidae	*Raja clavata*	Thornback ray	Lusitanian	Demersal eggs	90	Bentho-piscivore	3.8	Inner shelf	Demersal	Yang (1982a)
Rajidae	*Raja microocellata*	Small-eyed ray	Lusitanian	Demersal eggs	80	Piscivore	3.9	Inner shelf	Demersal	Yang (1982a)
Rajidae	*Raja montagui*	Spotted ray	Lusitanian	Demersal eggs	80	Bentho-piscivore	3.7	Inner shelf	Demersal	Yang (1982a)
Rajidae	*Raja undulata*	Undulate ray	Lusitanian	Demersal eggs	100	Bentho-piscivore	3.5	Inner shelf	Demersal	Yang (1982a)
Rajidae	*Rajella fyllae*	Round skate	Boreal	Demersal eggs	55	Bentho-piscivore	3.3	Slope	Bathydemersal	Yang (1982a)
Myliobatidae	*Myliobatis aquila*	Eagle ray	Lusitanian	Viviparous	83 [2]	Benthivore	3.6	Shelf	Benthopelagic	Yang (1982a)
Dasyatidae	*Dasyatis pastinaca*	Sting ray	Lusitanian	Viviparous	60 [2]	Bentho-piscivore	4.1	Shelf	Demersal	Yang (1982a)
Dasyatidae	*Pteroplatytrygon violacea*	Pelagic sting ray	Atlantic	Viviparous	80 [2]	Piscivore	4.4	Oceanic	Epipelagic	Ellis (2007)
Chimaeridae	*Chimaera monstrosa*	Rabbitfish	Atlantic	Demersal eggs	100	Benthivore	3.5	Slope	Bathydemersal	Yang (1982a)
Acipenseridae	*Acipenser sturio*	Sturgeon	Lusitanian	Fluvial spawner	350	Benthivore	3.5	Coastal	Demersal	Yang (1982a)
Anguillidae	*Anguilla anguilla*	European eel	Atlantic	Leptocephalus larvae	100	Bentho-piscivore	3.5	Coastal	Demersal	Yang (1982a)

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[2] Disc width.

Family	**Species**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	**L_{MAX} (cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Muraenidae	*Muraena helena*	Moray eel	Lusitanian	Leptocephalus larvae	130	Piscivore	4.2	Coastal	Reef-associated	Yang (1982a)
Congridae	*Conger conger*	Conger eel	Lusitanian	Leptocephalus larvae	300	Piscivore	4.3	Shelf	Reef-associated	Yang (1982a)
Clupeidae	*Alosa alosa*	Allis shad	Lusitanian	Fluvial spawner	70	Planktivore	3.6	Shelf	Pelagic	Yang (1982a)
Clupeidae	*Alosa fallax*	Twaite shad	Lusitanian	Fluvial spawner	50	Planktivore	3.6	Shelf	Pelagic	Yang (1982a)
Clupeidae	*Clupea harengus*	Herring	Boreal	Demersal eggs	40	Planktivore	3.2	Shelf	Benthopelagic	Yang (1982a)
Clupeidae	*Sardina pilchardus*	Pilchard	Lusitanian	Planktonic eggs	25	Planktivore	2.6	Shelf	Pelagic	Yang (1982a)
Clupeidae	*Sprattus sprattus*	Sprat	Lusitanian	Planktonic eggs	16	Planktivore	3.0	Shelf	Pelagic	Yang (1982a)
Engraulidae	*Engraulis encrasicolus*	European anchovy	Lusitanian	Planktonic eggs	20	Planktivore	3.1	Shelf	Pelagic	Yang (1982a)
Argentinidae	*Argentina silus*	Great silversmelt	Boreal	Planktonic eggs	60	Planktivore	3.3	Slope	Benthopelagic	Yang (1982a)
Argentinidae	*Argentina sphyraena*	Lesser silversmelt	Lusitanian	Planktonic eggs	32	Planktivore	3.6	Shelf	Benthopelagic	Yang (1982a)
Osmeridae	*Osmerus eperlanus*	Smelt	Boreal	Demersal eggs	45	Benthivore	3.1	Coastal	Pelagic	Yang (1982a)
Osmeridae	*Mallotus villosus*	Capelin	Boreal	Demersal eggs	22	Planktivore	3.1	Inner shelf	Pelagic	Yang (1982a)
Salmonidae	*Coregonus oxyrinchus*	Houting	Boreal	Fluvial spawner	57	Planktivore	3.3	Coastal	Demersal	Yang (1982a)
Salmonidae	*Salmo salar*	Atlantic salmon	Atlantic	Fluvial spawner	150	Piscivore	4.4	Inner shelf	Pelagic	Yang (1982a)
Salmonidae	*Salmo trutta*	Trout	Boreal	Fluvial spawner	140	Piscivore	3.2	Inner shelf	Pelagic	Yang (1982a)
Salmonidae	*Salvelinus alpinus*	Charr	Boreal	Fluvial spawner	88	Piscivore	4.3	Coastal	Benthopelagic	Yang (1982a)
Sternoptychidae	*Argyropelecus olfersi*	Hatchetfish	Atlantic	Planktonic eggs	7	Planktivore	3.4	Slope	Bathypelagic	Yang (1982a)
Sternoptychidae	*Maurolicus muelleri*	Pearlside	Atlantic	Planktonic eggs	7	Planktivore	3.0	Slope	Bathypelagic	Yang (1982a)
Myctophidae	*Myctophum punctatum*	Spotted lanternfish	Atlantic	Planktonic eggs	11	Planktivore	3.4	Slope	Bathypelagic	FishBase (2007)
Nemichthyidae	*Nemichthys scolopaceus*	Slender snipe eel	Atlantic	Leptocephalus larvae	130	Planktivore	3.5	Slope	Bathypelagic	FishBase (2007)
Paralepididae	*Paralepis coregonoides*	Sharpchin barracudina	Atlantic	Planktonic eggs	30	Piscivore	4.5	Oceanic	Mesopelagic	FishBase (2007)
Gadidae (Gadinae)	*Gadiculus argenteus*	Silvery pout	Lusitanian	Planktonic eggs	15	Planktivore	3.5	Slope	Pelagic	Yang (1982a)
Gadidae (Gadinae)	*Gadus morhua*	Cod	Boreal	Planktonic eggs	190	Piscivore	4.4	Shelf	Demersal	Yang (1982a)
Gadidae (Gadinae)	*Melanogrammus aeglefinus*	Haddock	Boreal	Planktonic eggs	112	Benthivore	4.1	Shelf	Demersal	Yang (1982a)
Gadidae (Gadinae)	*Merlangius merlangus*	Whiting	Lusitanian	Planktonic eggs	70	Piscivore	4.4	Shelf	Demersal	Yang (1982a)
Gadidae (Gadinae)	*Micromesistius poutassou*	Blue whiting	Atlantic	Planktonic eggs	47	Planktivore	4.0	Slope	Mesopelagic	Yang (1982a)
Gadidae (Gadinae)	*Pollachius pollachius*	Pollack	Boreal	Planktonic eggs	130	Piscivore	4.2	Shelf	Demersal	Yang (1982a)
Gadidae (Gadinae)	*Pollachius virens*	Saithe	Boreal	Planktonic eggs	120	Piscivore	4.4	Shelf	Demersal	Yang (1982a)
Gadidae (Gadinae)	*Trisopterus esmarkii*	Norway pout	Boreal	Planktonic eggs	26	Bentho-piscivore	3.2	Outer shelf	Benthopelagic	Yang (1982a)
Gadidae (Gadinae)	*Trisopterus luscus*	Bib	Lusitanian	Planktonic eggs	45	Benthivore	3.7	Inner shelf	Demersal	Yang (1982a)
Gadidae (Gadinae)	*Trisopterus minutus*	Poor cod	Lusitanian	Planktonic eggs	26	Benthivore	3.8	Shelf	Demersal	Yang (1982a)

Family	**Species**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} (cm)	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Gadidae (Lotinae)	*Brosme brosme*	Tusk	Boreal	Planktonic eggs	100	Benthivore	4.0	Outer shelf	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Ciliata mustela*	Five-bearded rockling	Boreal	Planktonic eggs	45	Benthivore	3.5	Shelf	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Ciliata septentrionalis*	Northern rockling	Boreal	Planktonic eggs	17	Benthivore	3.5	Shelf	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Enchelyopus cimbrius*	Four-bearded rockling	Boreal	Planktonic eggs	41	Benthivore	3.5	Shelf	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Gaidropsarus macrophthalmus*	Big-eyed rockling	Lusitanian	Planktonic eggs	10	Benthivore	3.5	Outer shelf	Demersal	Uncertain[3]
Gadidae (Lotinae)	*Gaidropsarus mediterraneus*	Shore rockling	Lusitanian	Planktonic eggs	25	Benthivore	3.4	Shelf	Demersal	Wheeler (1978)
Gadidae (Lotinae)	*Gaidropsarus vulgaris*	Three-bearded rockling	Lusitanian	Planktonic eggs	43	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Molva dypterygia*	Blue ling	Boreal	Planktonic eggs	130	Piscivore	4.5	Slope	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Molva molva*	Common ling	Boreal	Planktonic eggs	200	Piscivore	4.3	Slope	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Phycis blennoides*	Greater forkbeard	Lusitanian	Planktonic eggs	75	Bentho-piscivore	3.7	Outer shelf	Demersal	Yang (1982a)
Gadidae (Lotinae)	*Raniceps raninus*	Tadpolefish	Boreal	Planktonic eggs	30	Benthivore	3.8	Inner shelf	Demersal	Yang (1982a)
Merlucciidae	*Merluccius merluccius*	European hake	Lusitanian	Planktonic eggs	120	Piscivore	4.4	Shelf	Demersal	Yang (1982a)
Macrouridae	*Caelorinchus caelorhincus*	Hollow-nosed rattail	Atlantic	Planktonic eggs	38	Benthivore	3.6	Slope	Bathydemersal	Yang (1982a)
Macrouridae	*Coryphaenoides rupestris*	Round-head rattail	Boreal	Planktonic eggs	150	Benthivore	3.5	Slope	Bathydemersal	Yang (1982a)
Macrouridae	*Macrourus berglax*	Rough rattail	Boreal	Planktonic eggs	100	Benthivore	4.5	Slope	Bathydemersal	Yang (1982a)
Macrouridae	*Malacocephalus laevis*	Soft-head rattail	Atlantic	Planktonic eggs	50	Benthivore	4.2	Slope	Bathydemersal	Wheeler (1978)
Carapidae	*Echiodon drummondii*	Pearlfish	Lusitanian	Planktonic eggs (?)	30	Piscivore	4.0	Slope	Bathydemersal	Yang (1982a)
Lophiidae	*Lophius budegassa*	Black-bellied anglerfish	Lusitanian	Planktonic eggs (rafts)	100	Piscivore	4.5	Outer shelf	Bathydemersal	Muus *et al.* (1998)
Lophiidae	*Lophius piscatorius*	Anglerfish	Lusitanian	Planktonic eggs (rafts)	200	Piscivore	4.4	Shelf	Demersal	Yang (1982a)
Gobiesocidae	*Apletodon microcephalus*	Small-headed clingfish	Lusitanian	Demersal eggs	4	Benthivore	3.1	Coastal	Demersal	Foster-Smith (2000)
Gobiesocidae	*Diplecogaster bimaculata*	Two-spotted clingfish	Lusitanian	Demersal eggs	4	Benthivore	3.3	Inner shelf	Demersal	Yang (1982a)
Gobiesocidae	*Lepadogaster lepadogaster*	Shore clingfish	Lusitanian	Demersal eggs	6.5	Benthivore	3.3	Coastal	Demersal	Harding and Nichols (1987)[4]

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[3] Distributed along the edge of the continental shelf of the Celtic Seas eco-region, the distribution may extend to the northwestern North Sea.

[4] Larvae recorded in plankton samples.

Family	**Species**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	**L_{MAX} (cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Exocoetidae	*Cypselurus heterurus*	Atlantic flyingfish	Atlantic	Attached eggs	34	Planktivore	3.4	Oceanic	Epipelagic	Yang (1982a)
Belonidae	*Belone belone*	Garfish	Lusitanian	Attached eggs	90	Piscivore	4.2	Shelf	Epipelagic	Yang (1982a)
Scomberesocidae	*Scomberesox saurus*	Saurey pike	Atlantic	Planktonic eggs	45	Planktivore	3.6	Oceanic	Epipelagic	Yang (1982a)
Atherinidae	*Atherina boyeri*	Big-scale sandsmelt	Lusitanian	Attached eggs	13	Benthivore	2.3	Coastal	Pelagic	Yang (1982a)
Atherinidae	*Atherina presbyter*	Sandsmelt	Lusitanian	Attached eggs	20	Benthivore	3.7	Coastal	Pelagic	Yang (1982a)
Lampridae	*Lampris guttatus*	Opah	Atlantic	Planktonic eggs	185	Piscivore	4.2	Oceanic	Epipelagic	Yang (1982a)
Trachipteridae	*Trachipterus arcticus*	Dealfish	Atlantic	Planktonic eggs	250	Piscivore	4.5	Oceanic	Mesopelagic	Yang (1982a)
Regalecidae	*Regalecus glesne*	Ribbonfish	Atlantic	Planktonic eggs	700	Planktivore	3.2	Oceanic	Mesopelagic	Yang (1982a)
Berycidae	*Beryx decadactylus*	Beryx	Atlantic	Planktonic eggs	40	Piscivore	4.1	Slope	Bathydemersal	Yang (1982a)
Zeidae	*Zeus faber*	John dory	Lusitanian	Planktonic eggs	66	Piscivore	4.5	Shelf	Benthopelagic	Yang (1982a)
Caproidae	*Capros aper*	Boarfish	Lusitanian	Planktonic eggs	16	Planktivore	3.1	Slope	Bathydemersal	Yang (1982a)
Gasterosteidae	*Gasterosteus aculeatus*	Three-spined stickleback	Boreal	Nest-forming	8	Benthivore	3.5	Coastal	Demersal	Yang (1982a)
Gasterosteidae	*Spinachia spinachia*	Sea stickleback	Boreal	Nest-forming	22	Benthivore	3.5	Coastal	Demersal	Yang (1982a)
Centriscidae	*Macroramphosus scolopax*	Snipefish	Lusitanian	Planktonic eggs	20	Planktivore	3.5	Slope	Bathydemersal	Yang (1982a)
Syngnathidae	*Entelurus aequoreus*	Snake pipefish	Lusitanian	Egg brooder	60	Planktivore	3.5	Oceanic/shelf	Pelagic	Yang (1982a)
Syngnathidae	*Hippocampus guttulatus*	Sea horse	Lusitanian	Egg brooder	16	Planktivore	3.5	Coastal	Demersal	Yang (1982a)
Syngnathidae	*Hippocampus hippocampus*	Short-snouted sea horse	Lusitanian	Egg brooder	16	Planktivore	3.2	Coastal	Demersal	Pinnegar *et al.* (2008)
Syngnathidae	*Nerophis lumbriciformis*	Worm pipefish	Lusitanian	Egg brooder	17	Planktivore	4.0	Coastal	Demersal	Yang (1982a)
Syngnathidae	*Nerophis ophidion*	Straight-nosed pipefish	Lusitanian	Egg brooder	30	Planktivore	4.0	Coastal	Demersal	Yang (1982a)
Syngnathidae	*Syngnathus acus*	Great pipefish	Lusitanian	Egg brooder	46	Planktivore	3.4	Coastal	Demersal	Yang (1982a)
Syngnathidae	*Syngnathus rostellatus*	Nilsson's pipefish	Lusitanian	Egg brooder	17	Planktivore	3.7	Coastal	Demersal	Yang (1982a)
Syngnathidae	*Syngnathus typhle*	Deep-snouted pipefish	Lusitanian	Egg brooder	35	Planktivore	4.3	Coastal	Demersal	Yang (1982a)
Sebastidae	*Helicolenus dactylopterus*	Blue-mouth redfish	Atlantic	Viviparous	44	Bentho-piscivore	3.8	Slope	Bathydemersal	Yang (1982a)
Sebastidae	*Scorpaena scrofa*	Red scorpionfish	Lusitanian	Planktonic eggs	50	Piscivore	4.3	Slope	Bathydemersal	Uncertain [5]
Sebastidae	*Sebastes norvegicus* (=*S. marinus*)	Redfish	Boreal	Viviparous	100	Plankto-piscivore	4.0	Slope	Pelagic	Yang (1982a)
Sebastidae	*Sebastes viviparus*	Norway haddock	Boreal	Viviparous	35	Piscivore	4.0	Slope	Demersal	Yang (1982a)

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[5] Distributed along the edge of the continental shelf of the Celtic Seas eco-region, the distribution may extend to the northwestern North Sea.

Family	Species	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)	Source
Triglidae	*Aspitrigla cuculus*	Red gurnard	Lusitanian	Planktonic eggs	50	Benthivore	3.8	Shelf	Demersal	Yang (1982a)
Triglidae	*Eutrigla gurnardus*	Grey gurnard	Lusitanian	Planktonic eggs	50	Benthivore	3.6	Shelf	Demersal	Yang (1982a)
Triglidae	*Trigla lucerna*	Tub gurnard	Lusitanian	Planktonic eggs	75	Benthivore	3.7	Shelf	Demersal	Yang (1982a)
Triglidae	*Trigla lyra*	Piper	Lusitanian	Planktonic eggs	60	Benthivore	3.5	Outer shelf	Bathydemersal	Yang (1982a)
Triglidae	*Trigloporus lastoviza*	Streaked gurnard	Lusitanian	Planktonic eggs	40	Benthivore	3.4	Shelf	Demersal	Yang (1982a)
Cottidae	*Artediellus atlanticus*	Atlantic hook-ear sculpin	Boreal	Demersal eggs	13	Benthivore	3.4	Shelf	Demersal	Yang (1982a)
Cottidae	*Icelus bicornis*	Two-horn sculpin	Boreal	Demersal eggs	16	Benthivore	3.1	Shelf	Demersal	Yang (1982a)
Cottidae	*Micrenophrys lilljeborgii*	Norway bullhead	Boreal	Demersal eggs	7	Benthivore	3.8	Inner shelf	Demersal	Yang (1982a)
Cottidae	*Myoxocephalus scorpius*	Bullrout	Boreal	Demersal eggs	60	Bentho-piscivore	3.9	Inner shelf	Demersal	Yang (1982a)
Cottidae	*Taurulus bubalis*	Sea scorpion	Boreal	Demersal eggs	17.5	Benthivore	3.6	Inner shelf	Demersal	Yang (1982a)
Cottidae	*Triglops murrayi*	Sculpin	Boreal	Demersal eggs	19	Benthivore	3.5	Outer shelf	Demersal	Yang (1982a)
Agonidae	*Agonus cataphractus*	Pogge (armed bullhead)	Boreal	Demersal eggs	21	Benthivore	3.4	Inner shelf	Demersal	Yang (1982a)
Cyclopteridae	*Cyclopterus lumpus*	Lumpsucker	Boreal	Demersal eggs	61	Bentho-piscivore	3.9	Shelf	Benthopelagic	Yang (1982a)
Liparidae	*Liparis liparis*	Seasnail	Boreal	Demersal eggs	18	Benthivore	3.6	Inner shelf	Demersal	Yang (1982a)
Liparidae	*Liparis montagui*	Montagu's seasnail	Boreal	Demersal eggs	10	Benthivore	3.5	Inner shelf	Demersal	Yang (1982a)
Percichthyidae	*Dicentrarchus labrax*	European sea bass	Lusitanian	Planktonic eggs	100	Piscivore	3.8	Shelf	Benthopelagic	Yang (1982a)
Serranidae	*Polyprion americanus*	Wreckfish	Lusitanian	Planktonic eggs	200	Piscivore	3.8	Shelf	Benthopelagic	Yang (1982a)
Serranidae	*Serranus cabrilla*	Comber	Lusitanian	Planktonic eggs	40	Piscivore	3.3	Shelf	Demersal	Yang (1982a)
Carangidae	*Naucrates ductor*	Pilotfish	Atlantic	Planktonic eggs	63	Scavenger	4.0	Oceanic	Epipelagic	Yang (1982a)
Carangidae	*Trachinotus ovatus*	Derbio	Lusitanian	Planktonic eggs	70	Piscivore	3.7	Shelf	Pelagic	Yang (1982a)
Carangidae	*Trachurus trachurus*	Horse mackerel	Lusitanian	Planktonic eggs	60	Piscivore	3.6	Shelf	Pelagic	Yang (1982a)
Echneidae	*Remora remora*	Sharksucker	Atlantic	Planktonic eggs	62	Planktivore[6]	3.1	Oceanic	Epipelagic	Carl *et al.* (2004)[7]
Coryphaenidae	*Coryphaena equiselis*	Pompano dolphinfish	Atlantic	Planktonic eggs	75	Piscivore	4.5	Oceanic	Epipelagic	Uncertain[8]
Bramidae	*Brama brama*	Ray's bream	Atlantic	Planktonic eggs	70	Piscivore	4.1	Oceanic	Mesopelagic	Yang (1982a)
Bramidae	*Pterycombus brama*	Silver pomfret	Atlantic	Planktonic eggs	40	Piscivore	4.0	Oceanic	Epipelagic	Yang (1982a)

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[6] Feed on ectoparasites of larger fish/marine mammals and also consumes zooplankton and small fish.

[7] Reported for Danish waters, and so would have had to pass through the North Sea.

[8] Uncertain record.

Family	**Species**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	**L_{MAX} (cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Bramidae	*Taractes asper*	Rough pomfret	Atlantic	Planktonic eggs	50	Piscivore	4.1	Oceanic	Epipelagic	Yang (1982a)
Bramidae	*Taractichthys longipinnis*	Long-finned bream	Atlantic	Planktonic eggs	100	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Sparidae	*Boops boops*	Bogue	Lusitanian	Planktonic eggs	36	Omnivore	3.0	Coastal	Benthopelagic	Yang (1982a)
Sparidae	*Dentex dentex*	Dentex	Lusitanian	Planktonic eggs	100	Piscivore	4.5	Inner shelf	Reef-associated	Yang (1982a)
Sparidae	*Dentex maroccanus*	Morocco dentex	Lusitanian	Planktonic eggs	41	Piscivore	3.8	Inner shelf	Demersal	Uncertain[9]
Sparidae	*Pagellus acarne*	Auxillary sea bream	Lusitanian	Planktonic eggs	36	Bentho-piscivore	3.5	Inner shelf	Demersal	Yang (1982a)
Sparidae	*Pagellus bogaraveo*	Red sea bream	Lusitanian	Planktonic eggs	70	Piscivore	3.7	Shelf	Demersal	Yang (1982a)
Sparidae	*Pagellus erythrinus*	Pandora	Lusitanian	Planktonic eggs	60	Bentho-piscivore	3.4	Inner shelf	Demersal	Yang (1982a)
Sparidae	*Sarpa salpa*	Saupe	Lusitanian	Planktonic eggs	46	Herbivore	2.0	Inner shelf	Benthopelagic	Yang (1982a)
Sparidae	*Sparus aurata*	Gilt-head sea bream	Lusitanian	Planktonic eggs	70	Bentho-piscivore	3.4	Inner shelf	Demersal	Yang (1982a)
Sparidae	*Spondyliosoma cantharus*	Black sea bream	Lusitanian	Nest-forming	60	Benthivore	3.3	Inner shelf	Demersal	Yang (1982a)
Sciaenidae	*Argyrosomus regius*	Meagre	Lusitanian	Planktonic eggs	140	Piscivore	4.3	Shelf	Benthopelagic	Yang (1982a)
Mullidae	*Mullus barbatus*	Red mullet	Lusitanian	Planktonic eggs	30	Benthivore	3.2	Inner shelf	Demersal	Uncertain[10]
Mullidae	*Mullus surmuletus*	Striped red mullet	Lusitanian	Planktonic eggs	40	Benthivore	3.4	Inner shelf	Demersal	Yang (1982a)
Cepolidae	*Cepola rubescens*	Red bandfish	Lusitanian	Planktonic eggs (?)	70	Benthivore	3.1	Shelf	Demersal	Yang (1982a)
Mugilidae	*Chelon labrosus*	Thick-lipped mullet	Lusitanian	Planktonic eggs	60	Detritivore	2.4	Coastal	Pelagic	Yang (1982a)
Mugilidae	*Liza aurata*	Golden mullet	Lusitanian	Planktonic eggs	50	Detritivore	2.5	Coastal	Pelagic	Yang (1982a)
Mugilidae	*Liza ramada*	Thin-lipped mullet	Lusitanian	Planktonic eggs	50	Detritivore	2.2	Coastal	Pelagic	Yang (1982a)
Labridae	*Acantholabrus palloni*	Scale-rayed wrasse	Lusitanian	Nest-forming	25	Benthivore	3.5	Coastal	Reef-associated	Yang (1982a)
Labridae	*Centrolabrus exoletus*	Small-mouthed wrasse	Lusitanian	Nest-forming	15	Benthivore	3.5	Coastal	Reef-associated	Yang (1982a)
Labridae	*Coris julis*	Rainbow wrasse	Lusitanian	Planktonic eggs	25	Benthivore	3.2	Coastal	Reef-associated	Whitehead *et al.* (1984–1986)
Labridae	*Symphodus bailloni*	Baillon's wrasse	Lusitanian	Nest-forming	20	Benthivore	3.3	Coastal	Reef-associated	Uncertain[11]
Labridae	*Symphodus melops*	Corkwing	Lusitanian	Nest-forming	28	Benthivore	3.2	Coastal	Reef-associated	Yang (1982a)
Labridae	*Ctenolabrus rupestris*	Goldsinny	Lusitanian	Planktonic eggs	18	Benthivore	3.3	Coastal	Reef-associated	Yang (1982a)
Labridae	*Labrus bergylta*	Ballan wrasse	Lusitanian	Nest-forming	60	Benthivore	3.1	Coastal	Reef-associated	Yang (1982a)
Labridae	*Labrus mixtus*	Cuckoo wrasse	Lusitanian	Nest-forming	35	Bentho-	3.9	Coastal	Reef-associated	Yang (1982a)

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[9] Vagrants may occur as far north as the southern North Sea. Listed in the Danish fish fauna by Carl *et al.* (2004).

[10] Listed as a North Sea species, though taxonomy uncertain.

[11] Occurs in eastern English Channel, and distribution may extend to the southern North Sea.

Family	**Species**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} (cm)	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
						piscivore				
Zoarcidae	*Lycenchelys sarsii*	Sar's eelpout	Boreal	Demersal eggs	19	Benthivore	3.2	Outer shelf	Demersal	Yang (1982a)
Zoarcidae	*Lycodes esmarkii*	Esmark's eelpout	Boreal	Demersal eggs	75	Benthivore	3.4	Outer shelf	Demersal	Yang (1982a)
Zoarcidae	*Lycodes vahlii*	Vahl's eelpout	Boreal	Demersal eggs	52	Benthivore	3.4	Outer shelf	Demersal	Yang (1982a)
Zoarcidae	*Zoarces viviparus*	Eelpout	Boreal	Viviparous	52	Benthivore	3.5	Inner shelf	Demersal	Yang (1982a)
Stichaeidae	*Chirolophis ascanii*	Yarrell's blenny	Boreal	Demersal eggs	25	Benthivore	3.0	Shelf	Demersal	Yang (1982a)
Stichaeidae	*Leptoclinus maculatus*	Spotted snake blenny	Boreal	Demersal eggs	20	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Stichaeidae	*Lumpenus lampretaeformis*	Snake blenny	Boreal	Demersal eggs	49	Benthivore	3.6	Shelf	Demersal	Yang (1982a)
Pholidae	*Pholis gunnellus*	Butterfish	Boreal	Demersal eggs	25	Benthivore	3.5	Inner shelf	Demersal	Yang (1982a)
Anarhichadidae	*Anarhichas denticulatus*	Jelly cat	Boreal	Demersal eggs	138	Plankto-piscivore	3.8	Shelf	Benthopelagic	Yang (1982a)
Anarhichadidae	*Anarhichas lupus*	Wolffish	Boreal	Demersal eggs	125	Benthivore	3.2	Shelf	Demersal	Yang (1982a)
Anarhichadidae	*Anarhichas minor*	Spotted catfish	Boreal	Demersal eggs	144	Benthivore	3.5	Shelf	Demersal	Yang (1982a)
Trachinidae	*Echiichthys vipera*	Lesser weever	Lusitanian	Planktonic eggs	15	Bentho-piscivore	4.4	Inner shelf	Demersal	Yang (1982a)
Trachinidae	*Trachinus draco*	Greater weever	Lusitanian	Planktonic eggs	40	Bentho-piscivore	4.2	Inner shelf	Demersal	Yang (1982a)
Blenniidae	*Lipophrys pholis*	Shanny	Lusitanian	Demersal eggs	16	Benthivore	3.1	Coastal	Reef-associated	Yang (1982a)
Blenniidae	*Parablennius gattorugine*	Tompot blenny	Lusitanian	Demersal eggs	30	Benthivore	2.9	Inner shelf	Reef-associated	Poll (1947)
Ammodytidae	*Ammodytes marinus*	Sandeel	Boreal	Demersal eggs	25	Planktivore	2.7	Inner shelf	Benthopelagic	Yang (1982a)
Ammodytidae	*Ammodytes tobianus*	Sandeel	Boreal	Demersal eggs	20	Planktivore	3.2	Inner shelf	Benthopelagic	Yang (1982a)
Ammodytidae	*Gymnammodytes semisquamatus*	Smooth sandeel	Lusitanian	Demersal eggs	28	Planktivore	2.7	Inner shelf	Benthopelagic	Yang (1982a)
Ammodytidae	*Hyperoplus immaculatus*	Immaculate sandeel	Lusitanian	Demersal eggs	35	Piscivore	4.4	Inner shelf	Benthopelagic	Yang (1982a)
Ammodytidae	*Hyperoplus lanceolatus*	Great sandeel	Boreal	Demersal eggs	40	Piscivore	4.2	Inner shelf	Benthopelagic	Yang (1982a)
Callionymidae	*Callionymus lyra*	Common dragonet	Lusitanian	Planktonic eggs	32	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Callionymidae	*Callionymus maculatus*	Spotted dragonet	Lusitanian	Planktonic eggs	16	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Callionymidae	*Callionymus reticulatus*	Reticulate dragonet	Lusitanian	Planktonic eggs	11	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Gobiidae	*Aphia minuta*	Transparent goby	Lusitanian	Demersal eggs	6	Planktivore	3.1	Inner shelf	Pelagic	Yang (1982a)
Gobiidae	*Buenia jeffreysii*	Jeffrey's goby	Boreal	Demersal eggs	6	Benthivore	3.6	Outer shelf	Demersal	Yang (1982a)
Gobiidae	*Crystallogobius linearis*	Crystal goby	Lusitanian	Demersal eggs	5	Planktivore	3.4	Outer shelf	Pelagic	Yang (1982a)
Gobiidae	*Gobius cobitis*	Giant goby	Lusitanian	Demersal eggs	27	Benthivore	3.0	Coastal	Demersal	Rogers *et al.* (1998a)
Gobiidae	*Gobius niger*	Black goby	Lusitanian	Demersal eggs	15	Benthivore	3.2	Inner shelf	Demersal	Yang (1982a)

FAMILY	SPECIES	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{MAX} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)	SOURCE
Gobiidae	*Gobius paganellus*	Rock goby	Lusitanian	Demersal eggs	12	Benthivore	3.3	Coastal	Demersal	Rogers *et al.* (1998a)
Gobiidae	*Gobiusculus flavescens*	Two-spot goby	Lusitanian	Demersal eggs	6	Benthivore	3.2	Coastal	Demersal	Yang (1982a)
Gobiidae	*Lebetus guilleti*	Guillet's goby	Boreal	Demersal eggs	2.5	Benthivore	3.1	Inner shelf	Reef-associated	Yang (1982a)
Gobiidae	*Lebetus scorpioides*	Diminutive goby	Boreal	Demersal eggs	4	Benthivore	3.2	Shelf	Reef-associated	Yang (1982a)
Gobiidae	*Lesueurigobius friesii*	Fries's goby	Boreal	Demersal eggs	10	Benthivore	3.2	Shelf	Demersal	Yang (1982a)
Gobiidae	*Pomatoschistus lozanoi*	Lozano's goby	Lusitanian	Demersal eggs	8	Benthivore	3.1	Inner shelf	Demersal	Whitehead *et al.* (1984–1986)
Gobiidae	*Pomatoschistus microps*	Common goby	Lusitanian	Demersal eggs	6	Benthivore	3.3	Inner shelf	Demersal	Yang (1982a)
Gobiidae	*Pomatoschistus minutus*	Sand goby	Lusitanian	Demersal eggs	9.5	Benthivore	3.2	Inner shelf	Demersal	Yang (1982a)
Gobiidae	*Pomatoschistus norvegicus*	Norwegian goby	Boreal	Demersal eggs	6.5	Benthivore	3.5	Outer shelf	Demersal	Yang (1982a)
Gobiidae	*Pomatoschistus pictus*	Painted goby	Lusitanian	Demersal eggs	6	Benthivore	3.1	Inner shelf	Demersal	Yang (1982a)
Gobiidae	*Thorogobius ephippiatus*	Leopard-spotted goby	Lusitanian	Demersal eggs	13	Benthivore	3.0	Inner shelf	Reef-associated	Foster-Smith (2000)
Trichiuridae	*Aphanopus carbo*	Black scabbardfish	Atlantic	Planktonic eggs	110	Piscivore	4.5	Slope	Benthopelagic	Yang (1982a)
Trichiuridae	*Lepidopus caudatus*	Scabbard fish	Atlantic	Planktonic eggs	205	Piscivore	3.8	Slope	Benthopelagic	Yang (1982a)
Scombridae	*Auxis rochei*	Frigate mackerel	Atlantic	Planktonic eggs	50	Piscivore	4.1	Oceanic	Epipelagic	Yang (1982a)
Scombridae	*Euthynnus alletteratus*	Little tunny	Atlantic	Planktonic eggs	100	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Scombridae	*Katsuwonus pelamis*	Skipjack tuna	Atlantic	Planktonic eggs	108	Piscivore	4.3	Oceanic	Epipelagic	Yang (1982a)
Scombridae	*Orcynopsis unicolor*	Plain bonito	Atlantic	Planktonic eggs	130	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Scombridae	*Sarda sarda*	Bonito	Atlantic	Planktonic eggs	90	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Scombridae	*Scomber scombrus*	Atlantic mackerel	Atlantic	Planktonic eggs	55	Piscivore	3.7	Shelf	Pelagic	Yang (1982a)
Scombridae	*Thunnus alalunga*	Albacore	Atlantic	Planktonic eggs	127	Piscivore	4.3	Oceanic	Epipelagic	Yang (1982a)
Scombridae	*Thunnus thynnus*	Blue-fin tunny	Atlantic	Planktonic eggs	300	Piscivore	4.4	Oceanic	Epipelagic	Yang (1982a)
Xiphiidae	*Xiphias gladius*	Swordfish	Atlantic	Planktonic eggs	450	Piscivore	4.5	Oceanic	Epipelagic	Yang (1982a)
Luvaridae	*Luvarus imperialis*	Louvar	Atlantic	No data	180	Planktivore	4.0	Oceanic	Mesopelagic	Yang (1982a)
Centrolophidae	*Centrolophus niger*	Blackfish	Atlantic	Planktonic eggs	150	Piscivore	4.0	Oceanic	Mesopelagic	Yang (1982a)
Centrolophidae	*Schedophilus medusophagus*	Cornish blackfish	Atlantic	Planktonic eggs	50	Planktivore	4.0	Oceanic	Mesopelagic	Yang (1982a)
Stromateidae	*Pampus argenteus*	White pomfret	Indo-Pacific	Planktonic eggs	30	Planktivore	3.1	oceanic	Epi/mesopelagic	Davis and Wheeler (1985)
Scophthalmidae	*Lepidorhombus boscii*	Four-spotted megrim	Lusitanian	Planktonic eggs	40	Piscivore	3.7	Outer shelf	Demersal	Uncertain [12]
Scophthalmidae	*Lepidorhombus whiffiagonis*	Megrim	Lusitanian	Planktonic eggs	59	Piscivore	4.2	Outer shelf	Demersal	Yang (1982a)

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[12] Distributed along the edge of the continental shelf of the Celtic Seas eco-region, the distribution may extend to the northwestern North Sea.

FAMILY	SPECIES	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{MAX} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)	SOURCE
Scophthalmidae	*Phrynorhombus norvegicus*	Norwegian topknot	Boreal	Planktonic eggs	12	Bentho-piscivore	4.0	Shelf	Demersal	Yang (1982a)
Scophthalmidae	*Psetta maxima*	Turbot	Lusitanian	Planktonic eggs	100	Piscivore	4.0	Shelf	Demersal	Yang (1982a)
Scophthalmidae	*Scophthalmus rhombus*	Brill	Lusitanian	Planktonic eggs	75	Piscivore	3.8	Shelf	Demersal	Yang (1982a)
Scophthalmidae	*Zeugopterus punctatus*	Topknot	Lusitanian	Planktonic eggs	25	Bentho-piscivore	4.0	Shelf	Demersal	Yang (1982a)
Bothidae	*Arnoglossus imperialis*	Imperial scaldfish	Lusitanian	Planktonic eggs	25	Benthivore	3.8	Outer shelf	Demersal	Uncertain[13]
Bothidae	*Arnoglossus laterna*	Scaldfish	Lusitanian	Planktonic eggs	20	Benthivore	3.6	Inner shelf	Demersal	Yang (1982a)
Pleuronectidae	*Glyptocephalus cynoglossus*	Witch	Boreal	Planktonic eggs	60	Benthivore	3.1	Shelf	Demersal	Yang (1982a)
Pleuronectidae	*Hippoglossoides platessoides*	Long rough dab	Boreal	Planktonic eggs	50	Bentho-piscivore	3.7	Shelf	Demersal	Yang (1982a)
Pleuronectidae	*Hippoglossus hippoglossus*	Halibut	Boreal	Planktonic eggs	200	Piscivore	4.5	Slope	Demersal	Yang (1982a)
Pleuronectidae	*Limanda limanda*	Dab	Boreal	Planktonic eggs	40	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Pleuronectidae	*Microstomus kitt*	Lemon sole	Boreal	Planktonic eggs	45	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Pleuronectidae	*Platichthys flesus*	Flounder	Lusitanian	Planktonic eggs	50	Benthivore	3.2	Coastal	Demersal	Yang (1982a)
Pleuronectidae	*Pleuronectes platessa*	European plaice	Boreal	Planktonic eggs	100	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Pleuronectidae	*Reinhardtius hippoglossoides*	Greenland halibut	Boreal	Planktonic eggs	100	Piscivore	4.5	Slope	Benthopelagic	Yang (1982a)
Soleidae	*Buglossidium luteum*	Solenette	Lusitanian	Planktonic eggs	15	Benthivore	3.3	Inner shelf	Demersal	Yang (1982a)
Soleidae	*Microchirus variegatus*	Thick-back sole	Lusitanian	Planktonic eggs	20	Benthivore	3.3	Shelf	Demersal	Yang (1982a)
Soleidae	*Pegusa lascaris*	Sand sole	Lusitanian	Planktonic eggs	40	Benthivore	3.2	Inner shelf	Demersal	Yang (1982a)
Soleidae	*Solea solea*	Sole	Lusitanian	Planktonic eggs	70	Benthivore	3.1	Inner shelf	Demersal	Yang (1982a)
Balistidae	*Balistes capriscus*	Grey triggerfish	Lusitanian	Demersal eggs	40	Benthivore	3.5	Shelf	Reef-associated	Yang (1982a)
Tetraodontidae	*Lagocephalus lagocephalus*	Pufferfish	Atlantic	Demersal eggs (?)	60	Benthivore	3.7	Shelf	Benthopelagic	Yang (1982a)
Molidae	*Mola mola*	Sunfish	Atlantic	Planktonic eggs	300	Planktivore	3.9	Oceanic	Epipelagic	Yang (1982a)
Molidae	*Ranzania laevis*	Truncated sunfish	Atlantic	Planktonic eggs	80	Planktivore	3.7	Oceanic	Epipelagic	Yang (1982a)

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[13] More common in Celtic Seas ecoregion. Some records from the northwestern North Sea.

Annex 2. Ecotypes of Baltic fish

Taxonomic list of brackish water and freshwater fish recorded from the Baltic, including their reproductive mode, maximum length, trophic guild, trophic level (from FishBase), and habitat type.

FAMILY	SCIENTIFIC NAME	COMMON NAME	REPRODUCTIVE MODE	L_{MAX} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT
Petromyzontidae	*Eudontomyzon mariae*	Ukrainian brook lamprey	Fluvial spawner	22	Ectoparasite	3.4	Demersal
Acipenseridae	*Acipenser gueldenstaedtii*	Russian sturgeon	Fluvial spawner	235	Benthivore	3.1	Demersal
Acipenseridae	*Acipenser ruthenus*	Sterlet	Fluvial spawner	125	Benthivore	3.6	Demersal
Clupeidae	*Clupea harengus membras*	Baltic herring	Demersal eggs	24	Planktivore	3.1	Pelagic
Clupeidae	*Sprattus sprattus balticus*	Baltic sprat	Planktonic eggs	16	Planktivore	3.0	Pelagic
Cyprinidae	*Abramis brama*	Common bream	Attached eggs	82	Benthivore	2.9	Benthopelagic
Cyprinidae	*Alburnoides bipunctatus*	Spirlin	Attached eggs	16	Benthivore	2.9	Benthopelagic
Cyprinidae	*Alburnus alburnus*	Bleak	Attached eggs	25	Bentho-planktivore	3.0	Benthopelagic
Cyprinidae	*Aspius aspius*	Asp	Attached eggs	100	Piscivore	4.5	Benthopelagic
Cyprinidae	*Ballerus ballerus*	Zope	Attached eggs	35	Planktivore	3.2	Benthopelagic
Cyprinidae	*Barbus barbus*	Barbel	Attached eggs	120	Benthivore	3.1	Benthopelagic
Cyprinidae	*Blicca bjoerkna*	White bream	Attached eggs	36	Omnivore	3.1	Demersal
Cyprinidae	*Carassius carassius*	Crucian carp	Attached eggs	64	Omnivore	3.1	Demersal
Cyprinidae	*Carassius gibelio*	Prussian carp	Attached eggs	45	Omnivore	2.5	Benthopelagic
Cyprinidae	*Chondrostoma nasus*	Sneep	Attached eggs	50	Herbivore	2.0	Benthopelagic
Cyprinidae	*Cyprinus carpio carpio*	Common carp	Attached eggs	146	Omnivore	3.0	Benthopelagic
Cyprinidae	*Hypophthalmichthys molitrix*	Silver carp	Attached eggs	105	Omnivore	2.0	Benthopelagic
Cyprinidae	*Leucaspius delineatus*	Belica	Attached eggs	12	Planktivore	3.1	Pelagic
Cyprinidae	*Leuciscus idus*	Ide	Attached eggs	76	Bentho-piscivore	3.8	Benthopelagic
Cyprinidae	*Leuciscus leuciscus*	Common dace	Attached eggs	40	Benthivore	2.6	Benthopelagic
Cyprinidae	*Pelecus cultratus*	Ziege	Attached eggs	60	Bentho-piscivore	3.3	Pelagic
Cyprinidae	*Phoxinus phoxinus*	Eurasian minnow	Attached eggs	14	Omnivore	3.1	Demersal
Cyprinidae	*Rutilus rutilus*	Roach	Attached eggs	46	Omnivore	2.8	Benthopelagic
Cyprinidae	*Scardinius erythrophthalmus*	Rudd	Attached eggs	51	Omnivore	2.9	Benthopelagic
Cyprinidae	*Squalius cephalus*	European chub	Attached eggs	60	Omnivore	3.0	Benthopelagic
Cyprinidae	*Tinca tinca*	Tench	Attached eggs	85	Benthivore	3.5	Demersal
Cyprinidae	*Vimba vimba*	Vimba	Attached eggs	50	Omnivore	2.8	Benthopelagic
Cobitidae	*Misgurnus fossilis*	Weatherfish	Attached eggs	30	Benthivore	3.4	Demersal
Cobitidae	*Sabanejewia aurata aurata*	Golden-spined loach	Attached eggs	14	Benthivore	3.2	Demersal

Family	Scientific name	Common name	Reproductive mode	L_{MAX} (cm)	Trophic guild	Trophic level	Habitat
Balitoridae	*Barbatula barbatula*	Stone loach	Attached eggs	21	Benthivore	3.2	Demersal
Siluridae	*Silurus glanis*	Wels catfish	Demersal eggs	500	Piscivore	4.4	Demersal
Esocidae	*Esox lucius*	Northern pike	Attached eggs	150	Piscivore	4.4	Demersal
Salmonidae	*Coregonus albula*	Vendace	Demersal eggs	45	Benthivore	3.0	Pelagic
Salmonidae	*Coregonus lavaretus*	Common whitefish	Demersal eggs	73	Benthivore	3.1	Demersal
Salmonidae	*Coregonus nasus*	Broad whitefish	Demersal eggs	71	Benthivore	3.3	Demersal
Salmonidae	*Coregonus pallasii*	Asp houting	Demersal eggs	46	Benthivore	3.3	Demersal
Salmonidae	*Coregonus peled*	Peled	Demersal eggs	50	Benthivore	3.0	Demersal
Salmonidae	*Salvelinus fontinalis*	Brook trout	Demersal eggs	105	Benthivore	3.1	Demersal
Salmonidae	*Thymallus thymallus*	Grayling	Demersal eggs	60	Benthivore	3.1	Benthopelagic
Lotidae	*Lota lota*	Burbot	Demersal eggs	55	Piscivore	4.0	Demersal
Gasterosteidae	*Pungitius pungitius*	Nine-spined stickleback	Nest-forming	9	Benthivore	3.3	Benthopelagic
Cottidae	*Cottus gobio*	Bullhead	Demersal eggs	18	Benthivore	3.2	Demersal
Cottidae	*Cottus poecilopus*	Alpine bullhead	Demersal eggs	18	Benthivore	3.0	Demersal
Cottidae	*Triglopsis quadricornis*	Four-horn sculpin	Demersal eggs	60	Benthivore	3.7	Demersal
Liparidae	*Liparis liparis barbatus*	Seasnail	Demersal eggs	19	Benthivore	3.4	Demersal
Percidae	*Gymnocephalus cernuus*	Ruffe	Attached eggs	25	Benthivore	3.3	Demersal
Percidae	*Perca fluviatilis*	European perch	Attached eggs	51	Piscivore	4.3	Demersal
Percidae	*Sander lucioperca*	Pike-perch	Attached eggs	130	Piscivore	4.3	Pelagic
Gobiidae	*Neogobius melanostomus*	Round goby	Demersal eggs	25	Benthivore	3.3	Demersal

Annex 3. Ecotypes of Irish Sea fish

Taxonomic list of fish recorded from the Irish Sea, including their biogeographical affinities, reproductive mode, maximum length, trophic guild, trophic level (from FishBase), and habitat type. For references, see Section 25.

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{MAX} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)	Source
Myxinidae	*Myxine glutinosa*	Hagfish	Atlantic	Demersal eggs	45	Scavenger	3.5	Shelf	Demersal	Ellis *et al.* (2002)
Petromyzontidae	*Lampetra fluviatilis*	River lamprey	Boreal	Fluvial spawner	45	Ectoparasite	4.5	Coastal	Demersal	Ellis *et al.* (2002)
Petromyzontidae	*Petromyzon marinus*	Sea lamprey	Boreal	Fluvial spawner	120	Ectoparasite	4.4	Shelf	Demersal	Ellis *et al.* (2002)
Lamnidae	*Lamna nasus*	Porbeagle shark	Atlantic	Viviparous	370	Piscivore	4.5	Shelf	Epipelagic	Ellis *et al.* (2002)
Cetorhinidae	*Cetorhinus maximus*	Basking shark	Atlantic	Viviparous	980	Planktivore	3.2	Shelf	Epipelagic	Ellis *et al.* (2002)
Alopiidae	*Alopias vulpinus*	Thresher shark	Atlantic	Viviparous	560	Piscivore	4.5	Oceanic	Epipelagic	Ellis *et al.* (2002)
Scyliorhinidae	*Galeus melastomus*	Black-mouthed dogfish	Lusitanian	Demersal eggs	90	Bentho-piscivore	4.2	Slope	Bathydemersal	Ellis *et al.* (2002)
Scyliorhinidae	*Scyliorhinus canicula*	Lesser spotted dogfish	Lusitanian	Demersal eggs	80	Bentho-piscivore	3.7	Inner shelf	Demersal	Ellis *et al.* (2002)
Scyliorhinidae	*Scyliorhinus stellaris*	Nurse hound	Lusitanian	Demersal eggs	162	Piscivore	4.0	Inner shelf	Reef-associated	Ellis *et al.* (2002)
Triakidae	*Galeorhinus galeus*	Tope shark	Lusitanian	Viviparous	200	Piscivore	4.2	Shelf	Benthopelagic	Ellis *et al.* (2002)
Triakidae	*Mustelus asterias*	Starry smooth hound	Lusitanian	Viviparous	140	Carcinophage	3.7	Shelf	Demersal	Ellis *et al.* (2002)
Triakidae	*Mustelus mustelus*	Smooth hound	Lusitanian	Viviparous	150	Carcinophage	3.8	Shelf	Demersal	Ellis *et al.* (2002)
Carcharhinidae	*Prionace glauca*	Blue shark	Atlantic	Viviparous	383	Piscivore	4.2	Oceanic	Epipelagic	Ellis *et al.* (2002)
Squalidae	*Squalus acanthias*	Spurdog	Boreal	Viviparous	105	Piscivore	4.3	Shelf	Benthopelagic	Ellis *et al.* (2002)
Echinorhinidae	*Echinorhinus brucus*	Bramble shark	Atlantic	Viviparous	250	Piscivore	4.4	Slope	Bathydemersal	Ellis *et al.* (2002)
Squatinidae	*Squatina squatina*	Angel shark	Lusitanian	Viviparous	250	Piscivore	4.1	Inner shelf	Demersal	Ellis *et al.* (2002)
Torpedinidae	*Torpedo nobiliana*	Electric ray	Lusitanian	Viviparous	180[14]	Piscivore	4.5	Shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Amblyraja radiata*	Starry ray	Boreal	Demersal eggs	90[14]	Piscivore	4.0	Shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Dipturus batis*	Common skate	Boreal	Demersal eggs	250	Piscivore	4.0	Shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Leucoraja circularis*	Sandy ray	Lusitanian	Demersal eggs	120[14]	Piscivore	3.5	Outer shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Leucoraja fullonica*	Shagreen ray	Boreal	Demersal eggs	100[14]	Piscivore	3.5	Outer shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Leucoraja naevus*	Cuckoo ray	Lusitanian	Demersal eggs	70[14]	Piscivore	3.9	Shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Raja brachyura*	Blonde ray	Lusitanian	Demersal eggs	120[14]	Piscivore	4.0	Inner shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Raja clavata*	Thornback ray	Lusitanian	Demersal eggs	90[14]	Bentho-piscivore	3.8	Inner shelf	Demersal	Ellis *et al.* (2002)

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[14] Disc width.

FAMILY	SCIENTIFIC NAME	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{max} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)	SOURCE
Rajidae	*Raja microocellata*	Small-eyed ray	Lusitanian	Demersal eggs	80(14)	Piscivore	3.9	Inner shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Raja montagui*	Spotted ray	Lusitanian	Demersal eggs	80(14)	Bentho-piscivore	3.7	Inner shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Raja undulata*	Undulate ray	Lusitanian	Demersal eggs	100(14)	Bentho-piscivore	3.5	Inner shelf	Demersal	Ellis *et al.* (2002)
Rajidae	*Rostroraja alba*	Bottle-nosed skate	Lusitanian	Demersal eggs	230	Bentho-piscivore	4.4	Shelf	Demersal	Ellis *et al.* (2002)
Dasyatidae	*Dasyatis pastinaca*	Sting ray	Lusitanian	Viviparous	60 (DW) (14)	Bentho-piscivore	4.1	Shelf	Demersal	Ellis *et al.* (2002)
Acipenseridae	*Acipenser sturio*	Sturgeon	Lusitanian	Fluvial spawner	350	Benthivore	3.5	Coastal	Demersal	Ellis *et al.* (2002)
Anguillidae	*Anguilla anguilla*	European eel	Atlantic	Leptocephalus larvae	100	Bentho-piscivore	3.5	Coastal	Demersal	Ellis *et al.* (2002)
Congridae	*Conger conger*	Conger eel	Lusitanian	Leptocephalus larvae	300	Piscivore	4.3	Shelf	Reef-associated	Ellis *et al.* (2002)
Clupeidae	*Alosa alosa*	Allis shad	Lusitanian	Fluvial spawner	70	Planktivore	3.6	Shelf	Pelagic	Ellis et al. (2002)
Clupeidae	*Alosa fallax*	Twaite shad	Lusitanian	Fluvial spawner	50	Planktivore	3.6	Shelf	Pelagic	Ellis et al. (2002)
Clupeidae	*Clupea harengus*	Herring	Boreal	Demersal eggs	40	Planktivore	3.2	Shelf	Benthopelagic	Ellis *et al.* (2002)
Clupeidae	*Sardina pilchardus*	Pilchard	Lusitanian	Planktonic eggs	25	Planktivore	2.6	Shelf	Pelagic	Ellis *et al.* (2002)
Clupeidae	*Sprattus sprattus*	Sprat	Lusitanian	Planktonic eggs	16	Planktivore	3	Shelf	Pelagic	Ellis *et al.* (2002)
Engraulidae	*Engraulis encrasicolus*	European anchovy	Lusitanian	Planktonic eggs	20	Planktivore	3.1	Shelf	Pelagic	Ellis *et al.* (2002)
Argentinidae	*Argentina sphyraena*	Lesser silversmelt	Lusitanian	Planktonic eggs	32	Planktivore	3.6	Shelf	Benthopelagic	Ellis *et al.* (2002)
Osmeridae	*Osmerus eperlanus*	Smelt	Boreal	Demersal eggs	45	Bentho-piscivore	3.1	Coastal	Pelagic	Ellis *et al.* (2002)
Salmonidae	*Salmo salar*	Atlantic salmon	Boreal	Fluvial spawner	150	Piscivore	4.4	Inner shelf	Pelagic	Ellis *et al.* (2002)
Salmonidae	*Salmo trutta*	Trout	Boreal	Fluvial spawner	140	Piscivore	3.2	Inner shelf	Pelagic	Ellis *et al.* (2002)
Sternoptychidae	*Maurolicus muelleri*	Pearlside	Atlantic	Planktonic eggs	7	Planktivore	3.0	Slope	Bathypelagic	Ellis *et al.* (2002)
Lampridae	*Lampris guttatus*	Opah	Atlantic	Planktonic eggs	185	Piscivore	4.2	Oceanic	Epipelagic	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Gadus morhua*	Cod	Boreal	Planktonic eggs	190	Piscivore	4.4	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Melanogrammus aeglefinus*	Haddock	Boreal	Planktonic eggs	112	Benthivore	4.1	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Merlangius merlangus*	Whiting	Lusitanian	Planktonic eggs	70	Piscivore	4.4	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Micromesistius poutassou*	Blue whiting	Atlantic	Planktonic eggs	47	Planktivore	4.0	Slope	Mesopelagic	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Pollachius pollachius*	Pollack	Boreal	Planktonic eggs	130	Piscivore	4.2	Shelf	Demersal	Ellis et al. (2002)
Gadidae (Gadinae)	*Pollachius virens*	Saithe	Boreal	Planktonic eggs	120	Piscivore	4.4	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Trisopterus esmarkii*	Norway pout	Boreal	Planktonic eggs	26	Bentho-piscivore	3.2	Outer shelf	Benthopelagic	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Trisopterus luscus*	Bib	Lusitanian	Planktonic eggs	45	Benthivore	3.7	Inner shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Gadinae)	*Trisopterus minutus*	Poor cod	Lusitanian	Planktonic eggs	26	Benthivore	3.8	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Lotinae)	*Ciliata mustela*	Five-bearded rockling	Boreal	Planktonic eggs	45	Benthivore	3.5	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Lotinae)	*Ciliata septentrionalis*	Northern rockling	Boreal	Planktonic eggs	17	Benthivore	3.5	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Lotinae)	*Enchelyopus cimbrius*	Four-bearded rockling	Boreal	Planktonic eggs	41	Benthivore	3.5	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Lotinae)	*Gaidropsarus*	Shore rockling	Lusitanian	Planktonic eggs	25	Benthivore	3.4	Shelf	Demersal	Ellis *et al.* (2002)

FAMILY	SCIENTIFIC NAME	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{max} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)	SOURCE
	mediterraneus									
Gadidae (Lotinae)	*Gaidropsarus vulgaris*	Three-bearded rockling	Lusitanian	Planktonic eggs	43	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Lotinae)	*Molva molva*	Common ling	Boreal	Planktonic eggs	200	Piscivore	4.3	Slope	Demersal	Ellis *et al.* (2002)
Gadidae (Lotinae)	*Phycis blennoides*	Greater forkbeard	Lusitanian	Planktonic eggs	75	Bentho-piscivore	3.7	Outer shelf	Demersal	Ellis *et al.* (2002)
Gadidae (Lotinae)	*Raniceps raninus*	Tadpolefish	Boreal	Planktonic eggs	30	Benthivore	3.8	Inner shelf	Demersal	Ellis *et al.* (2002)
Merlucciidae	*Merluccius merluccius*	European hake	Lusitanian	Planktonic eggs	120	Piscivore	4.4	Shelf	Demersal	Ellis *et al.* (2002)
Lophiidae	*Lophius piscatorius*	Anglerfish	Lusitanian	Planktonic eggs (rafts)	200	Piscivore	4.4	Shelf	Demersal	Ellis *et al.* (2002)
Gobiesocidae	*Apletodon dentatus*	Small-headed clingfish	Lusitanian	Demersal eggs	4	Benthivore	3.1	Coastal	Demersal	Ellis *et al.* (2002)
Gobiesocidae	*Diplecogaster bimaculata*	Two-spotted clingfish	Lusitanian	Demersal eggs	4	Benthivore	3.3	Inner shelf	Demersal	Ellis *et al.* (2002)
Gobiesocidae	*Lepadogaster candollei*	Connemara clingfish	Lusitanian	Demersal eggs	9	Benthivore	2.8	Shelf	Demersal	Ellis *et al.* (2002)
Atherinidae	*Atherina presbyter*	Sandsmelt	Lusitanian	Attached eggs	20	Bentho-planktivore	3.7	Coastal	Pelagic	Ellis *et al.* (2002)
Scomberesocidae	*Scomberesox saurus*	Saurey pike	Atlantic	Planktonic eggs	45	Planktivore	3.6	Oceanic	Epipelagic	Ellis *et al.* (2002)
Belonidae	*Belone belone*	Garfish	Lusitanian	Attached eggs	90	Piscivore	4.2	Shelf	Epipelagic	Ellis *et al.* (2002)
Zeidae	*Zeus faber*	John dory	Lusitanian	Planktonic eggs	66	Piscivore	4.5	Shelf	Benthopelagic	Ellis *et al.* (2002)
Caproidae	*Capros aper*	Boarfish	Lusitanian	Planktonic eggs	16	Planktivore	3.1	Slope	Bathydemersal	Ellis *et al.* (2002)
Gasterosteidae	*Gasterosteus aculeatus*	Three-spined stickleback	Boreal	Nest-forming	8	Benthivore	3.5	Coastal	Demersal	Ellis *et al.* (2002)
Gasterosteidae	*Pungitius pungitius*	Nine-spined stickleback	Boreal	Nest-forming	8	Benthivore	3.3	Coastal	Demersal	Ellis *et al.* (2002)
Gasterosteidae	*Spinachia spinachia*	Fifteen-spined stickleback	Boreal	Nest-forming	22	Benthivore	3.5	Coastal	Demersal	Ellis *et al.* (2002)
Syngnathidae	*Entelurus aequoreus*	Snake pipefish	Lusitanian	Egg brooder	60	Planktivore	3.5	Oceanic/ shelf	Pelagic	Ellis *et al.* (2002)
Syngnathidae	*Nerophis lumbriciformis*	Worm pipefish	Lusitanian	Egg brooder	17	Planktivore	4.0	Coastal	Demersal	Ellis *et al.* (2002)
Syngnathidae	*Nerophis ophidion*	Straight-nosed pipefish	Lusitanian	Egg brooder	30	Planktivore	4.0	Coastal	Demersal	Ellis *et al.* (2002)
Syngnathidae	*Syngnathus acus*	Great pipefish	Lusitanian	Egg brooder	46	Planktivore	3.4	Coastal	Demersal	Ellis *et al.* (2002)
Syngnathidae	*Syngnathus rostellatus*	Nilsson's pipefish	Lusitanian	Egg brooder	17	Planktivore	3.7	Coastal	Demersal	Ellis *et al.* (2002)
Syngnathidae	*Syngnathus typhle*	Deep-snouted pipefish	Lusitanian	Egg brooder	35	Planktivore	4.3	Coastal	Demersal	Ellis *et al.* (2002)
Syngnathidae	*Hippocampus hippocampus*	Short-snouted sea horse	Lusitanian	Egg brooder	16	Planktivore	3.2	Coastal	Demersal	Ellis *et al.* (2002)
Sebastidae	*Helicolenus dactylopterus*	Blue-mouth redfish	Atlantic	Planktonic eggs	44	Plankto-piscivore	3.8	Slope	Bathydemersal	Ellis *et al.* (2002)
Sebastidae	*Sebastes marinus*	Redfish	Boreal	Viviparous	100	Plankto-piscivore	4.0	Slope	Pelagic	Ellis *et al.* (2002)
Triglidae	*Aspitrigla cuculus*	Red gurnard	Lusitanian	Planktonic eggs	50	Benthivore	3.8	Shelf	Demersal	Ellis *et al.* (2002)

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)	Source
Triglidae	*Eutrigla gurnardus*	Grey gurnard	Lusitanian	Planktonic eggs	50	Benthivore	3.6	Shelf	Demersal	Ellis *et al.* (2002)
Triglidae	*Trigla lucerna*	Tub gurnard	Lusitanian	Planktonic eggs	75	Benthivore	3.7	Shelf	Demersal	Ellis *et al.* (2002)
Triglidae	*Trigla lyra*	Piper	Lusitanian	Planktonic eggs	60	Benthivore	3.5	Outer shelf	Bathydemersal	Ellis *et al.* (2002)
Triglidae	*Trigloporus lastoviza*	Streaked gurnard	Lusitanian	Planktonic eggs	40	Benthivore	3.4	Shelf	Demersal	Ellis *et al.* (2002)
Cottidae	*Micrenophrys lilljeborgii*	Norway bullhead	Boreal	Demersal eggs	7	Benthivore	3.8	Inner shelf	Demersal	Ellis *et al.* (2002)
Cottidae	*Myoxocephalus scorpius*	Bullrout	Boreal	Demersal eggs	60	Bentho-piscivore	3.9	Inner shelf	Demersal	Ellis *et al.* (2002)
Cottidae	*Taurulus bubalis*	Sea scorpion	Boreal	Demersal eggs	17.5	Benthivore	3.6	Inner shelf	Demersal	Ellis *et al.* (2002)
Agonidae	*Agonus cataphractus*	Pogge (armed bullhead)	Boreal	Demersal eggs	21	Benthivore	3.4	Inner shelf	Demersal	Ellis *et al.* (2002)
Cyclopteridae	*Cyclopterus lumpus*	Lumpsucker	Boreal	Demersal eggs	61	Bentho-piscivore	3.9	Shelf	Benthopelagic	Ellis *et al.* (2002)
Cyclopteridae (Liparidae)	*Liparis liparis*	Seasnail	Boreal	Demersal eggs	18	Benthivore	3.6	Inner shelf	Demersal	Ellis *et al.* (2002)
Cyclopteridae (Liparidae)	*Liparis montagui*	Montagu's seasnail	Boreal	Demersal eggs	10	Benthivore	3.5	Inner shelf	Demersal	Ellis *et al.* (2002)
Moronidae	*Dicentrarchus labrax*	European sea bass	Lusitanian	Planktonic eggs	100	Piscivore	3.8	Shelf	Benthopelagic	Ellis *et al.* (2002)
Serranidae	*Serranus cabrilla*	Comber	Lusitanian	Planktonic eggs	40	Bentho-piscivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Echeneidae	*Remora remora*	Sharksucker	Atlantic	Planktonic eggs	62	Plankto-piscivore	3.1	Oceanic	Epipelagic	Ellis *et al.* (2002)
Carangidae	*Naucrates ductor*	Pilotfish	Atlantic	Planktonic eggs	63	Scavenger	4.0	Oceanic	Epipelagic	Ellis *et al.* (2002)
Carangidae	*Trachurus trachurus*	Horse mackerel	Lusitanian	Planktonic eggs	60	Piscivore	3.6	Shelf	Pelagic	Ellis *et al.* (2002)
Bramidae	*Brama brama*	Ray's bream	Atlantic	Planktonic eggs	70	Piscivore	4.1	Oceanic	Mesopelagic	Ellis *et al.* (2002)
Sparidae	*Pagellus bogaraveo*	Red sea bream	Lusitanian	Planktonic eggs	70	Piscivore	3.7	Shelf	Demersal	Ellis *et al.* (2002)
Sparidae	*Spondyliosoma cantharus*	Black sea bream	Lusitanian	Nest-forming	60	Benthivore	3.3	Inner shelf	Demersal	Ellis *et al.* (2002)
Sciaenidae	*Argyrosomus regius*	Meagre	Lusitanian	Planktonic eggs	140	Piscivore	4.3	Shelf	Benthopelagic	Ellis *et al.* (2002)
Mullidae	*Mullus surmuletus*	Striped red mullet	Lusitanian	Planktonic eggs	40	Benthivore	3.4	Inner shelf	Demersal	Ellis *et al.* (2002)
Cepolidae	*Cepola rubescens*	Red bandfish	Lusitanian	Planktonic eggs (?)	70	Benthivore	3.1	Shelf	Demersal	Ellis *et al.* (2002)
Mugilidae	*Chelon labrosus*	Thick-lipped mullet	Lusitanian	Planktonic eggs	60	Detritivore	2.4	Coastal	Pelagic	Ellis *et al.* (2002)
Labridae	*Centrolabrus exoletus*	Small-mouthed wrasse	Lusitanian	Nest-forming	15	Benthivore	3.5	Coastal	Reef-associated	Ellis *et al.* (2002)
Labridae	*Coris julis*	Rainbow wrasse	Lusitanian	Planktonic eggs	25	Benthivore	3.2	Coastal	Reef-associated	Ellis *et al.* (2002)
Labridae	*Ctenolabrus rupestris*	Goldsinny	Lusitanian	Planktonic eggs	18	Benthivore	3.3	Coastal	Reef-associated	Ellis *et al.* (2002)
Labridae	*Labrus bergylta*	Ballan wrasse	Lusitanian	Nest-forming	60	Benthivore	3.1	Coastal	Reef-associated	Ellis *et al.* (2002)
Labridae	*Labrus bimaculatus*	Cuckoo wrasse	Lusitanian	Nest-forming	35	Bentho-piscivore	3.9	Coastal	Reef-associated	Ellis *et al.* (2002)
Labridae	*Symphodus (Crenilabrus) melops*	Corkwing	Lusitanian	Nest-forming	28	Benthivore	3.2	Coastal	Reef-associated	Ellis *et al.* (2002)
Zoarcidae	*Zoarces viviparus*	Eelpout	Boreal	Viviparous	52	Benthivore	3.5	Inner shelf	Demersal	Ellis *et al.* (2002)

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)	Source
Stichaeidae	*Chirolophis ascanii*	Yarrell's blenny	Boreal	Demersal eggs	25	Benthivore	3	Shelf	Demersal	Ellis *et al.* (2002)
Stichaeidae (Lumpenidae)	*Lumpenus lumpretaeformis*	Snake blenny	Boreal	Demersal eggs	40	Benthivore	3.6	Shelf	Demersal	Ellis *et al.* (2002)
Pholidae	*Pholis gunnellus*	Butterfish	Boreal	Demersal eggs	25	Benthivore	3.5	Inner shelf	Demersal	Ellis *et al.* (2002)
Anarhichadidae	*Anarhichas lupus*	Wolf-fish	Boreal	Demersal eggs	125	Benthivore	3.2	Shelf	Demersal	Ellis *et al.* (2002)
Ammodytidae	*Ammodytes marinus*	Sandeel	Boreal	Demersal eggs	25	Planktivore	2.7	Inner shelf	Benthopelagic	Ellis *et al.* (2002)
Ammodytidae	*Ammodytes tobianus*	Sandeel	Boreal	Demersal eggs	20	Planktivore	3.2	Inner shelf	Benthopelagic	Ellis *et al.* (2002)
Ammodytidae	*Gymnammodytes semisquamatus*	Smooth sandeel	Lusitanian	Demersal eggs	28	Planktivore	2.7	Inner shelf	Benthopelagic	Ellis *et al.* (2002)
Ammodytidae	*Hyperoplus immaculatus*	Immaculate sandeel	Lusitanian	Demersal eggs	35	Piscivore	4.4	Inner shelf	Benthopelagic	Ellis *et al.* (2002)
Ammodytidae	*Hyperoplus lanceolatus*	Great sandeel	Boreal	Demersal eggs	40	Piscivore	4.2	Inner shelf	Benthopelagic	Ellis *et al.* (2002)
Trachinidae	*Echiichthys vipera*	Lesser weever	Lusitanian	Planktonic eggs	15	Bentho-piscivore	4.4	Inner shelf	Demersal	Ellis *et al.* (2002)
Trachinidae	*Trachinus draco*	Greater weever	Lusitanian	Planktonic eggs	40	Bentho-piscivore	4.2	Inner shelf	Demersal	Ellis *et al.* (2002)
Blenniidae	*Blennius ocellaris*	Butterfly blenny	Lusitanian	Demersal eggs	20	Benthivore	3.5	Shelf	Demersal	Ellis *et al.* (2002)
Blenniidae	*Coryphoblennius galerita*	Montagu's blenny	Lusitanian	Demersal eggs	9	Benthivore	2.2	Inner shelf	Reef-associated	Ellis *et al.* (2002)
Blenniidae	*Lipophrys pholis*	Shanny	Lusitanian	Demersal eggs	16	Benthivore	3.1	Coastal	Reef-associated	Ellis *et al.* (2002)
Blenniidae	*Parablennius gattorugine*	Tompot blenny	Lusitanian	Demersal eggs	30	Benthivore	2.9	Inner shelf	Reef-associated	Ellis *et al.* (2002)
Callionymidae	*Callionymus lyra*	Common dragonet	Lusitanian	Planktonic eggs	32	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Callionymidae	*Callionymus maculatus*	Spotted dragonet	Lusitanian	Planktonic eggs	16	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Callionymidae	*Callionymus reticulatus*	Reticulate dragonet	Lusitanian	Planktonic eggs	11	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Gobiidae	*Aphia minuta*	Transparent goby	Lusitanian	Demersal eggs	6	Planktivore	3.1	Inner shelf	Pelagic	Ellis *et al.* (2002)
Gobiidae	*Buenia jeffreysii*	Jeffrey's goby	Boreal	Demersal eggs	6	Benthivore	3.6	Outer shelf	Demersal	Ellis *et al.* (2002)
Gobiidae	*Crystallogobius linearis*	Crystal goby	Lusitanian	Demersal eggs	5	Planktivore	3.4	Outer shelf	Pelagic	Ellis *et al.* (2002)
Gobiidae	*Gobius niger*	Black goby	Lusitanian	Demersal eggs	15	Benthivore	3.2	Inner shelf	Demersal	Ellis *et al.* (2002)
Gobiidae	*Gobius paganellus*	Rock goby	Lusitanian	Demersal eggs	12	Benthivore	3.3	Coastal	Demersal	Ellis *et al.* (2002)
Gobiidae	*Gobiusculus flavescens*	Two-spot goby	Lusitanian	Demersal eggs	6	Benthivore	3.2	Coastal	Demersal	Ellis *et al.* (2002)
Gobiidae	*Lebetus scorpioides*	Diminutive goby	Boreal	Demersal eggs	4	Benthivore	3.2	Shelf	Reef-associated	Ellis *et al.* (2002)
Gobiidae	*Lesueurigobius friesii*	Fries's goby	Boreal	Demersal eggs	10	Benthivore	3.2	Shelf	Demersal	Ellis *et al.* (2002)

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Gobiidae	*Pomatoschistus microps*	Common goby	Lusitanian	Demersal eggs	6	Benthivore	3.3	Inner shelf	Demersal	Ellis *et al.* (2002)
Gobiidae	*Pomatoschistus minutus*	Sand goby	Lusitanian	Demersal eggs	9.5	Benthivore	3.2	Inner shelf	Demersal	Ellis *et al.* (2002)
Gobiidae	*Pomatoschistus norvegicus*	Norwegian goby	Boreal	Demersal eggs	6.5	Benthivore	3.5	Outer shelf	Demersal	Ellis *et al.* (2002)
Gobiidae	*Pomatoschistus pictus*	Painted goby	Lusitanian	Demersal eggs	6	Benthivore	3.1	Inner shelf	Demersal	Ellis *et al.* (2002)
Gobiidae	*Thorogobius ephippiatus*	Leopard-spotted goby	Lusitanian	Demersal eggs	13	Benthivore	3	Inner shelf	Reef-associated	Ellis *et al.* (2002)
Scombridae	*Katsuwonus pelamis*	Skipjack tuna	Atlantic	Planktonic eggs	108	Piscivore	4.3	Oceanic	Epipelagic	Ellis *et al.* (2002)
Scombridae	*Sarda sarda*	Bonito	Atlantic	Planktonic eggs	90	Piscivore	4.5	Oceanic	Epipelagic	Ellis *et al.* (2002)
Scombridae	*Scomber japonicus*	Chub mackerel	Lusitanian	Planktonic eggs	64	Planktivore	3.1	Outer shelf	Epipelagic	Ellis *et al.* (2002)
Scombridae	*Scomber scombrus*	Atlantic mackerel	Atlantic	Planktonic eggs	55	Piscivore	3.7	Shelf	Epipelagic	Ellis *et al.* (2002)
Scombridae	*Thunnus alalunga*	Albacore	Atlantic	Planktonic eggs	127	Piscivore	4.3	Oceanic	Epipelagic	Ellis *et al.* (2002)
Scombridae	*Thunnus thynnus*	Blue-fin tunny	Atlantic	Planktonic eggs	300	Piscivore	4.4	Oceanic	Epipelagic	Ellis *et al.* (2002)
Centrolophidae	*Centrolophus niger*	Blackfish	Atlantic	Planktonic eggs	150	Piscivore	4	Oceanic	Mesopelagic	Ellis *et al.* (2002)
Scophthalmidae	*Lepidorhombus whiffiagonis*	Megrim	Lusitanian	Planktonic eggs	59	Piscivore	4.2	Outer shelf	Demersal	Ellis *et al.* (2002)
Scophthalmidae	*Phrynorhombus norvegicus*	Norwegian topknot	Boreal	Planktonic eggs	12	Bentho-piscivore	4	Shelf	Demersal	Ellis *et al.* (2002)
Scophthalmidae	*Phrynorhombus regius*	Eckström's topknot	Lusitanian	Planktonic eggs	20	Benthivore	3.4	Shelf	Demersal	Ellis *et al.* (2002)
Scophthalmidae	*Scophthalmus maximus*	Turbot	Lusitanian	Planktonic eggs	100	Piscivore	4	Shelf	Demersal	Ellis *et al.* (2002)
Scophthalmidae	*Scophthalmus rhombus*	Brill	Lusitanian	Planktonic eggs	75	Piscivore	3.8	Shelf	Demersal	Ellis *et al.* (2002)
Scophthalmidae	*Zeugopterus punctatus*	Topknot	Lusitanian	Planktonic eggs	25	Bentho-piscivore	4	Shelf	Demersal	Ellis *et al.* (2002)
Bothidae	*Arnoglossus laterna*	Scaldfish	Lusitanian	Planktonic eggs	20	Benthivore	3.6	Inner shelf	Demersal	Ellis *et al.* (2002)
Pleuronectidae	*Glyptocephalus cynoglossus*	Witch	Boreal	Planktonic eggs	60	Benthivore	3.1	Shelf	Demersal	Ellis *et al.* (2002)
Pleuronectidae	*Hippoglossoides platessoides*	Long rough dab	Boreal	Planktonic eggs	50	Bentho-piscivore	3.7	Shelf	Demersal	Ellis *et al.* (2002)
Pleuronectidae	*Hippoglossus hippoglossus*	Halibut	Boreal	Planktonic eggs	200	Piscivore	4.5	Slope	Demersal	Ellis *et al.* (2002)
Pleuronectidae	*Limanda limanda*	Dab	Boreal	Planktonic eggs	40	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Pleuronectidae	*Microstomus kitt*	Lemon sole	Boreal	Planktonic eggs	45	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Pleuronectidae	*Platichthys flesus*	Flounder	Lusitanian	Planktonic eggs	50	Benthivore	3.2	Coastal	Demersal	Ellis *et al.* (2002)

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**	**Source**
Pleuronectidae	*Pleuronectes platessa*	European plaice	Boreal	Planktonic eggs	100	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Soleidae	*Buglossidium luteum*	Solenette	Lusitanian	Planktonic eggs	15	Benthivore	3.3	Inner shelf	Demersal	Ellis *et al.* (2002)
Soleidae	*Microchirus variegatus*	Thick-back sole	Lusitanian	Planktonic eggs	20	Benthivore	3.3	Shelf	Demersal	Ellis *et al.* (2002)
Soleidae	*Pegusa lascaris*	Sand sole	Lusitanian	Planktonic eggs	40	Benthivore	3.2	Inner shelf	Demersal	Ellis *et al.* (2002)
Soleidae	*Solea solea*	Sole	Lusitanian	Planktonic eggs	70	Benthivore	3.1	Inner shelf	Demersal	Ellis *et al.* (2002)
Balistidae	*Balistes capriscus*	Grey triggerfish	Lusitanian	Demersal eggs	40	Benthivore	3.5	Shelf	Reef-associated	Ellis *et al.* (2002)
Molidae	*Mola mola*	Sunfish	Atlantic	Planktonic eggs	300	Planktivore	3.9	Oceanic	Epipelagic	Ellis *et al.* (2002)

Annex 4. Ecotypes of European marine fish

Taxonomic list of fish recorded from European seas (adapted from the European Register of Marine Species), including their biogeographical affinities, reproductive mode, maximum length, trophic guild, trophic level (from FishBase), and habitat types.

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
Myxinidae	*Myxine glutinosa*	Hagfish	Atlantic	Demersal eggs	45	Scavenger	3.5	Shelf	Demersal
Myxinidae	*Myxine ios*	White-headed hagfish	Atlantic	Demersal eggs	57	Scavenger	3.3	Oceanic	Bathydemersal
Petromyzontidae	*Lampetra fluviatilis*	River lamprey	Boreal	Fluvial spawner	45	Ectoparasite	4.5	Coastal	Demersal
Petromyzontidae	*Lethenteron camtschaticum*	Arctic lamprey	Arctic	Fluvial spawner	63	Ectoparasite	4.5	Inner shelf	Demersal
Petromyzontidae	*Petromyzon marinus*	Sea lamprey	Boreal	Fluvial spawner	120	Ectoparasite	4.4	Shelf	Demersal
Hexanchidae	*Heptranchias perlo*	Sharp-nose seven-gilled shark	Atlantic	Viviparous	140	Piscivore	4.2	Slope	Bathydemersal
Hexanchidae	*Hexanchus griseus*	Six-gilled shark	Atlantic	Viviparous	500	Piscivore	4.3	Slope	Bathydemersal
Hexanchidae	*Hexanchus nakamurai*	Big-eye six-gilled shark	Atlantic	Viviparous	180	Piscivore	4.2	Slope	Bathydemersal
Chlamydoselachidae	*Chlamydoselachus anguineus*	Frilled shark	Atlantic	Viviparous	200	Piscivore	4.2	Slope	Bathydemersal
Rhincodontidae	*Rhincodon typus*	Whale shark	Atlantic (African)	Viviparous	2000	Planktivore	3.5	Oceanic/shelf	Pelagic
Ginglymostomatidae	*Ginglymostoma cirratum*	Nurse shark	Atlantic (African)	Viviparous	430	Benthivore	3.8	Inner shelf	Demersal
Odontaspididae	*Carcharias taurus*	Sand tiger shark	Atlantic (African)	Viviparous	320	Piscivore	4.5	Inner shelf	Demersal
Odontaspididae	*Odontaspis ferox*	Small-tooth sand tiger	Lusitanian	Viviparous	367	Piscivore	4.2	Shelf	Demersal
Odontaspididae	*Odontaspis noronhai*	Big-eye sand tiger	Atlantic	Viviparous	360	Piscivore	4.3	Slope	Demersal
Mitsukurinidae	*Mitsukurina owstoni*	Goblin shark	Atlantic	Viviparous	385	Piscivore	4.1	Slope	Demersal
Lamnidae	*Carcharodon carcharias*	Great white shark	Atlantic	Viviparous	720	Piscivore	4.5	Shelf	Pelagic
Lamnidae	*Isurus oxyrinchus*	Short-fin mako shark	Atlantic	Viviparous	400	Piscivore	4.5	Oceanic	Epipelagic
Lamnidae	*Isurus paucus*	Long-fin mako shark	Atlantic	Viviparous	417	Piscivore	4.5	Oceanic	Epipelagic
Lamnidae	*Lamna nasus*	Porbeagle shark	Atlantic	Viviparous	370	Piscivore	4.5	Shelf	Epipelagic
Cetorhinidae	*Cetorhinus maximus*	Basking shark	Atlantic	Viviparous	980	Planktivore	3.2	Shelf	Epipelagic
Alopiidae	*Alopias superciliosus*	Big-eye thresher shark	Atlantic	Viviparous	488	Piscivore	4.5	Oceanic	Epipelagic
Alopiidae	*Alopias vulpinus*	Thresher shark	Atlantic	Viviparous	560	Piscivore	4.5	Oceanic	Epipelagic
Scyliorhinidae	*Apristurus aphyodes*	–	Atlantic	Demersal eggs	NA	Unknown	NA	Oceanic	Bathydemersal
Scyliorhinidae	*Apristurus laurussonii*	Iceland cat shark	Atlantic	Demersal eggs	68	Bentho-piscivore	3.9	Slope	Demersal
Scyliorhinidae	*Apristurus manis*	Ghost cat shark	Atlantic	Demersal eggs	85	Unknown	NA	Slope	Bathydemersal
Scyliorhinidae	*Apristurus microps*	Smalleye cat shark	Atlantic	Demersal eggs	61	Bentho-piscivore	3.8	Oceanic	Bathydemersal
Scyliorhinidae	*Apristurus nasutus*	Largenose cat shark	Uncertain	Demersal eggs	70	Unknown	3.1	Slope	Bathydemersal
Scyliorhinidae	*Galeus atlanticus*	Atlantic sawtail cat shark	Atlantic	Demersal eggs	51	Unknown	4.1	Slope	Bathydemersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Scyliorhinidae	*Galeus melastomus*	Black-mouthed dogfish	Lusitanian	Demersal eggs	90	Bentho-piscivore	4.2	Slope	Bathydemersal
Scyliorhinidae	*Galeus murinus*	Mouse cat shark	Boreal	Demersal eggs	63	Bentho-piscivore	4	Slope	Bathydemersal
Scyliorhinidae	*Scyliorhinus canicula*	Lesser spotted dogfish	Lusitanian	Demersal eggs	80	Bentho-piscivore	3.7	Inner shelf	Demersal
Scyliorhinidae	*Scyliorhinus stellaris*	Nurse hound	Lusitanian	Demersal eggs	162	Piscivore	4.0	Inner shelf	Reef-associated
Pseudotriakidae	*Pseudotriakis microdon*	False cat shark	Atlantic	Viviparous	295	Piscivore	4.3	Slope	Demersal
Leptochariidae	*Leptocharias smithii*	Barbelled hound shark	African	Viviparous	80	Piscivore	3.8	Inner shelf	Demersal
Triakidae	*Galeorhinus galeus*	Tope shark	Lusitanian	Viviparous	200	Piscivore	4.2	Shelf	Benthopelagic
Triakidae	*Mustelus asterias*	Starry smooth hound	Lusitanian	Viviparous	140	Carcinophage	3.7	Shelf	Demersal
Triakidae	*Mustelus mustelus*	Smooth hound	Lusitanian	Viviparous	150	Carcinophage	3.8	Shelf	Demersal
Triakidae	*Mustelus punctulatus*	Black-spotted smooth-hound	Lusitanian	Viviparous	190	Carcinophage	3.8	Inner shelf	Demersal
Hemigaleidae	*Paragaleus pectoralis*	Atlantic weasel shark	African	Viviparous	138	Piscivore	4.3	Inner shelf	Demersal
Carcharhinidae	*Carcharhinus altimus*	Big-nose shark	Atlantic (African)	Viviparous	300	Piscivore	4.5	Shelf	Reef-associated
Carcharhinidae	*Carcharhinus brevipinna*	Spinner shark	Lusitanian	Viviparous	300	Piscivore	4.2	Oceanic/shelf	Pelagic
Carcharhinidae	*Carcharhinus falciformis*	Silky shark	Atlantic	Viviparous	350	Piscivore	4.5	Oceanic	Pelagic
Carcharhinidae	*Carcharhinus galapagensis*	Galapagos shark	Atlantic (African)	Viviparous	370	Piscivore	4.2	Shelf	Reef-associated
Carcharhinidae	*Carcharhinus isodon*	Finetooth shark	African	Viviparous	190	Piscivore	4.2	Shelf	Pelagic
Carcharhinidae	*Carcharhinus leucas*	Bull shark	Atlantic (African)	Viviparous	300	Piscivore	4.3	Shelf	Demersal
Carcharhinidae	*Carcharhinus limbatus*	Black-tip shark	Lusitanian	Viviparous	275	Piscivore	4.2	Oceanic/shelf	Pelagic
Carcharhinidae	*Carcharhinus longimanus*	Oceanic white-tip shark	Atlantic	Viviparous	350	Piscivore	4.2	Oceanic	Epipelagic
Carcharhinidae	*Carcharhinus melanopterus*	Black-tip reef shark	Indo-Pacific	Viviparous	200	Piscivore	3.9	Shelf	Reef-associated
Carcharhinidae	*Carcharhinus obscurus*	Dusky shark	Lusitanian	Viviparous	420	Piscivore	4.5	Oceanic/shelf	Pelagic
Carcharhinidae	*Carcharhinus plumbeus*	Sand-bar shark	Lusitanian	Viviparous	250	Piscivore	4.5	Shelf	Demersal
Carcharhinidae	*Carcharhinus signatus*	Night shark	Atlantic	Viviparous	280	Piscivore	4.5	Oceanic	Pelagic
Carcharhinidae	*Galeocerdo cuvier*	Tiger shark	Atlantic (African)	Viviparous	740	Piscivore	4.5	Oceanic/shelf	Benthopelagic
Carcharhinidae	*Negaprion brevirostris*	Lemon shark	Atlantic (African)	Viviparous	320	Piscivore	4.4	Shelf	Demersal
Carcharhinidae	*Prionace glauca*	Blue shark	Atlantic	Viviparous	383	Piscivore	4.2	Oceanic	Epipelagic
Carcharhinidae	*Rhizoprionodon acutus*	Milk shark	Atlantic (African)	Viviparous	105	Bentho-piscivore	4.3	Inner shelf	Demersal
Sphyrnidae	*Sphyrna lewini*	Scalloped hammerhead	Lusitanian	Viviparous	430	Piscivore	4.1	Oceanic/shelf	Pelagic
Sphyrnidae	*Sphyrna mokarran*	Great hammerhead	Atlantic (African)	Viviparous	610	Piscivore	4.3	Oceanic/shelf	Pelagic
Sphyrnidae	*Sphyrna tudes*	Small-eye hammerhead	Mediterranean (?)	Viviparous	148	Piscivore	3.6	Inner shelf	Pelagic
Sphyrnidae	*Sphyrna zygaena*	Common hammerhead	Lusitanian	Viviparous	400	Piscivore	4.5	Oceanic/shelf	Epipelagic

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
Dalatiidae	*Centroscyllium fabricii*	Black dogfish	Arctic	Viviparous	107	Benthivore	3.9	Slope	Bathydemersal
Dalatiidae	*Etmopterus princeps*	Great lantern-shark	Atlantic	Viviparous	75	Piscivore	4.2	Slope	Bathydemersal
Dalatiidae	*Etmopterus pusillus*	Smooth lantern-shark	Atlantic	Viviparous	50	Piscivore	4.2	Slope	Bathydemersal
Dalatiidae	*Etmopterus spinax*	Velvet belly	Atlantic	Viviparous	45	Piscivore	3.8	Slope	Bathydemersal
Dalatiidae	*Centroscymnus coelolepis*	Portuguese dogfish	Atlantic	Viviparous	120	Piscivore	4.3	Slope	Bathydemersal
Dalatiidae	*Centroscymnus crepidater*	Long-nose velvet dogfish	Atlantic	Viviparous	130	Piscivore	4.2	Slope	Bathydemersal
Dalatiidae	*Centroscymnus cryptacanthus*	Short-nose velvet dogfish	Atlantic	Viviparous	70	Piscivore	NA	Slope	Bathydemersal
Dalatiidae	*Scymnodalatias garricki*	Azores dogfish	Atlantic	Viviparous	NA	Unknown	NA	Unknown	Bathypelagic
Dalatiidae	*Scymnodon obscurus*	Small-mouth velvet dogfish	Atlantic	Viviparous	70	Piscivore	4.0	Slope	Bathydemersal
Dalatiidae	*Scymnodon ringens*	Knife-tooth dogfish	Atlantic	Viviparous	110	Piscivore	3.9	Slope	Bathydemersal
Dalatiidae	*Somniosus microcephalus*	Greenland shark	Boreal	Viviparous	650	Piscivore	4.2	Slope	Benthopelagic
Dalatiidae	*Somniosus rostratus*	Little sleeper shark	Lusitanian	Viviparous	143	Piscivore	4.2	Slope	Bathydemersal
Dalatiidae	*Oxynotus centrina*	Angular rough-shark	Atlantic	Viviparous	150	Unknown	3.1	Slope	Bathydemersal
Dalatiidae	*Oxynotus paradoxus*	Sail-fin rough-shark	Atlantic	Viviparous	120	Unknown	4.0	Slope	Bathydemersal
Dalatiidae	*Dalatias licha*	Darkie charlie	Atlantic	Viviparous	180	Piscivore	4.2	Slope	Bathydemersal
Dalatiidae	*Squaliolus laticaudus*	Spined pygmy shark	Atlantic	Viviparous	25	Piscivore	4.2	Slope	Bathypelagic
Centrophoridae	*Centrophorus granulosus*	Gulper shark	Atlantic	Viviparous	160	Piscivore	4.1	Slope	Bathydemersal
Centrophoridae	*Centrophorus lusitanicus*	Low-fin gulper shark	Atlantic	Viviparous	160	Piscivore	4.4	Slope	Bathydemersal
Centrophoridae	*Centrophorus squamosus*	Leaf-scale gulper shark	Atlantic	Viviparous	160	Piscivore	4.2	Slope	Bathydemersal
Centrophoridae	*Centrophorus uyato*	Little gulper shark	Atlantic	Viviparous	110	Piscivore	4.5	Slope	Bathydemersal
Centrophoridae	*Deania calcea*	Bird-beak dogfish	Atlantic	Viviparous	122	Piscivore	4.2	Slope	Bathydemersal
Centrophoridae	*Deania hystricosa*	Rough long-nose dogfish	Atlantic	Viviparous	109	Unknown	4.5	Slope	Bathydemersal
Centrophoridae	*Deania profundorum*	Arrow-head dogfish	Atlantic	Viviparous	79	Piscivore	4.5	Slope	Bathydemersal
Squalidae	*Squalus acanthias*	Spurdog	Boreal	Viviparous	105	Piscivore	4.3	Shelf	Benthopelagic
Squalidae	*Squalus blainvillei*	Long-nose spurdog	Lusitanian	Viviparous	100	Piscivore	4.0	Shelf	Demersal
Squalidae	*Squalus megalops*	Short-nose spurdog	Uncertain	Viviparous	71	Piscivore	4.3	Outer shelf	Demersal
Echinorhinidae	*Echinorhinus brucus*	Bramble shark	Atlantic	Viviparous	250	Piscivore	4.4	Slope	Bathydemersal
Squatinidae	*Squatina aculeata*	Saw-back angel shark	Lusitanian	Viviparous	188	Piscivore	4.0	Shelf	Demersal
Squatinidae	*Squatina oculata*	Smooth-back angel shark	Lusitanian	Viviparous	160	Piscivore	4.0	Shelf	Demersal
Squatinidae	*Squatina squatina*	Angel shark	Lusitanian	Viviparous	250	Piscivore	4.1	Inner shelf	Demersal
Pristidae	*Pristis pectinata*	Small-tooth sawfish	Atlantic (African)	Viviparous	760	Bentho-piscivore	4.5	Inner shelf	Demersal
Pristidae	*Pristis pristis*	Common sawfish	African	Viviparous	500	Bentho-piscivore	4.0	Inner shelf	Demersal
Torpedinidae	*Torpedo marmorata*	Marbled electric ray	Lusitanian	Viviparous	60	Piscivore	4.5	Shelf	Demersal
Torpedinidae	*Torpedo nobiliana*	Common electric ray	Lusitanian	Viviparous	180	Piscivore	4.5	Shelf	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Torpedinidae	*Torpedo torpedo*	Common torpedo	Lusitanian	Viviparous	60	Piscivore	4.5	Shelf	Demersal
Rhinobatidae	*Rhinobatos cemiculus*	Black-chin guitarfish	Lusitanian	Viviparous	242	Bentho-piscivore	4.0	Shelf	Demersal
Rhinobatidae	*Rhinobatos rhinobatos*	Common guitarfish	Lusitanian	Viviparous	100	Bentho-piscivore	4.1	Shelf	Demersal
Rajidae	*Amblyraja hyperborea*	Arctic skate	Arctic	Demersal eggs	106	Bentho-piscivore	3.5	Slope	Demersal
Rajidae	*Amblyraja jenseni*	Jensen's skate	Boreal	Demersal eggs	74	Bentho-piscivore	3.6	Slope	Bathydemersal
Rajidae	*Amblyraja radiata*	Starry ray	Boreal	Demersal eggs	90	Piscivore	4.0	Shelf	Demersal
Rajidae	*Bathyraja pallida*	Pale ray	Atlantic	Demersal eggs	160	Unknown	3.6	Slope	Bathydemersal
Rajidae	*Bathyraja richardsoni*	Richardson's ray	Atlantic	Demersal eggs	175	Bentho-piscivore	4.0	Slope	Bathydemersal
Rajidae	*Bathyraja spinicauda*	Spine-tail ray	Arctic	Demersal eggs	170	Bentho-piscivore	3.5	Slope	Bathydemersal
Rajidae	*Dipturus batis*	Common skate	Boreal	Demersal eggs	250	Piscivore	4.0	Shelf	Demersal
Rajidae	*Dipturus linteus*	Sail ray	Boreal	Demersal eggs	110	Benthivore	3.5	Slope	Demersal
Rajidae	*Dipturus nidarosiensis*	Black skate	Boreal	Demersal eggs	200	Piscivore	3.5	Slope	Bathydemersal
Rajidae	*Dipturus oxyrinchus*	Long-nose skate	Lusitanian	Demersal eggs	150	Piscivore	3.5	Slope	Bathydemersal
Rajidae	*Leucoraja circularis*	Sandy ray	Lusitanian	Demersal eggs	120	Piscivore	3.5	Outer shelf	Demersal
Rajidae	*Leucoraja fullonica*	Shagreen ray	Boreal	Demersal eggs	100	Piscivore	3.5	Outer shelf	Demersal
Rajidae	*Leucoraja melitensis*	Maltese ray	Mediterranean	Demersal eggs	50	Benthivore	3.3	Shelf	Demersal
Rajidae	*Leucoraja naevus*	Cuckoo ray	Lusitanian	Demersal eggs	70	Piscivore	3.9	Shelf	Demersal
Rajidae	*Malacoraja kreffti*	Krefft's ray	Atlantic	Demersal eggs	70	Unknown	3.8	Slope	Bathydemersal
Rajidae	*Malacoraja spinacidermis*	Rough-skin skate	Atlantic	Demersal eggs	70	Unknown	3.8	Slope	Bathydemersal
Rajidae	*Neoraja caerulea*	Blue ray	Atlantic	Demersal eggs	30	Bentho-piscivore	3.5	Slope	Bathydemersal
Rajidae	*Raja africana*	African ray	African	Demersal eggs	80	Bentho-piscivore	4.0	Shelf	Demersal
Rajidae	*Raja asterias*	Starry ray	Mediterranean/African	Demersal eggs	70	Bentho-piscivore	3.5	Shelf	Demersal
Rajidae	*Raja brachyura*	Blonde ray	Lusitanian	Demersal eggs	120	Piscivore	4.0	Inner shelf	Demersal
Rajidae	*Raja clavata*	Thornback ray	Lusitanian	Demersal eggs	90	Bentho-piscivore	3.8	Inner shelf	Demersal
Rajidae	*Raja maderensis*	Madeira ray	Macaronesia	Demersal eggs	85	Benthivore	3.5	Shelf	Demersal
Rajidae	*Raja microocellata*	Small-eyed ray	Lusitanian	Demersal eggs	80	Piscivore	3.9	Inner shelf	Demersal
Rajidae	*Raja miraletus*	Brown ray	Lusitanian	Demersal eggs	63	Bentho-piscivore	3.8	Shelf	Demersal
Rajidae	*Raja montagui*	Spotted ray	Lusitanian	Demersal eggs	80	Bentho-piscivore	3.7	Inner shelf	Demersal
Rajidae	*Raja polystigma*	Speckled ray	African	Demersal eggs	60	Bentho-piscivore	4.0	Shelf	Demersal
Rajidae	*Raja radula*	Rough ray	Mediterranean/African	Demersal eggs	70	Bentho-piscivore	3.7	Shelf	Demersal
Rajidae	*Raja rondeleti*	Rondelet's ray	Mediterranean	Demersal eggs	50	Unknown	3.5	Shelf	Demersal
Rajidae	*Raja undulata*	Undulate ray	Lusitanian	Demersal eggs	100	Bentho-piscivore	3.5	Inner shelf	Demersal
Rajidae	*Rajella bathyphila*	Deep-water ray	Atlantic	Demersal eggs	90	Unknown	3.9	Slope	Demersal
Rajidae	*Rajella bigelowi*	Bigelow's ray	Atlantic	Demersal eggs	55	Unknown	3.8	Slope	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Rajidae	*Rajella fyllae*	Round skate	Boreal	Demersal eggs	55	Bentho-piscivore	3.3	Slope	Bathydemersal
Rajidae	*Rajella kukujevi*	Mid-Atlantic skate	Atlantic	Demersal eggs	NA	Unknown	NA	Slope	Bathydemersal
Rajidae	*Rostroraja alba*	Bottle-nosed skate	Lusitanian	Demersal eggs	230	Bentho-piscivore	4.4	Shelf	Demersal
Dasyatidae	*Dasyatis centroura*	Rough-tail sting ray	Lusitanian	Viviparous	205	Bentho-piscivore	3.8	Shelf	Demersal
Dasyatidae	*Dasyatis pastinaca*	Sting ray	Lusitanian	Viviparous	60 (DW)	Bentho-piscivore	4.1	Shelf	Demersal
Dasyatidae	*Dasyatis tortonesei*	Tortonese's sting ray	Mediterranean	Viviparous	205	Bentho-piscivore	4.0	Shelf	Demersal
Dasyatidae	*Dasyatis violacea*	Pelagic sting ray	Atlantic	Viviparous	80 (DW)	Piscivore	4.4	Oceanic	Epipelagic
Dasyatidae	*Himantura uarnak*	Honeycomb sting ray	Indo-Pacific	Viviparous	236	Bentho-piscivore	3.6	Shelf	Demersal
Dasyatidae	*Taeniura grabata*	Round sting ray	African	Viviparous	250	Bentho-piscivore	4.0	Inner shelf	Demersal
Gymnuridae	*Gymnura altavela*	Spiny butterfly ray	Lusitanian	Viviparous	77	Bentho-piscivore	4.5	Inner shelf	Demersal
Myliobatidae	*Myliobatis aquila*	Eagle ray	Lusitanian	Viviparous	83 (DW)	Benthivore	3.6	Shelf	Benthopelagic
Myliobatidae	*Pteromylaeus bovinus*	Bull ray	African	Viviparous	250	Benthivore	3.8	Inner shelf	Benthopelagic
Myliobatidae	*Rhinoptera marginata*	Lusitanian cow-nose ray	Lusitanian	Viviparous	99	Benthivore	3.8	Shelf	Benthopelagic
Myliobatidae	*Manta birostris*	Giant manta	Atlantic (African)	Viviparous	134	Plankto-piscivore	3.5	Shelf	Pelagic
Myliobatidae	*Mobula mobular*	Devilfish	Lusitanian	Viviparous	140	Plankto-piscivore	3.7	Shelf	Pelagic
Myliobatidae	*Mobula tarapacana*	Chilean devilray	Atlantic (African)	Viviparous	300 (DW)	Plankto-piscivore	3.8	Shelf	Pelagic
Chimaeridae	*Chimaera monstrosa*	Rabbitfish	Atlantic	Demersal eggs	100	Benthivore	3.5	Slope	Bathydemersal
Chimaeridae	*Hydrolagus affinis*	Small-eyed rabbitfish	Atlantic	Demersal eggs	130	Benthivore	4.0	Slope	Bathydemersal
Chimaeridae	*Hydrolagus mirabilis*	Large-eyed rabbitfish	Atlantic	Demersal eggs	50	Benthivore	3.9	Slope	Bathydemersal
Chimaeridae	*Hydrolagus pallidus*	-	Atlantic	Demersal eggs	NA	Unknown	NA	Slope	Bathydemersal
Rhinochimaeridae	*Harriotta haeckeli*	Small-spine spookfish	Atlantic	Demersal eggs	65	Unknown	3.5	Oceanic	Bathydemersal
Rhinochimaeridae	*Harriotta raleighana*	Narrow-nose chimaera	Atlantic	Demersal eggs	65	Benthivore	3.5	Slope	Bathydemersal
Rhinochimaeridae	*Rhinochimaera atlantica*	Spear nose chimaera	Atlantic	Demersal eggs	140	Benthivore	3.5	Slope	Bathydemersal
Acipenseridae	*Acipenser gueldenstaedtii*	Danube sturgeon	Sarmatic	Fluvial spawner	235	Benthivore	3.1	Coastal	Demersal
Acipenseridae	*Acipenser naccarii*	Adriatic sturgeon	Mediterranean	Fluvial spawner	200	Benthivore	3.4	Coastal	Demersal
Acipenseridae	*Acipenser nudiventris*	Fringe-barbel sturgeon	Sarmatic	Fluvial spawner	200	Benthivore	3.3	Coastal	Demersal
Acipenseridae	*Acipenser stellatus*	Starry sturgeon	Mediterranean	Fluvial spawner	220	Benthivore	3.1	Coastal	Demersal
Acipenseridae	*Acipenser sturio*	Sturgeon	Lusitanian	Fluvial spawner	350	Benthivore	3.5	Coastal	Demersal
Acipenseridae	*Huso huso*	Beluga	Samatic	Fluvial spawner	500	Bentho-piscivore	4.1	Coastal	Demersal
Megalopidae	*Megalops atlanticus*	Tarpon	Atlantic	Demersal eggs	250	Piscivore	4.5	Inner shelf	Pelagic
Halosauridae	*Aldrovandia affinis*	-	Atlantic	Leptocephalus larvae	55	Benthivore	3.3	Slope	Benthopelagic
Halosauridae	*Aldrovandia phalacra*	Hawaiian halosaurid fish	Atlantic	Leptocephalus	50	Benthivore	3.2	Slope	Benthopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
				larvae					
Halosauridae	*Halosauropsis macrochir*	Abyssal halosaur	Atlantic	Leptocephalus larvae	90	Benthivore	3.3	Slope	Benthopelagic
Halosauridae	*Halosaurus johnsonianus*	Halosaur	Atlantic	Leptocephalus larvae	50	Benthivore	3.1	Slope	Benthopelagic
Halosauridae	*Halosaurus ovenii*	-	Atlantic	Leptocephalus larvae	60	Benthivore	3.5	Slope	Benthopelagic
Notacanthidae	*Notacanthus bonapartei*	Short-fin spiny eel	Boreal	Leptocephalus larvae	26	Benthivore	3.3	Slope	Benthopelagic
Notacanthidae	*Notacanthus chemnitzii*	Spiny eel	Atlantic	Leptocephalus larvae	120	Benthivore	3.5	Slope	Benthopelagic
Notacanthidae	*Polyacanthonotus challengeri*	Long-nose tapirfish	Atlantic	Leptocephalus larvae	60	Benthivore	3.2	Oceanic	Benthopelagic
Notacanthidae	*Polyacanthonotus rissoanus*	Small-mouth spiny eel	Atlantic	Leptocephalus larvae	55	Benthivore	3.5	Slope	Benthopelagic
Anguillidae	*Anguilla anguilla*	European eel	Atlantic	Leptocephalus larvae	100	Bentho-piscivore	3.5	Coastal	Demersal
Heterenchelyidae	*Panturichthys fowleri*	Fowler's short-face eel	Mediterranean	Leptocephalus larvae	89	Unknown	3.9	Inner shelf	Demersal
Heterenchelyidae	*Panturichthys mauritanicus*	Mauritanean short-face eel	African	Leptocephalus larvae	84	Benthivore	3.2	Inner shelf	Demersal
Chlopsidae (Xenocongridae)	*Chlopsis bicolor*	Bicoloured false moray	Lusitanian	Leptocephalus larvae	42	Unknown	3.7	Shelf	Demersal
Muraenidae	*Anarchias euryurus*	-	African	Leptocephalus larvae	25	Piscivore	NA	Shelf	Demersal
Muraenidae	*Enchelycore anatina*	Fang-tooth moray	Macaronesia	Leptocephalus larvae	120	Piscivore	4.0	Shelf	Reef-associated
Muraenidae	*Gymnothorax maderensis*	Shark-tooth moray	African	Leptocephalus larvae	100	Piscivore	4.1	Shelf	Reef-associated
Muraenidae	*Gymnothorax polygonius*	Polygon moray	Atlantic (African)	Leptocephalus larvae	84	Piscivore	4.1	Shelf	Reef-associated
Muraenidae	*Gymnothorax unicolor*	Brown moray	Lusitanian	Leptocephalus larvae	100	Piscivore	3.4	Shelf	Reef-associated
Muraenidae	*Gymnothorax vicinus*	Purple-mouth moray	Atlantic (African)	Leptocephalus larvae	122	Piscivore	4.3	Shelf	Reef-associated
Muraenidae	*Muraena helena*	Moray eel	Lusitanian	Leptocephalus larvae	130	Piscivore	4.2	Coastal	Reef-associated
Synaphobranchidae	*Dysomma brevirostre*	Pig-nosed arrow-tooth eel	Lusitanian	Leptocephalus larvae	30	Unknown	3.5	Slope	Benthopelagic
Synaphobranchidae	*Ilyophis arx*	-	Atlantic	Leptocephalus	45	Unknown	3.6	Oceanic	Bathydemersal

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
				larvae					
Synaphobranchidae	*Ilyophis blachei*	–	Atlantic	Leptocephalus larvae	79	Benthivore	3.7	Slope	Benthopelagic
Synaphobranchidae	*Ilyophis brunneus*	Muddy arrow-tooth eel	Atlantic	Leptocephalus larvae	58	Unknown	3.2	Slope	Benthopelagic
Synaphobranchidae	*Haptenchelys texis*	–	Atlantic	Leptocephalus larvae	51	Unknown	3.6	Oceanic	Bathydemersal
Synaphobranchidae	*Histiobranchus bathybius*	Deepwater arrow-tooth eel	Atlantic	Leptocephalus larvae	137	Unknown	3.8	Oceanic	Benthopelagic
Synaphobranchidae	*Synaphobranchus kaupi*	Kaup's arrow-tooth eel	Atlantic	Leptocephalus larvae	100	Bentho-piscivore	4.1	Slope	Benthopelagic
Synaphobranchidae	*Simenchelys parasiticus*	Snub-nosed eel	Atlantic	Leptocephalus larvae	61	Benthivore	3.7	Slope	Benthopelagic
Ophichthidae	*Apterichtthus anguiformis*	Slender finless eel	Lusitanian	Leptocephalus larvae	49	Unknown	4.0	Shelf	Demersal
Ophichthidae	*Apterihcthus caecus*	European finless eel	Lusitanian	Leptocephalus larvae	60	Unknown	4.1	Shelf	Demersal
Ophichthidae	*Dalophis imberbis*	Armless snake eel	Lusitanian	Leptocephalus larvae	150	Unknown	4.0	Shelf	Demersal
Ophichthidae	*Echelus myrus*	Painted eel	Lusitanian	Leptocephalus larvae	100	Unknown	3.9	Shelf	Demersal
Ophichthidae	*Ophichthus ophis*	Spotted snake eel	African	Leptocephalus larvae	210	Unknown	4.3	Inner shelf	Demersal
Ophichthidae	*Ophichthus rufus*	Rufus snake eel	Mediterranean	Leptocephalus larvae	60	Unknown	4.0	Shelf	Demersal
Ophichthidae	*Ophisurus serpens*	Serpent eel	Lusitanian	Leptocephalus larvae	250	Unknown	4.1	Shelf	Demersal
Ophichthidae	*Pisodonophis semicinctus*	Saddled snake eel	African	Leptocephalus larvae	80	Benthivore	3.5	Inner shelf	Demersal
Congridae	*Bathyuroconger vicinus*	Large-toothed conger	Atlantic	Leptocephalus larvae	88	Unknown	4.0	Slope	Bathydemersal
Congridae	*Conger conger*	Conger eel	Lusitanian	Leptocephalus larvae	300	Piscivore	4.3	Shelf	Reef-associated
Congridae	*Gnathophis codoniphorus*	–	Macaronesia	Leptocephalus larvae	NA	Unknown	NA	Slope	Demersal
Congridae	*Gnathophis mystax*	Thin-lip conger	Mediterranean	Leptocephalus larvae	60	Bentho-piscivore	3.6	Outer shelf	Demersal
Congridae	*Pseudophichthys splendens*	Purple-mouthed conger	African	Leptocephalus larvae	50	Unknown	3.8	Slope	Demersal
Congridae	*Ariosoma balearicum*	Band-tooth conger	Lusitanian	Leptocephalus	35	Unknown	3.9	Shelf	Demersal

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
				larvae					
Congridae	*Paraconger macrops*	Black-spot conger	Macaronesia	Leptocephalus larvae	50	Piscivore	4.0	Shelf	Demersal
Congridae	*Heteroconger longissimus*	Garden conger	African	Leptocephalus larvae	60	Benthivore	3.1	Shelf	Demersal
Muraenesocidae	*Cynoponticus ferox*	Guinea pike conger	African	Leptocephalus larvae	200	Piscivore	3.6	Shelf	Demersal
Muraenesocidae	*Muraenesox cinereus*	Dagger-tooth pike conger	Indo-Pacific	Leptocephalus larvae	220	Piscivore	4.1	Shelf	Demersal
Derichthyidae	*Derichthys serpentinus*	Narrow-necked oceanic eel	Atlantic	Leptocephalus larvae	40	Benthivore	3.1	Oceanic	Bathypelagic
Derichthyidae	*Nessorhamphus ingolfianus*	Duckbill oceanic eel	Atlantic	Leptocephalus larvae	60	Benthivore	3.5	Oceanic	Bathypelagic
Nemichthyidae	*Avocettina infans*	Avocet snipe eel	Atlantic	Leptocephalus larvae	75	Planktivore	3.5	Oceanic	Bathypelagic
Nemichthyidae	*Nemichthys curvirostris*	Spotted snipe eel	Atlantic	Leptocephalus larvae	150	Planktivore	3.3	Oceanic	Bathypelagic
Nemichthyidae	*Nemichthys scolopaceus*	Slender snipe eel	Atlantic	Leptocephalus larvae	130	Planktivore	3.5	Slope	Bathypelagic
Serrivomeridae	*Serrivomer beanii*	Bean's saw-toothed eel	Atlantic	Leptocephalus larvae	78	Bentho-piscivore	3.9	Oceanic	Bathypelagic
Serrivomeridae	*Serrivomer lanceolatoides*	Short-tooth saw-palate eel	Atlantic	Leptocephalus larvae	65	Unknown	3.5	Oceanic	Bathypelagic
Nettastomatidae	*Facciolella oxyrhyncha*	Facciola's sorcerer	African	Leptocephalus larvae	79	Benthivore	3.5	Slope	Bathydemersal
Nettastomatidae	*Nettastoma melanurum*	Black-fin sorcerer	African	Leptocephalus larvae	77	Benthivore	3.5	Slope	Bathydemersal
Nettastomatidae	*Saurenchelys cancrivora*	Slender sorcerer	African	Leptocephalus larvae	65	Unknown	3.4	Slope	Demersal
Nettastomatidae	*Venefica proboscidea*	Whip-snout sorcerer	African	Leptocephalus larvae	100	Unknown	3.5	Slope	Demersal
Cyematidae (Cyemidae)	*Cyema atrum*	-	Atlantic	Leptocephalus larvae	13	Unknown	NA	Oceanic	Bathypelagic
Saccopharyngidae	*Saccopharynx ampullaceus*	Gulper eel	Atlantic	Leptocephalus larvae	161	Piscivore	4.5	Oceanic	Bathypelagic
Saccopharyngidae	*Saccopharynx harrisoni*	-	Atlantic	Leptocephalus larvae	166	Piscivore	NA	Oceanic	Bathypelagic
Saccopharyngidae	*Saccopharynx hjorti*	-	Atlantic	Leptocephalus larvae	NA	Unknown	NA	Oceanic	Bathypelagic
Saccopharyngidae	*Saccopharynx*	-	Atlantic	Leptocephalus	NA	Unknown	NA	Oceanic	Bathypelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
	paucovertebratis			larvae					
Saccopharyngidae	*Saccopharynx ramosus*	–	Atlantic	Leptocephalus larvae	62	Piscivore	4.0	Oceanic	Bathypelagic
Saccopharyngidae	*Saccopharynx thalassa*	–	Atlantic	Leptocephalus larvae	107	Piscivore	4.2	Oceanic	Bathypelagic
Saccopharyngidae	*Saccopharynx trilobatus*	–	Atlantic	Leptocephalus larvae	NA	Unknown	NA	Oceanic	Bathypelagic
Eurypharyngidae	*Eurypharynx pelecanoides*	Pelican eel	Atlantic	Leptocephalus larvae	100	Piscivore	4.5	Oceanic	Bathypelagic
Monognathidae	*Monognathus bertini*	–	Atlantic	Leptocephalus larvae	10	Unknown	3.2	Oceanic	Bathypelagic
Monognathidae	*Monognathus boehlkei*	–	Atlantic	Leptocephalus larvae	7	Unknown	3.6	Oceanic	Bathypelagic
Monognathidae	*Monognathus herringi*	–	Atlantic	Leptocephalus larvae	5	Unknown	3.2	Oceanic	Bathypelagic
Monognathidae	*Monognathus jesperseni*	–	Atlantic	Leptocephalus larvae	11	Unknown	3.6	Oceanic	Bathypelagic
Monognathidae	*Monognathus nigeli*	–	Atlantic	Leptocephalus larvae	6	Unknown	NA	Oceanic	Bathypelagic
Clupeidae	*Alosa alosa*	Allis shad	Lusitanian	Fluvial spawner	70	Planktivore	3.6	Shelf	Pelagic
Clupeidae	*Alosa caspia*	Caspian shad	Sarmatic	Fluvial spawner	32	Planktivore	3.5	Inner shelf	Pelagic
Clupeidae	*Alosa fallax*	Twaite shad	Lusitanian	Fluvial spawner	50	Planktivore	3.6	Shelf	Pelagic
Clupeidae	*Alosa pontica*	Pontic shad	Sarmatic	Fluvial spawner	39	Planktivore	3.9	Inner shelf	Pelagic
Clupeidae	*Clupea harengus*	Herring	Boreal	Demersal eggs	40	Planktivore	3.2	Shelf	Benthopelagic
Clupeidae	*Clupeonella cultriventris*	Black Sea sprat	Sarmatic	Planktonic eggs	18	Planktivore	3.0	Coastal	Pelagic
Clupeidae	*Dussumieria acuta*	Rainbow sardine	Indo-Pacific	Planktonic eggs	24	Planktivore	3.4	Coastal	Pelagic
Clupeidae	*Herklotsichthys punctatus*	Spot-back herring	Indo-Pacific	Planktonic eggs	10	Planktivore	3.2	Coastal	Pelagic
Clupeidae	*Sardina pilchardus*	Pilchard	Lusitanian	Planktonic eggs	25	Planktivore	2.6	Shelf	Pelagic
Clupeidae	*Sardinella aurita*	Round sardinella	Lusitanian	Planktonic eggs	31	Planktivore	3.0	Shelf	Pelagic
Clupeidae	*Sardinella maderensis*	Madeiran sardinella	Lusitanian	Planktonic eggs	41	Planktivore	3.2	Shelf	Pelagic
Clupeidae	*Spratelloides delicatulus*	Delicate round herring	Indo-Pacific	Planktonic eggs	9	Planktivore	3.1	Coastal	Pelagic
Clupeidae	*Sprattus sprattus*	Sprat	Lusitanian	Planktonic eggs	16	Planktivore	3.0	Shelf	Pelagic
Engraulidae	*Engraulis encrasicolus*	European anchovy	Lusitanian	Planktonic eggs	20	Planktivore	3.1	Shelf	Pelagic
Argentinidae	*Argentina silus*	Great silversmelt	Boreal	Planktonic eggs	60	Planktivore	3.3	Slope	Benthopelagic
Argentinidae	*Argentina sphyraena*	Lesser silversmelt	Lusitanian	Planktonic eggs	32	Planktivore	3.6	Shelf	Benthopelagic
Argentinidae	*Glossanodon leioglossus*	Small-toothed argentine	African	Planktonic eggs	20	Planktivore	3.5	Outer shelf	Benthopelagic
Microstomatidae	*Microstoma microstoma*	Slender argentine	Atlantic	Planktonic eggs	21	Planktivore	3.4	Slope	Mesopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Microstomatidae	*Nansenia groenlandica*	Greenland argentine	Atlantic	Planktonic eggs	30	Planktivore	3.3	Oceanic	Mesopelagic
Microstomatidae	*Nansenia iberica*	–	Mediterranean	Planktonic eggs	31	Planktivore	3.3	Slope	Mesopelagic
Microstomatidae	*Nansenia longicauda*	–	Atlantic	Planktonic eggs	13	Planktivore	NA	Slope	Mesopelagic
Microstomatidae	*Nansenia oblita*	–	Atlantic	Planktonic eggs	22	Planktivore	3.2	Oceanic	Mesopelagic
Microstomatidae	*Nansenia tenera*	–	Atlantic	Planktonic eggs	11	Planktivore	NA	Slope	Mesopelagic
Bathylagidae	*Bathylagichthys greyae*	–	Atlantic	Planktonic eggs	20	Planktivore	3.4	Oceanic	Bathypelagic
Bathylagidae	*Bathylagus euryops*	Golter blacksmelt	Boreal	Planktonic eggs	13	Planktivore	3.4	Oceanic	Bathypelagic
Bathylagidae	*Dolicholagus longirostris*	Long-snout blacksmelt	Atlantic	Planktonic eggs	21	Planktivore	3.4	Oceanic	Bathypelagic
Bathylagidae	*Melanolagus bericoides*	–	Atlantic	Planktonic eggs	24	Planktivore	3.4	Oceanic	Bathypelagic
Opisthoproctidae	*Bathylychnops exilis*	Javelin spookfish	Atlantic	Planktonic eggs	50	Unknown	NA	Oceanic	Mesopelagic
Opisthoproctidae	*Dolichopteryx longipes*	Brown-snout spookfish	Atlantic	Planktonic eggs	18	Unknown	3.0	Oceanic	Mesopelagic
Opisthoproctidae	*Opisthoproctus grimaldii*	Mirrorbelly	Atlantic	Planktonic eggs	10	Unknown	4.0	Oceanic	Mesopelagic
Opisthoproctidae	*Opisthoproctus soleatus*	Barrel-eye	Atlantic	Planktonic eggs	13	Unknown	3.6	Oceanic	Mesopelagic
Opisthoproctidae	*Rhynchohyalus natalensis*	–	Atlantic	Planktonic eggs	20	Unknown	3.7	Oceanic	Mesopelagic
Alepocephalidae	*Alepocephalus agassizii*	Agassiz' slickhead	Atlantic	Demersal eggs (?)	96	Plankto-piscivore	3.4	Oceanic	Bathydemersal
Alepocephalidae	*Alepocephalus australis*	Southern Atlantic smooth-head	Atlantic	Demersal eggs (?)	73	Plankto-piscivore	3.5	Oceanic	Bathydemersal
Alepocephalidae	*Alepocephalus bairdii*	Baird's smooth-head	Atlantic	Demersal eggs (?)	122	Plankto-piscivore	3.6	Oceanic	Bathydemersal
Alepocephalidae	*Alepocephalus productus*	Smalleye smooth-head	Atlantic	Demersal eggs (?)	50	Plankto-piscivore	3.5	Oceanic	Bathydemersal
Alepocephalidae	*Alepocephalus rostratus*	Risso's smooth-head	Atlantic	Demersal eggs (?)	61	Plankto-piscivore	3.5	Oceanic	Bathydemersal
Alepocephalidae	*Asquamiceps velaris*	Fan-fin smooth-head	Atlantic	Demersal eggs (?)	17	Unknown	NA	Oceanic	Bathypelagic
Alepocephalidae	*Bajacalifornia calcarata*	Brown slickhead	Atlantic	Demersal eggs (?)	39	Unknown	NA	Slope	Bathypelagic
Alepocephalidae	*Bajacalifornia megalops*	Big-eye smooth-head	Atlantic	Demersal eggs (?)	49	Unknown	3.4	Oceanic	Bathypelagic
Alepocephalidae	*Bathylaco nigricans*	Black warrior	Atlantic	Demersal eggs (?)	41	Unknown	3.4	Oceanic	Bathypelagic
Alepocephalidae	*Bathyprion danae*	Fangtooth smooth-head	Atlantic	Uncertain	46	Unknown	3.4	Oceanic	Bathypelagic
Alepocephalidae	*Bathytroctes macrognathus*	–	Atlantic	Uncertain	25	Unknown	NA	Oceanic	Bathypelagic
Alepocephalidae	*Bathytroctes macrolepis*	Koefoed's smooth-head	Atlantic	Uncertain	49	Unknown	3.4	Oceanic	Bathypelagic
Alepocephalidae	*Bathytroctes michaelsarsi*	Michael Sars' smooth-head	Atlantic	Uncertain	45	Unknown	3.4	Oceanic	Bathypelagic
Alepocephalidae	*Bathytroctes microlepis*	Small-scale smooth-head	Atlantic	Uncertain	39	Unknown	3.4	Oceanic	Bathypelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Alepocephalidae	*Conocara fiolenti*	Fiolenti's smooth-head	Atlantic	Uncertain	37	Unknown	NA	Oceanic	Bathydemersal
Alepocephalidae	*Conocara macropterum*	Long-fin smooth-head	Atlantic	Uncertain	41	Unknown	3.4	Oceanic	Bathydemersal
Alepocephalidae	*Conocara microlepis*	Elongate smooth-head	Atlantic	Uncertain	33	Unknown	3.3	Oceanic	Bathydemersal
Alepocephalidae	*Conocara murrayi*	Murray's smooth-head	Atlantic	Uncertain	41	Unknown	3.4	Oceanic	Bathydemersal
Alepocephalidae	*Conocara salmoneum*	Salmon smooth-head	Atlantic	Uncertain	89	Unknown	3.5	Oceanic	Bathydemersal
Alepocephalidae	*Conocara werneri*	Werner's smooth-head	Atlantic	Uncertain	41	Unknown	3.4	Oceanic	Bathydemersal
Alepocephalidae	*Einara edentula*	Toothless smooth-head	Atlantic	Uncertain	25	Unknown	3.3	Oceanic	Mesopelagic
Alepocephalidae	*Einara macrolepis*	Loose-scale smooth-head	Atlantic	Uncertain	27	Unknown	3.3	Oceanic	Bathypelagic
Alepocephalidae	*Herwigia kreffti*	Krefft's smooth-head	Atlantic	Uncertain	49	Unknown	3.4	Oceanic	Bathypelagic
Alepocephalidae	*Leptoderma macrops*	Grenadier smooth-head	Atlantic	Uncertain	29	Unknown	3.3	Oceanic	Bathydemersal
Alepocephalidae	*Mirognathus normani*	Norman's smooth-head	Atlantic	Uncertain	24	Unknown	3.3	Oceanic	Bathypelagic
Alepocephalidae	*Narcetes erimelas*	–	Atlantic	Uncertain	29	Unknown	NA	Oceanic	Bathypelagic
Alepocephalidae	*Narcetes stomias*	Blackhead salmon	Atlantic	Uncertain	70	Unknown	3.4	Oceanic	Bathydemersal
Alepocephalidae	*Photostylus pycnopterus*	Starry smooth-head	Atlantic	Uncertain	13	Unknown	3.2	Oceanic	Bathypelagic
Alepocephalidae	*Rinoctes nasutus*	Abyssal smooth-head	Atlantic	Uncertain	23	Benthivore	3.2	Oceanic	Bathydemersal
Alepocephalidae	*Rouleina attrita*	Soft-skin smooth-head	Atlantic	Uncertain	59	Unknown	3.4	Oceanic	Bathydemersal
Alepocephalidae	*Rouleina maderensis*	Madeiran smooth-head	Atlantic	Uncertain	39	Unknown	3.3	Oceanic	Bathydemersal
Alepocephalidae	*Talismania antillarum*	Antillean smooth-head	Atlantic	Uncertain	20	Unknown	3.3	Oceanic	Bathydemersal
Alepocephalidae	*Talismania homoptera*	Hair-fin smooth-head	Atlantic	Uncertain	35	Unknown	3.3	Oceanic	Bathydemersal
Alepocephalidae	*Talismania mekistonema*	Thread-fin smooth-head	Atlantic	Uncertain	33	Unknown	3.3	Oceanic	Bathydemersal
Alepocephalidae	*Xenodermichthys copei*	Blunt-snout smooth-head	Atlantic	Uncertain	25	Unknown	3.2	Oceanic	Mesopelagic
Platytroctidae	*Barbantus curvifrons*	Pale-belly searsid	Atlantic	Uncertain	16	Unknown	3.2	Oceanic	Bathypelagic
Platytroctidae	*Holtbyrnia anomala*	Big-head searsid	Atlantic	Uncertain	31	Unknown	3.3	Oceanic	Mesopelagic
Platytroctidae	*Holtbyrnia macrops*	Big-eye searsid	Atlantic	Uncertain	24	Unknown	3.2	Oceanic	Mesopelagic
Platytroctidae	*Maulisia argipalla*	Pale-gold searsid	Atlantic	Uncertain	23	Unknown	3.2	Oceanic	Mesopelagic
Platytroctidae	*Maulisia mauli*	Maul's searsid	Atlantic	Uncertain	24	Unknown	3.2	Oceanic	Mesopelagic
Platytroctidae	*Maulisia microlepis*	Small-scale searsid	Atlantic	Uncertain	31	Unknown	3.3	Oceanic	Bathypelagic
Platytroctidae	*Mentodus rostratus*	–	Atlantic	Uncertain	32	Unknown	NA	Oceanic	Bathypelagic
Platytroctidae	*Normichthys operosus*	Multipore searsid	Atlantic	Uncertain	20	Unknown	3.2	Oceanic	Mesopelagic
Platytroctidae	*Platytroctes apus*	Legless searsid	Atlantic	Uncertain	22	Unknown	3.2	Oceanic	Bathypelagic
Platytroctidae	*Platytroctes mirus*	Leaf searsid	Atlantic	Uncertain	12	Unknown	NA	Oceanic	Bathypelagic
Platytroctidae	*Sagamichthys schnakenbecki*	Schnakenbeck's searsid	Atlantic	Uncertain	33	Unknown	3.3	Oceanic	Benthopelagic
Platytroctidae	*Searsia koefoedi*	Koefoed's searsid	Atlantic	Uncertain	18	Unknown	3.2	Oceanic	Mesopelagic
Osmeridae	*Mallotus villosus*	Capelin	Boreal	Demersal eggs	22	Planktivore	3.1	Inner shelf	Pelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Osmeridae	*Osmerus eperlanus*	Smelt	Boreal	Demersal eggs	45	Bentho-piscivore	3.1	Coastal	Pelagic
Osmeridae	*Osmerus mordax*	Rainbow smelt	Arctic	Fluvial spawner	30	Bentho-piscivore	4.2	Coastal	Pelagic
Leptochilichthyidae	*Leptochilichthys agassizii*	Agassiz' smooth-head	Atlantic	Demersal eggs (?)	38	Unknown	3.3	Oceanic	Bathypelagic
Leptochilichthyidae	*Leptochilichthys pinguis*	Vaillant's smooth-head	Atlantic	Demersal eggs (?)	30	Unknown	3.3	Oceanic	Mesopelagic
Salmonidae	*Coregonus albula*	Vendace	Boreal	Fluvial spawner	45	Planktivore	3.0	Coastal	Pelagic
Salmonidae	*Coregonus autumnalis*	Arctic cisco	Arctic	Fluvial spawner	64	Planktivore	3.6	Coastal	Pelagic
Salmonidae	*Coregonus lavaretus*	Houting	Boreal	Fluvial spawner	57	Planktivore	3.3	Coastal	Pelagic
Salmonidae	*Coregonus sardinella*	Sardine cisco	Arctic	Fluvial spawner	47	Planktivore	3.2	Coastal	Pelagic
Salmonidae	*Stenodus leucichthys*	Guldenstadt's whitefish	Arctic	Fluvial spawner	150	Piscivore	4.2	Coastal	Pelagic
Salmonidae	*Oncorhynchus gorbuscha*	Pink salmon	Pacific (introduced)	Fluvial spawner	76	Piscivore	4.2	Inner shelf	Pelagic
Salmonidae	*Oncorhynchus keta*	Chum salmon	Pacific (introduced)	Fluvial spawner	111	Plankto-piscivore	3.5	Inner shelf	Pelagic
Salmonidae	*Oncorhynchus kisutch*	Coho salmon	Pacific (introduced)	Fluvial spawner	88	Piscivore	4.2	Coastal	Pelagic
Salmonidae	*Oncorhynchus mykiss*	Rainbow trout	Pacific (introduced)	Fluvial spawner	120	Piscivore	4.4	Shelf	Pelagic
Salmonidae	*Salmo salar*	Atlantic salmon	Boreal	Fluvial spawner	150	Piscivore	4.4	Inner shelf	Pelagic
Salmonidae	*Salmo trutta*	Trout	Boreal	Fluvial spawner	140	Piscivore	3.2	Inner shelf	Pelagic
Salmonidae	*Salvelinus alpinus*	Charr	Boreal	Fluvial spawner	88	Piscivore	4.3	Coastal	Benthopelagic
Gonostomatidae	*Bonapartia pedaliota*	–	African	Planktonic eggs	9	Unknown	3.4	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone acclinidens*	Bent-tooth bristlemouth	Atlantic	Planktonic eggs	8	Planktivore	3.0	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone alba*	Bristlemouth	Atlantic	Planktonic eggs	4	Unknown	3.1	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone braueri*	–	Atlantic	Planktonic eggs	5	Planktivore	3.1	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone livida*	–	Atlantic	Planktonic eggs	6	Planktivore	3.1	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone microdon*	Veiled anglemouth	Atlantic	Planktonic eggs	8	Planktivore	3.0	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone obscura*	–	Atlantic	Planktonic eggs	8	Planktivore	3.1	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone pallida*	Tan bristlemouth	Atlantic	Planktonic eggs	9	Planktivore	3.2	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone pseudopallida*	Slender bristlemouth	Atlantic	Planktonic eggs	7	Planktivore	3.1	Oceanic	Mesopelagic
Gonostomatidae	*Cyclothone pygmaea*	–	Mediterranean	Planktonic eggs	4	Planktivore	3.4	Oceanic	Mesopelagic
Gonostomatidae	*Diplophos maderensis*	–	Atlantic	Planktonic eggs	22	Unknown	3.5	Oceanic	Mesopelagic
Gonostomatidae	*Diplophos taenia*	Pacific portholefish	Atlantic	Planktonic eggs	34	Unknown	3.2	Oceanic	Mesopelagic
Gonostomatidae	*Gonostoma atlanticum*	Atlantic fangjaw	Atlantic	Planktonic eggs	8	Planktivore	3.0	Oceanic	Mesopelagic
Gonostomatidae	*Gonostoma bathyphilum*	–	Atlantic	Planktonic eggs	24	Unknown	3.3	Oceanic	Bathypelagic
Gonostomatidae	*Gonostoma denudatum*	–	Atlantic	Planktonic eggs	17	Unknown	3.3	Oceanic	Mesopelagic
Gonostomatidae	*Gonostoma elongatum*	Elongated bristlemouth fish	Atlantic	Planktonic eggs	28	Plankto-piscivore	3.3	Oceanic	Mesopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Gonostomatidae	*Margrethia obtusirostra*	-	Atlantic	Planktonic eggs	10	Plankto-piscivore	3.5	Oceanic	Mesopelagic
Sternoptychidae	*Argyripnus atlanticus*	-	Atlantic	Planktonic eggs	8	Planktivore	3.5	Oceanic	Benthopelagic
Sternoptychidae	*Maurolicus muelleri*	Pearlside	Atlantic	Planktonic eggs	7	Planktivore	3.0	Slope	Bathypelagic
Sternoptychidae	*Valenciennellus tripunctulatus*	Constellationfish	Atlantic	Planktonic eggs	4	Planktivore	3.1	Oceanic	Mesopelagic
Sternoptychidae	*Argyropelecus aculeatus*	Lovely hatchetfish	Atlantic	Planktonic eggs	9	Planktivore	3.5	Oceanic	Mesopelagic
Sternoptychidae	*Argyropelecus affinis*	Pacific hatchetfish	Atlantic	Planktonic eggs	10	Planktivore	3.1	Oceanic	Mesopelagic
Sternoptychidae	*Argyropelecus gigas*	Hatchetfish	African	Planktonic eggs	15	Unknown	3.3	Oceanic	Mesopelagic
Sternoptychidae	*Argyropelecus hemigymnus*	Half-naked hatchetfish	Atlantic	Planktonic eggs	5	Planktivore	3.3	Oceanic	Mesopelagic
Sternoptychidae	*Argyropelecus olfersi*	Hatchetfish	Atlantic	Planktonic eggs	7	Planktivore	3.4	Slope	Bathypelagic
Sternoptychidae	*Polyipnus polli*	-	African	Planktonic eggs	6	Unknown	3.3	Slope	Mesopelagic
Sternoptychidae	*Sternoptyx diaphana*	Diaphanous hatchetfish	Atlantic	Planktonic eggs	7	Planktivore	3.4	Oceanic	Mesopelagic
Sternoptychidae	*Sternoptyx pseudobscura*	Highlight hatchetfish	Atlantic	Planktonic eggs	7	Planktivore	3.4	Oceanic	Mesopelagic
Photichthyidae	*Ichthyococcus ovatus*	Lightfish	Atlantic	Planktonic eggs	7	Planktivore	3.4	Oceanic	Mesopelagic
Photichthyidae	*Pollichthys mauli*	Star-eye lightfish	Atlantic	Planktonic eggs	7	Planktivore	3.7	Oceanic	Mesopelagic
Photichthyidae	*Polymetme corythaeola*	-	Atlantic	Planktonic eggs	32	Unknown	4.4	Slope	Benthopelagic
Photichthyidae	*Polymetme thaeocoryla*	-	Atlantic	Planktonic eggs	22	Unknown	NA	Slope	Bathydemersal
Photichthyidae	*Vinciguerria attenuata*	-	Atlantic	Planktonic eggs	5	Planktivore	3.0	Oceanic	Mesopelagic
Photichthyidae	*Vinciguerria nimbaria*	Oceanic lightfish	Atlantic	Planktonic eggs	6	Planktivore	3.2	Oceanic	Mesopelagic
Photichthyidae	*Vinciguerria poweriae*	Power's deepwater bristlemouth fish	Atlantic	Planktonic eggs	4	Planktivore	3.1	Oceanic	Mesopelagic
Stomiidae (Chauliodontidae)	*Chauliodus danae*	Dana viperfish	Atlantic	Planktonic eggs	18	Piscivore	4.0	Oceanic	Mesopelagic
Stomiidae (Chauliodontidae)	*Chauliodus sloani*	Sloane's viperfish	Atlantic	Planktonic eggs	43	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae	*Stomias boa*	Scaly dragonfish	Atlantic	Planktonic eggs	39	Piscivore	4.0	Oceanic	Mesopelagic
Stomiidae	*Stomias brevibarbatus*	-	Atlantic	Planktonic eggs	25	Piscivore	3.9	Oceanic	Mesopelagic
Stomiidae	*Stomias longibarbatus*	-	Atlantic	Planktonic eggs	52	Piscivore	4.1	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Astronesthes atlanticus*	-	Atlantic	Planktonic eggs	17	Unknown	NA	Slope	Bathypelagic
Stomiidae (Astronethidae)	*Astronesthes cyclophotus*	-	Atlantic	Planktonic eggs	7	Planktivore	3.5	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Astronesthes gemmifer*	Snaggletooth	Atlantic	Planktonic eggs	21	Unknown	4.0	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Astronesthes indicus*	-	Atlantic	Planktonic eggs	26	Unknown	3.5	Oceanic	Mesopelagic
Stomiidae	*Astronesthes leucopogon*	-	Atlantic	Planktonic eggs	15	Unknown	4.0	Oceanic	Mesopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
(Astronethidae)									
Stomiidae (Astronethidae)	*Astronesthes macropogon*	–	Atlantic	Planktonic eggs	17	Unknown	3.7	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Astronesthes micropogon*	–	Atlantic	Planktonic eggs	10	Unknown	3.7	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Astronesthes neopogon*	–	Atlantic	Planktonic eggs	23	Unknown	3.7	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Astronesthes niger*	–	Atlantic	Planktonic eggs	20	Unknown	3.8	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Borostomias antarcticus*	–	Atlantic	Planktonic eggs	37	Unknown	3.6	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Borostomias elucens*	–	Atlantic	Planktonic eggs	43	Unknown	4.0	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Borostomias mononema*	–	Atlantic	Planktonic eggs	38	Unknown	4.0	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Neonesthes capensis*	–	Atlantic	Planktonic eggs	21	Unknown	4.0	Oceanic	Mesopelagic
Stomiidae (Astronethidae)	*Rhadinesthes decimus*	–	Atlantic	Planktonic eggs	50	Unknown	4.1	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Bathophilus brevis*	–	Atlantic	Planktonic eggs	7	Unknown	3.7	Oceanic	Bathypelagic
Stomiidae (Melanostomiidae)	*Bathophilus digitatus*	–	Atlantic	Planktonic eggs	17	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Bathophilus nigerrimus*	Scaleless dragonfish	Atlantic	Planktonic eggs	15	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Bathophilus pawneei*	–	Atlantic	Planktonic eggs	15	Unknown	4.2	Oceanic	Bathypelagic
Stomiidae (Melanostomiidae)	*Bathophilus vaillanti*	–	Atlantic	Planktonic eggs	22	Piscivore	4.4	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Chirostomias pliopterus*	–	Atlantic	Planktonic eggs	25	Piscivore	4.3	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Echiostoma barbatum*	–	Atlantic	Planktonic eggs	45	Piscivore	4.1	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias braueri*	–	Atlantic	Planktonic eggs	14	Piscivore	NA	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias filifer*	–	Atlantic	Planktonic eggs	28	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias furcifer*	–	Atlantic	Planktonic eggs	21	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae	*Eustomias longibarba*	–	Atlantic	Planktonic eggs	23	Piscivore	4.4	Oceanic	Mesopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
(Melanostomiidae)									
Stomiidae (Melanostomiidae)	*Eustomias macronema*	–	Atlantic	Planktonic eggs	21	Piscivore	4.3	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias macrurus*	–	Atlantic	Planktonic eggs	28	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias obscurus*	–	Atlantic	Planktonic eggs	27	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias schmidti*	–	Atlantic	Planktonic eggs	26	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias simplex*	–	Atlantic	Planktonic eggs	27	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Eustomias tetranema*	–	Atlantic	Planktonic eggs	18	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Flagellostomias boureei*	–	Atlantic	Planktonic eggs	39	Piscivore	4.6	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Grammatostomias circularis*	–	Atlantic	Planktonic eggs	17	Piscivore	4.1	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Grammatostomias flagellibarba*	–	Atlantic	Planktonic eggs	18	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Leptostomias gladiator*	–	Atlantic	Planktonic eggs	46	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Leptostomias haplocaulus*	–	Atlantic	Planktonic eggs	46	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Leptostomias longibarba*	–	Atlantic	Planktonic eggs	40	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Melanostomias bartonbeani*	Scaleless black dragonfish	Atlantic	Planktonic eggs	32	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Melanostomias biseriatus*	–	Atlantic	Planktonic eggs	31	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Melanostomias macrophotus*	–	Atlantic	Planktonic eggs	28	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Melanostomias melanopogon*	–	Atlantic	Planktonic eggs	19	Piscivore	4.0	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Melanostomias melanops*	–	Atlantic	Planktonic eggs	32	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Melanostomias tentaculatus*	–	Atlantic	Planktonic eggs	29	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Melanostomias valdiviae*	Valdivia black dragonfish	Atlantic	Planktonic eggs	28	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae	*Pachystomias microdon*	–	Atlantic	Planktonic eggs	27	Piscivore	4.2	Oceanic	Mesopelagic

FAMILY	SCIENTIFIC NAME	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{MAX} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)
(Melanostomiidae)									
Stomiidae (Melanostomiidae)	*Photonectes braueri*	–	Atlantic	Planktonic eggs	34	Piscivore	4.1	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Photonectes dinema*	–	Atlantic	Planktonic eggs	31	Piscivore	4.1	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Photonectes margarita*	–	Atlantic	Planktonic eggs	40	Piscivore	4.0	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Photonectes parvimanus*	–	Atlantic	Planktonic eggs	30	Piscivore	4.1	Oceanic	Mesopelagic
Stomiidae (Melanostomiidae)	*Trigonolampa miriceps*	Three-light dragonfish	Atlantic	Planktonic eggs	39	Piscivore	4.5	Oceanic	Mesopelagic
Stomiidae (Malacosteidae)	*Aristostomias grimaldii*	–	Atlantic	Planktonic eggs	22	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Malacosteidae)	*Aristostomias lunifer*	–	Atlantic	Planktonic eggs	17	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Malacosteidae)	*Aristostomias tittmanni*	Loosejaw	Atlantic	Planktonic eggs	22	Piscivore	4.2	Oceanic	Mesopelagic
Stomiidae (Malacosteidae)	*Malacosteus niger*	Stop-light loosejaw	Atlantic	Planktonic eggs	29	Piscivore	3.7	Oceanic	Mesopelagic
Stomiidae (Malacosteidae)	*Photostomias guernei*	–	Atlantic	Planktonic eggs	16	Piscivore	3.5	Oceanic	Mesopelagic
Stomiidae (Idiacanthidae)	*Idiacanthus fasciola*	Ribbon sawtailfish	Atlantic	Planktonic eggs	60	Piscivore	3.9	Oceanic	Mesopelagic
Ateleopodidae	*Guentherus altivelis*	High-fin tadpolefish	Atlantic	Uncertain	200	Piscivore	4.5	Slope	Demersal
Ateleopodidae	*Ijimaia loppei*	Loppe's tadpolefish	Atlantic	Uncertain	200	Bentho-piscivore	4.3	Slope	Demersal
Aulopidae	*Aulopus filamentosus*	Royal flagfin	Lusitanian	Planktonic eggs	54	Unknown	4.2	Outer shelf	Demersal
Chlorophthalmidae	*Chlorophthalmus agassizi*	Short-nose greeneye	Atlantic	Planktonic eggs	40	Benthivore	3.7	Outer shelf	Demersal
Chlorophthalmidae (Ipnopidae)	*Bathymicrops regis*	–	Atlantic	Planktonic eggs	12	Benthivore	3.5	Oceanic	Bathydemersal
Chlorophthalmidae (Ipnopidae)	*Bathypterois dubius*	Spiderfish	Atlantic	Planktonic eggs	25	Benthivore	3.2	Slope	Demersal
Chlorophthalmidae (Ipnopidae)	*Bathypterois grallator*	Tripodfish	Atlantic	Planktonic eggs	45	Planktivore	3.1	Oceanic	Bathydemersal
Chlorophthalmidae (Ipnopidae)	*Bathypterois longipes*	Abyssal spiderfish	Atlantic	Planktonic eggs	30	Planktivore	3.1	Oceanic	Bathydemersal
Chlorophthalmidae (Ipnopidae)	*Bathypterois phenax*	Black-fin spiderfish	Atlantic	Planktonic eggs	22	Planktivore	3.4	Oceanic	Bathydemersal
Chlorophthalmidae (Ipnopidae)	*Bathytyphlops sewelli*	–	Atlantic	Uncertain	36	Planktivore	3.1	Oceanic	Bathydemersal

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
Scopelarchidae	*Benthalbella infans*	Zugmayer's pearleye	Atlantic	Uncertain	17	Piscivore	4.5	Oceanic	Mesopelagic
Scopelarchidae	*Rosenblattichthys hubbsi*	Hubb's pearleye	Atlantic	Uncertain	16	Piscivore	4.2	Oceanic	Mesopelagic
Scopelarchidae	*Scopelarchus analis*	Short-fin pearleye	Atlantic	Uncertain	14	Piscivore	4.2	Oceanic	Mesopelagic
Scopelarchidae	*Scopelarchus michaelsarsi*	Bigfin pearleye	Atlantic	Uncertain	12	Piscivore	4.2	Oceanic	Mesopelagic
Notosudidae	*Ahliesaurus berryi*	–	Atlantic	Uncertain	33	Planktivore	3.0	Oceanic	Bathypelagic
Notosudidae	*Scopelosaurus argenteus*	Waryfish	Atlantic	Uncertain	26	Planktivore	3.4	Oceanic	Mesopelagic
Notosudidae	*Scopelosaurus lepidus*	Black-fin waryfish	Atlantic	Uncertain	44	Planktivore	3.3	Oceanic	Mesopelagic
Notosudidae	*Scopelosaurus smithii*	–	Atlantic	Uncertain	25	Planktivore	3.4	Oceanic	Mesopelagic
Synodontidae	*Synodus saurus*	Atlantic lizardfish	Lusitanian	Planktonic eggs	49	Unknown	4.5	Shelf	Demersal
Synodontidae	*Synodus synodus*	Red lizardfish	African	Planktonic eggs	33	Unknown	4.2	Shelf	Demersal
Synodontidae	*Saurida undosquamis*	Brush-tooth lizardfish	Indo-Pacific	Planktonic eggs	61	Piscivore	4.5	Shelf	Demersal
Synodontidae	*Bathysaurus ferox*	Deep-sea lizardfish	Atlantic	Planktonic eggs	78	Bentho-piscivore	4.3	Oceanic	Bathydemersal
Synodontidae	*Bathysaurus mollis*	High-fin lizardfish	Atlantic	Planktonic eggs	95	Bentho-piscivore	4.5	Oceanic	Bathydemersal
Paralepididae	*Arctozenus risso*	Ribbon barracudina	Atlantic	Planktonic eggs	37	Piscivore	3.2	Oceanic	Mesopelagic
Paralepididae	*Lestidiops affinis*	Barracudina	Atlantic	Planktonic eggs	14	Planktivore	4.2	Oceanic	Pelagic
Paralepididae	*Lestidiops jayakari*	–	Atlantic	Planktonic eggs	20	Unknown	4.2	Oceanic	Pelagic
Paralepididae	*Lestidiops sphyrenoides*	–	Atlantic	Planktonic eggs	33	Unknown	4.5	Oceanic	Pelagic
Paralepididae	*Macroparalepis affinis*	–	Atlantic	Planktonic eggs	52	Piscivore	NA	Oceanic	Mesopelagic
Paralepididae	*Macroparalepis brevis*	–	Atlantic	Planktonic eggs	14	Planktivore	3.4	Oceanic	Mesopelagic
Paralepididae	*Macroparalepis nigra*	–	Atlantic	Planktonic eggs	46	Unknown	NA	Oceanic	Mesopelagic
Paralepididae	*Magnisudis atlantica*	Duck-bill barracudina	Atlantic	Planktonic eggs	68	Piscivore	4.1	Oceanic	Mesopelagic
Paralepididae	*Paralepis brevirostris*	–	Atlantic	Planktonic eggs	20	Piscivore	NA	Oceanic	Mesopelagic
Paralepididae	*Paralepis coregonoides*	Sharp-chin barracudina	Atlantic	Planktonic eggs	30	Piscivore	4.5	Oceanic	Mesopelagic
Paralepididae	*Sudis hyalina*	–	Atlantic	Planktonic eggs	100	Piscivore	4.1	Oceanic	Mesopelagic
Paralepididae	*Uncisudis longirostra*	–	Atlantic	Planktonic eggs	19	Unknown	NA	Oceanic	Mesopelagic
Paralepididae	*Uncisudis quadrimaculata*	–	Atlantic	Planktonic eggs	10	Unknown	NA	Slope	Bathypelagic
Evermannellidae	*Coccorella atlantica*	Atlantic sabre tooth	Atlantic	Uncertain	20	Piscivore	4.4	Oceanic	Mesopelagic
Evermannellidae	*Evermannella balbo*	Balbo sabretooth	Atlantic	Uncertain	21	Piscivore	4.2	Oceanic	Mesopelagic
Evermannellidae	*Evermannella indica*	Indian sabretooth	Atlantic	Uncertain	14	Piscivore	4.2	Oceanic	Mesopelagic
Evermannellidae	*Odontostomops normalops*	Undistinguished sabretooth	Atlantic	Uncertain	13	Piscivore	4.3	Oceanic	Mesopelagic
Omosudidae	*Omosudis lowei*	Hammerjaw	Atlantic	Planktonic eggs	28	Piscivore	4.3	Oceanic	Mesopelagic
Alepisauridae	*Alepisaurus brevirostris*	Short-nose lancetfish	Atlantic	Uncertain	96	Plankto-piscivore	3.8	Oceanic	Mesopelagic
Alepisauridae	*Alepisaurus ferox*	Long-nose lancetfish	Atlantic	Uncertain	215	Piscivore	4.2	Oceanic	Pelagic
Anotopteridae	*Anotopterus pharao*	Daggertooth	Atlantic	Uncertain	117	Piscivore	4.3	Oceanic	Bathypelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Neoscopelidae	*Neoscopelus macrolepidotus*	Large-scaled lanternfish	Atlantic	Uncertain	31	Unknown	4.2	Slope	Benthopelagic
Neoscopelidae	*Neoscopelus microchir*	–	Atlantic	Uncertain	37	Unknown	3.2	Slope	Benthopelagic
Neoscopelidae	*Scopelengys tristis*	Pacific blackchin	Atlantic	Uncertain	24	Unknown	3.1	Oceanic	Bathypelagic
Myctophidae	*Benthosema glaciale*	Glacier lanternfish	Atlantic	Planktonic eggs	13	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Benthosema suborbitale*	Small-fin lanternfish	Atlantic	Planktonic eggs	5	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Bolinichthys indicus*	Lanternfish	Atlantic	Planktonic eggs	5	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Bolinichthys supralateralis*	–	Atlantic	Planktonic eggs	14	Unknown	3.1	Oceanic	Mesopelagic
Myctophidae	*Centrobranchus nigroocellatus*	Round-nose lanternfish	Atlantic	Planktonic eggs	6	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Ceratoscopelus maderensis*	–	Atlantic	Planktonic eggs	10	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Ceratoscopelus warmingii*	–	Atlantic	Planktonic eggs	8	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Diaphus adenomus*	Gilbert's large lanternfish	Atlantic	Planktonic eggs	21	Unknown	3.2	Oceanic	Mesopelagic
Myctophidae	*Diaphus bertelseni*	–	Atlantic	Planktonic eggs	11	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Diaphus brachycephalus*	Short-headed lanternfish	Atlantic	Planktonic eggs	6	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Diaphus dumerilii*	–	Atlantic	Planktonic eggs	11	Unknown	3.0	Oceanic	Mesopelagic
Myctophidae	*Diaphus effulgens*	Headlight fish	Atlantic	Planktonic eggs	18	Unknown	3.0	Oceanic	Mesopelagic
Myctophidae	*Diaphus holti*	–	Atlantic	Planktonic eggs	9	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Diaphus lucidus*	–	Atlantic	Planktonic eggs	14	Unknown	3.0	Oceanic	Mesopelagic
Myctophidae	*Diaphus metopoclampus*	Spot-head lanternfish	Atlantic	Planktonic eggs	9	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Diaphus mollis*	–	Atlantic	Planktonic eggs	7	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Diaphus rafinesquii*	White-spotted lanternfish	Atlantic	Planktonic eggs	11	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Diaphus subtilis*	–	Atlantic	Planktonic eggs	9	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Diaphus termophilus*	Taaning's lanternfish	Atlantic	Planktonic eggs	10	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Diogenichthys atlanticus*	Long-fin lanternfish	Atlantic	Planktonic eggs	4	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Electrona risso*	Chubby flashlightfish	Atlantic	Planktonic eggs	10	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Gonichthys cocco*	–	Atlantic	Planktonic eggs	7	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Hygophum benoiti*	Benoit's lanternfish	Atlantic	Planktonic eggs	7	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Hygophum hygomii*	–	Atlantic	Planktonic eggs	8	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Hygophum reinhardtii*	–	Atlantic	Planktonic eggs	6	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Hygophum taaningi*	–	Atlantic	Planktonic eggs	7	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Lampadena anomala*	–	Atlantic	Planktonic eggs	22	Planktivore	3.3	Oceanic	Mesopelagic
Myctophidae	*Lampadena chavesi*	–	Atlantic	Planktonic eggs	10	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Lampadena speculigera*	Mirror lanternfish	Atlantic	Planktonic eggs	19	Unknown	3.3	Oceanic	Mesopelagic
Myctophidae	*Lampadena urophaos*	–	Atlantic	Planktonic eggs	24	Unknown	3.3	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus alatus*	–	Atlantic	Planktonic eggs	6	Planktivore	3.2	Oceanic	Mesopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Myctophidae	*Lampanyctus ater*	–	Atlantic	Planktonic eggs	13	Unknown	NA	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus crocodilus*	Jewel lanternfish	Atlantic	Planktonic eggs	37	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus cuprarius*	–	Atlantic	Planktonic eggs	4	Planktivore	3.3	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus festivus*	–	Atlantic	Planktonic eggs	17	Unknown	3.2	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus intricarius*	–	Atlantic	Planktonic eggs	24	Unknown	3.3	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus lineatus*	–	Atlantic	Planktonic eggs	24	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus macdonaldi*	Rakery beaconlamp	Atlantic	Planktonic eggs	20	Unknown	3.3	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus photonotus*	–	Atlantic	Planktonic eggs	9	Planktivore	NA	Oceanic	Mesopelagic
Myctophidae	*Lampanyctus pusillus*	–	Atlantic	Planktonic eggs	5	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Lepidophanes gaussi*	–	Atlantic	Planktonic eggs	6	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Lepidophanes guentheri*	–	Atlantic	Planktonic eggs	10	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Lobiancha dofleini*	–	Atlantic	Planktonic eggs	6	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Lobiancha gemellarii*	Cocco's lanternfish	Atlantic	Planktonic eggs	7	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Loweina interrupta*	–	Atlantic	Planktonic eggs	4	Planktivore	NA	Oceanic	Mesopelagic
Myctophidae	*Loweina rara*	Laura's lanternfish	Atlantic	Planktonic eggs	5	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Myctophum nitidulum*	Pearly lanternfish	Atlantic	Planktonic eggs	10	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Myctophum punctatum*	Spotted lanternfish	Atlantic	Planktonic eggs	11	Planktivore	3.4	Slope	Bathypelagic
Myctophidae	*Myctophum selenops*	Wisner's lanternfish	Atlantic	Planktonic eggs	8	Planktivore	3.3	Oceanic	Mesopelagic
Myctophidae	*Notolychnus valdiviae*	Topside lampfish	Atlantic	Planktonic eggs	6	Planktivore	3.1	Oceanic	Mesopelagic
Myctophidae	*Notoscopelus (Notoscopelus) caudispinosus*	–	Atlantic	Planktonic eggs	14	Unknown	NA	Oceanic	Mesopelagic
Myctophidae	*Notoscopelus (Notoscopelus) elongatus*	–	Mediterranean	Planktonic eggs	13	Unknown	3.4	Oceanic	Mesopelagic
Myctophidae	*Notoscopelus (Notoscopelus) kroeyeri*	Lancetfish	Atlantic	Planktonic eggs	17	Unknown	3.2	Oceanic	Mesopelagic
Myctophidae	*Notoscopelus (Notoscopelus) resplendens*	Patchwork lampfish	Atlantic	Planktonic eggs	12	Planktivore	3.0	Oceanic	Mesopelagic
Myctophidae	*Notoscopelus (Pareiophus) bolini*	–	Atlantic	Planktonic eggs	12	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Protomyctophum (Hierops) arcticum*	Arctic telescope	Boreal	Planktonic eggs	7	Planktivore	3.4	Oceanic	Mesopelagic
Myctophidae	*Symbolophorus veranyi*	Large-scale lanternfish	Atlantic	Planktonic eggs	15	Unknown	3.4	Oceanic	Mesopelagic
Myctophidae	*Taaningichthys bathyphilus*	–	Atlantic	Planktonic eggs	10	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Taaningichthys minimus*	–	Atlantic	Planktonic eggs	8	Planktivore	3.2	Oceanic	Mesopelagic
Myctophidae	*Taaningichthys paurolychnus*	–	Atlantic	Planktonic eggs	12	Planktivore	3.2	Oceanic	Mesopelagic
Lampridae	*Lampris guttatus*	Opah	Atlantic	Planktonic eggs	185	Piscivore	4.2	Oceanic	Epipelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Lophotidae	*Lophotus lacepede*	Crested oarfish	Atlantic	Planktonic eggs	200	Piscivore	4.5	Oceanic	Mesopelagic
Radiicephalidae	*Radiicephalus elongatus*	Tapertail	Atlantic	Planktonic eggs	76	Piscivore	3.9	Oceanic	Mesopelagic
Trachipteridae	*Trachipterus arcticus*	Dealfish	Atlantic	Planktonic eggs	250	Piscivore	4.5	Oceanic	Mesopelagic
Trachipteridae	*Trachipterus trachypterus*	Ribbonfish	Atlantic	Planktonic eggs	300	Piscivore	4.5	Oceanic	Mesopelagic
Trachipteridae	*Zu cristatus*	Scalloped ribbonfish	Atlantic	Planktonic eggs	144	Piscivore	4.5	Oceanic	Mesopelagic
Regalecidae	*Regalecus glesne*	Ribbonfish	Atlantic	Planktonic eggs	700	Planktivore	3.2	Oceanic	Mesopelagic
Stylephoridae	*Stylephorus chordatus*	Threadtail	Atlantic	Uncertain	34	Planktivore	3.0	Oceanic	Mesopelagic
Polymixiidae	*Polymixia nobilis*	Beardfish	Atlantic	Uncertain	48	Unknown	4.2	Outer shelf	Demersal
Bregmacerotidae	*Bregmaceros atlanticus*	Antenna codlet	Atlantic	Planktonic eggs	7	Planktivore	2.8	Oceanic	Pelagic
Macrouridae (Bathygadinae)	*Bathygadus favosus*	Bighead grenadier	African	Planktonic eggs	50	Unknown	3.2	Slope	Benthopelagic
Macrouridae (Bathygadinae)	*Bathygadus melanobranchus*	Vaillant's grenadier	Atlantic	Planktonic eggs	50	Benthivore	3.3	Slope	Benthopelagic
Macrouridae (Bathygadinae)	*Gadomus arcuatus*	Double-thread grenadier	Atlantic	Planktonic eggs	60	Unknown	3.1	Slope	Benthopelagic
Macrouridae (Bathygadinae)	*Gadomus dispar*	Long-beard grenadier	Atlantic	Planktonic eggs	39	Planktivore	3.0	Slope	Benthopelagic
Macrouridae (Bathygadinae)	*Gadomus longifilis*	Thread-fin grenadier	Atlantic	Planktonic eggs	30	Benthivore	3.2	Slope	Benthopelagic
Macrouridae (Trachyrhynchinae)	*Trachyrincus murrayi*	Rough-nose grenadier	Boreal	Planktonic eggs	37	Unknown	3.5	Slope	Benthopelagic
Macrouridae (Trachyrhynchinae)	*Trachyrincus scabrus*	Rough-snout grenadier	Atlantic	Planktonic eggs	60	Bentho-piscivore	3.5	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Caelorinchus caelorhincus*	Hollow-nosed rattail	Atlantic	Planktonic eggs	38	Benthivore	3.6	Slope	Bathydemersal
Macrouridae (Macrourinae)	*Caelorinchus caudani*	–	Atlantic	Planktonic eggs	36	Unknown	NA	Slope	Bathydemersal
Macrouridae (Macrourinae)	*Caelorinchus labiatus*	Spear-snouted grenadier	Atlantic	Planktonic eggs	50	Bentho-piscivore	4.0	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Cetonurus globiceps*	Globe-head grenadier	Atlantic	Planktonic eggs	50	Plankto-piscivore	3.8	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides (Chalinura) brevibarbis*	Short-beard grenadier	Boreal	Planktonic eggs	35	Benthivore	3.5	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides (Chalinura) leptolepis*	Ghostly grenadier	Atlantic	Planktonic eggs	62	Unknown	3.7	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides (Chalinura) mediterraneus*	Mediterranean grenadier	Atlantic	Planktonic eggs	73	Benthivore	3.4	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides (Chalinura) profundicolu*	Deep-water grenadier	Atlantic	Planktonic eggs	53	Unknown	3.5	Oceanic	Benthopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Macrouridae (Macrourinae)	*Coryphaenoides guentheri*	Gunther's grenadier	Atlantic	Planktonic eggs	48	Benthivore	3.3	Oceanic	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides rudis*	Rudis' rattail	Atlantic	Planktonic eggs	111	Piscivore	4.5	Slope	Bathypelagic
Macrouridae (Macrourinae)	*Coryphaenoides rupestris*	Round-head rattail	Boreal	Planktonic eggs	150	Benthivore	3.5	Slope	Bathydemersal
Macrouridae (Macrourinae)	*Coryphaenoides thelestomus*	Rough-lip grenadier	Macaronesia	Planktonic eggs	65	Unknown	NA	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides zaniophorus*	Slim-head grenadier	Atlantic	Planktonic eggs	43	Benthivore	3.2	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides (Lionurus) carapinus*	Carapine grenadier	Atlantic	Planktonic eggs	35	Benthivore	3.5	Oceanic	Benthopelagic
Macrouridae (Macrourinae)	*Coryphaenoides (Nematonurus) armatus*	Armed grenadier	Atlantic	Planktonic eggs	80	Benthivore	3.6	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Echinomacrurus mollis*	Button-scale grenadier	Atlantic	Planktonic eggs	40	Benthivore	3.2	Oceanic	Benthopelagic
Macrouridae (Macrourinae)	*Hymenocephalus italicus*	Glass-head grenadier	Atlantic	Planktonic eggs	25	Planktivore	3.4	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Hymenocephalus gracilis*	Graceful grenadier	Atlantic	Planktonic eggs	13	Planktivore	3.1	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Macrourus berglax*	Rough rattail	Boreal	Planktonic eggs	100	Bentho-piscivore	4.5	Slope	Bathydemersal
Macrouridae (Macrourinae)	*Malacocephalus laevis*	Soft-head rattail	Atlantic	Planktonic eggs	50	Benthivore	4.2	Slope	Bathydemersal
Macrouridae (Macrourinae)	*Nezumia aequalis*	Common Atlantic grenadier	Atlantic	Planktonic eggs	36	Benthivore	3.3	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Nezumia longebarbata*	Blunt-nose grenadier	Atlantic	Planktonic eggs	41	Unknown	NA	Oceanic	Benthopelagic
Macrouridae (Macrourinae)	*Nezumia sclerorhynchus*	Rough-tip grenadier	Atlantic	Planktonic eggs	36	Bentho-planktivore	3.2	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Odontomacrurus murrayi*	Round-head grenadier	Atlantic	Planktonic eggs	64	Piscivore	4.5	Oceanic	Bathypelagic
Macrouridae (Macrourinae)	*Pseudonezumia flagellicauda*	-	Atlantic	Planktonic eggs	39	Unknown	3.6	Slope	Bathydemersal
Macrouridae (Macrourinae)	*Sphagemacrurus grenadae*	Button-lip grenadier	Atlantic	Planktonic eggs	20	Unknown	NA	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Sphagemacrurus hirundo*	Swallow grenadier	African	Planktonic eggs	20	Unknown	NA	Slope	Benthopelagic
Macrouridae (Macrourinae)	*Trachonurus villosus*	Bristly grenadier	Atlantic	Planktonic eggs	45	Unknown	NA	Slope	Benthopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Moridae	*Antimora rostrata*	Blue antimora	Boreal	planktonic eggs	92	Bentho-planktivore	3.6	Slope	Benthopelagic
Moridae	*Erethmophorus kleinenbergi*	–	Mediterranean	planktonic eggs	11	Unknown	3.4	Slope	Pelagic
Moridae	*Gadella maraldi*	Gadella	Lusitanian	planktonic eggs	30	Unknown	3.5	Slope	Benthopelagic
Moridae	*Halargyreus johnsonii*	Slender codling	Atlantic	planktonic eggs	56	Unknown	3.4	Slope	Benthopelagic
Moridae	*Laemonema latifrons*	–	Boreal	planktonic eggs	16	Unknown	NA	Slope	Benthopelagic
Moridae	*Laemonema robustum*	Robust mora	Macaronesia	planktonic eggs	44	Unknown	3.5	Slope	Benthopelagic
Moridae	*Laemonema yarrellii*	–	African	planktonic eggs	22	Unknown	3.6	Slope	Benthopelagic
Moridae	*Lepidion eques*	North Atlantic codling	Atlantic	planktonic eggs	44	Benthivore	3.2	Slope	Benthopelagic
Moridae	*Lepidion guentheri*	–	Lusitanian	planktonic eggs	99	Unknown	3.6	Slope	Benthopelagic
Moridae	*Lepidion lepidion*	Mediterranean codling	Mediterranean	planktonic eggs	34	Unknown	3.6	Slope	Benthopelagic
Moridae	*Lepidion schmidti*	–	Atlantic	planktonic eggs	85	Unknown	NA	Slope	Bathydemersal
Moridae	*Mora moro*	Common mora	Atlantic	planktonic eggs	80	Bentho-piscivore	3.8	Slope	Benthopelagic
Moridae	*Physiculus dalwigki*	Black codling	Lusitanian	planktonic eggs	30	Unknown	3.8	Slope	Benthopelagic
Moridae	*Rhynchogadus hepaticus*	–	Mediterranean	planktonic eggs	12	Unknown	3.3	Slope	Benthopelagic
Moridae	*Svetovidovia lucullus*	–	Atlantic	planktonic eggs	50	Unknown	NA	Slope	Pelagic
Melanonidae	*Melanonus zugmayeri*	Arrowtail	Atlantic	Uncertain	28	Unknown	3.5	Oceanic	Mesopelagic
Gadidae (Gadinae)	*Arctogadus glacialis*	Arctic cod	Arctic	Planktonic eggs	48	Piscivore	3.8	Shelf	Pelagic
Gadidae (Gadinae)	*Boreogadus saida*	Polar cod	Arctic	Planktonic eggs	40	Planktivore	3.1	Shelf	Pelagic
Gadidae (Gadinae)	*Eleginus navaga*	Navaga	Arctic	Planktonic eggs	43	Bentho-piscivore	4.2	Shelf	Demersal
Gadidae (Gadinae)	*Gadiculus argenteus*	Silvery pout	Lusitanian	Planktonic eggs	15	Planktivore	3.5	Slope	Pelagic
Gadidae (Gadinae)	*Gadus morhua*	Cod	Boreal	Planktonic eggs	190	Piscivore	4.4	Shelf	Demersal
Gadidae (Gadinae)	*Melanogrammus aeglefinus*	Haddock	Boreal	Planktonic eggs	112	Benthivore	4.1	Shelf	Demersal
Gadidae (Gadinae)	*Merlangius merlangus*	Whiting	Lusitanian	Planktonic eggs	70	Piscivore	4.4	Shelf	Demersal
Gadidae (Gadinae)	*Micromesistius poutassou*	Blue whiting	Atlantic	Planktonic eggs	47	Planktivore	4.0	Slope	Mesopelagic
Gadidae (Gadinae)	*Pollachius pollachius*	Pollack	Boreal	Planktonic eggs	130	Piscivore	4.2	Shelf	Demersal
Gadidae (Gadinae)	*Pollachius virens*	Saithe	Boreal	Planktonic eggs	120	Piscivore	4.4	Shelf	Demersal
Gadidae (Gadinae)	*Theragra finnmarchica*	Norwegian pollock	Arctic	Planktonic eggs	50	Unknown	3.8	Shelf	Benthopelagic
Gadidae (Gadinae)	*Trisopterus esmarkii*	Norway pout	Boreal	Planktonic eggs	26	Bentho-piscivore	3.2	Outer shelf	Benthopelagic
Gadidae (Gadinae)	*Trisopterus luscus*	Bib	Lusitanian	Planktonic eggs	45	Benthivore	3.7	Inner shelf	Demersal
Gadidae (Gadinae)	*Trisopterus minutus*	Poor cod	Lusitanian	Planktonic eggs	26	Benthivore	3.8	Shelf	Demersal
Gadidae (Lotinae)	*Brosme brosme*	Tusk	Boreal	Planktonic eggs	100	Benthivore	4.0	Outer shelf	Demersal
Gadidae (Lotinae)	*Ciliata mustela*	Five-bearded rockling	Boreal	Planktonic eggs	45	Benthivore	3.5	Shelf	Demersal
Gadidae (Lotinae)	*Ciliata septentrionalis*	Northern rockling	Boreal	Planktonic eggs	17	Benthivore	3.5	Shelf	Demersal
Gadidae (Lotinae)	*Enchelyopus cimbrius*	Four-bearded rockling	Boreal	Planktonic eggs	41	Benthivore	3.5	Shelf	Demersal

FAMILY	SCIENTIFIC NAME	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{MAX} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)
Gadidae (Lotinae)	*Gaidropsarus argentatus*	Arctic rockling	Boreal	Planktonic eggs	43	Benthivore	3.6	Slope	Demersal
Gadidae (Lotinae)	*Gaidropsarus biscayensis*	Mediterranean big-eye rockling	Lusitanian	Planktonic eggs	40	Benthivore	3.6	Slope	Demersal
Gadidae (Lotinae)	*Gaidropsarus ensis*	Thread-fin rockling	Arctic	Planktonic eggs	35	Benthivore	3.4	Slope	Demersal
Gadidae (Lotinae)	*Gaidropsarus granti*	Azores rockling	Macaronesia	Planktonic eggs	44	Benthivore	3.6	Shelf	Demersal
Gadidae (Lotinae)	*Gaidropsarus guttatus*	–	Macaronesia	Planktonic eggs	32	Benthivore	2.8	Shelf	Demersal
Gadidae (Lotinae)	*Gaidropsarus macrophthalmus*	Big-eyed rockling	Lusitanian	Planktonic eggs	10	Benthivore	3.5	Outer shelf	Demersal
Gadidae (Lotinae)	*Gaidropsarus mediterraneus*	Shore rockling	Lusitanian	Planktonic eggs	25	Benthivore	3.4	Shelf	Demersal
Gadidae (Lotinae)	*Gaidropsarus vulgaris*	Three-bearded rockling	Lusitanian	Planktonic eggs	43	Benthivore	3.3	Shelf	Demersal
Gadidae (Lotinae)	*Molva dypterygia*	Blue ling	Boreal	Planktonic eggs	130	Piscivore	4.5	Slope	Demersal
Gadidae (Lotinae)	*Molva macrophthalma*	Spanish ling	Lusitanian	Planktonic eggs	108	Piscivore	4.5	Slope	Demersal
Gadidae (Lotinae)	*Molva molva*	Common ling	Boreal	Planktonic eggs	200	Piscivore	4.3	Slope	Demersal
Gadidae (Lotinae)	*Phycis blennoides*	Greater forkbeard	Lusitanian	Planktonic eggs	75	Bentho-piscivore	3.7	Outer shelf	Demersal
Gadidae (Lotinae)	*Phycis phycis*	Forkbeard	Lusitanian	Planktonic eggs	65	Bentho-piscivore	4.3	Shelf	Demersal
Gadidae (Lotinae)	*Raniceps raninus*	Tadpolefish	Boreal	Planktonic eggs	30	Benthivore	3.8	Inner shelf	Demersal
Gadidae (Lotinae)	*Urophycis chuss*	Squirrel hake	Atlantic	Planktonic eggs	50	Bentho-piscivore	3.6	Outer shelf	Demersal
Gadidae (Lotinae)	*Urophycis tenuis*	White hake	Boreal	Planktonic eggs	135	Bentho-piscivore	4.2	Outer shelf	Demersal
Merlucciidae	*Cynogadus brachycolus*	–	Atlantic	Planktonic eggs	24	Unknown	NA	Slope	Demersal
Merlucciidae	*Merluccius merluccius*	European hake	Lusitanian	Planktonic eggs	120	Piscivore	4.4	Shelf	Demersal
Merlucciidae	*Merluccius senegalensis*	Black hake	African	Planktonic eggs	90	Piscivore	4.5	Shelf	Demersal
Ophidiidae	*Brotulotaenia brevicauda*	–	Atlantic	Planktonic eggs	39	Unknown	3.6	Oceanic	Bathypelagic
Ophidiidae	*Brotulotaenia crassa*	Violet cuskeel	Atlantic	Planktonic eggs	105	Unknown	3.8	Oceanic	Bathypelagic
Ophidiidae	*Brotulotaenia nigra*	–	Atlantic	Planktonic eggs	37	Unknown	3.6	Oceanic	Bathypelagic
Ophidiidae	*Ophidion barbatum*	Snake blenny	Lusitanian	Planktonic eggs	31	Unknown	3.6	Shelf	Demersal
Ophidiidae	*Ophidion rochei*	–	Mediterranean	Planktonic eggs	29	Unknown	3.5	Shelf	Demersal
Ophidiidae	*Parophidion vassali*	–	Mediterranean	Planktonic eggs	31	Unknown	3.3	Outer shelf	Demersal
Ophidiidae	*Barathrites iris*	–	Atlantic	Planktonic eggs	63	Unknown	NA	Oceanic	Bathydemersal
Ophidiidae	*Bassozetus taenia*	–	Atlantic	Planktonic eggs	25	Unknown	3.5	Oceanic	Bathydemersal
Ophidiidae	*Bathyonus laticeps*	–	Atlantic	Planktonic eggs	25	Unknown	NA	Oceanic	Bathydemersal
Ophidiidae	*Benthocometes robustus*	–	Atlantic	Planktonic eggs	15	Unknown	3.1	Slope	Demersal
Ophidiidae	*Holcomycteronus squamosus*	–	Atlantic	Planktonic eggs	33	Unknown	3.6	Oceanic	Bathydemersal
Ophidiidae	*Lamprogrammus niger*	–	Atlantic	Planktonic eggs	61	Unknown	NA	Slope	Bathypelagic
Ophidiidae	*Lamprogrammus shcherbachevi*	–	Atlantic	Planktonic eggs	235	Unknown	4.0	Slope	Bathypelagic
Ophidiidae	*Monomitopus metriostoma*	–	Atlantic	Planktonic eggs	29	Unknown	3.5	Slope	Bathydemersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Ophidiidae	*Spectrunculus grandis*	Pudgy cuskeel	Atlantic	Planktonic eggs	155	Unknown	3.6	Oceanic	Bathydemersal
Carapidae	*Carapus acus*	Pearlfish	Mediterranean	Planktonic eggs (?)	21	Bentho-piscivore	4.0	Shelf	Demersal
Carapidae	*Echiodon dentatus*	-	Mediterranean	Planktonic eggs (?)	17	Unknown	3.7	Shelf	Demersal
Carapidae	*Echiodon drummondi*	Pearlfish	Lusitanian	Planktonic eggs (?)	30	Piscivore	4.0	Slope	Bathydemersal
Bythitidae	*Bellottia apoda*	-	Lusitanian	Viviparous	8	Unknown	3.3	Slope	Demersal
Bythitidae	*Bythites islandicus*	-	Uncertain	Viviparous	9	Unknown	NA	Slope	Demersal
Bythitidae	*Cataetyx alleni*	-	Lusitanian	Viviparous	12	Unknown	3.4	Slope	Demersal
Bythitidae	*Cataetyx laticeps*	-	Atlantic	Viviparous	65	Unknown	3.8	Slope	Demersal
Bythitidae	*Grammonus ater*	-	Mediterranean	Viviparous	15	Unknown	3.5	Slope	Demersal
Bythitidae	*Thalassobathia pelagica*	-	Atlantic	Viviparous	22	Unknown	NA	Slope	Demersal
Bythitidae	*Melodichthys hadrocephalus*	-	Atlantic	Viviparous	NA	Unknown	NA	Slope	Demersal
Aphyonidae	*Aphyonus gelatinosus*	Gelatinous blindfish	Atlantic	Viviparous	18	Unknown	3.5	Oceanic	Bathydemersal
Aphyonidae	*Barathronus multidens*	-	Atlantic	Viviparous	15	Unknown	3.4	Oceanic	Bathydemersal
Aphyonidae	*Barathronus parfaiti*	-	Atlantic	Viviparous	12	Unknown	3.4	Oceanic	Bathydemersal
Aphyonidae	*Meteoria erythrops*	-	Atlantic	Viviparous	8	Unknown	NA	Oceanic	Bathydemersal
Aphyonidae	*Nybelinella erikssoni*	-	Atlantic	Viviparous	8	Unknown	NA	Oceanic	Bathydemersal
Aphyonidae	*Sciadonus cryptophthalmus*	-	Atlantic	Viviparous	10	Unknown	3.3	Oceanic	Bathydemersal
Aphyonidae	*Sciadonus galatheae*	-	Atlantic	Viviparous	11	Unknown	3.3	Oceanic	Bathydemersal
Aphyonidae	*Sciadonus pedicellaris*	-	Atlantic	Viviparous	NA	Unknown	NA	Oceanic	Bathydemersal
Parabrotulidae	*Leucobrotula adipatus*	-	Atlantic	Viviparous	NA	Unknown	NA	Oceanic	Mesopelagic
Parabrotulidae	*Parabrotula plagiophthalma*	-	Atlantic	Viviparous	5	Unknown	NA	Oceanic	Mesopelagic
Batrachoididae	*Halobatrachus didactylus*	Lusitanian toadfish	Lusitanian	Uncertain	50	Bentho-piscivore	3.9	Inner shelf	Demersal
Lophiidae	*Lophius budegassa*	Black-bellied anglerfish	Lusitanian	Planktonic eggs (rafts)	100	Piscivore	4.5	Outer shelf	Bathydemersal
Lophiidae	*Lophius piscatorius*	Anglerfish	Lusitanian	Planktonic eggs (rafts)	200	Piscivore	4.4	Shelf	Demersal
Melanocetidae	*Melanocetus johnsoni*	Humpback anglerfish	Atlantic	Planktonic eggs (rafts)	18	Piscivore	4.2	Oceanic	Bathypelagic
Antennariidae	*Antennarius nummifer*	Spot-fin frogfish	Macaronesia	Planktonic eggs (rafts)	13	Unknown	4.2	Shelf	Demersal
Antennariidae	*Antennarius radiosus*	Single-spot frogfish	Atlantic	Planktonic eggs (rafts)	8	Unknown	3.7	Shelf	Demersal
Antennariidae	*Antennarius senegalensis*	Senegalese frogfish	African	Planktonic eggs (rafts)	35	Unknown	4.2	Shelf	Demersal

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
Antennariidae	*Histrio histrio*	Sargassum fish	Atlantic	Planktonic eggs (rafts)	20	Unknown	4.2	Oceanic	Pelagic
Chaunacidae	*Chaunax pictus*	Pink frogmouth	Atlantic	Planktonic eggs (rafts)	40	Unknown	4.4	Oceanic	Bathydemersal
Chaunacidae	*Chaunax suttkusi*	-	Atlantic	Planktonic eggs (rafts)	28	Unknown	4.2	Oceanic	Uncertain
Ogcocephalidae	*Dibranchus atlanticus*	Atlantic batfish	Atlantic	Planktonic eggs (rafts)	39	Unknown	3.5	Oceanic	Uncertain
Caulophrynidae	*Caulophryne jordani*	-	Atlantic	Planktonic eggs (rafts)	11	Piscivore	NA	Oceanic	Bathypelagic
Caulophrynidae	*Caulophryne polynema*	-	Atlantic	Planktonic eggs (rafts)	19	Piscivore	4.1	Oceanic	Bathypelagic
Melanocetidae	*Melanocetus murrayi*	Murray's abyssal anglerfish	Atlantic	Planktonic eggs (rafts)	2	Piscivore	NA	Oceanic	Bathypelagic
Himantolophidae	*Himantolophus albinares*	-	Atlantic	Planktonic eggs (rafts)	23	Piscivore	4.2	Oceanic	Bathypelagic
Himantolophidae	*Himantolophus compressus*	-	Atlantic	Planktonic eggs (rafts)	25	Piscivore	4.3	Oceanic	Bathypelagic
Himantolophidae	*Himantolophus groenlandicus*	Atlantic footballfish	Atlantic	Planktonic eggs (rafts)	73	Piscivore	4.3	Oceanic	Bathypelagic
Himantolophidae	*Himantolophus mauli*	-	Atlantic	Planktonic eggs (rafts)	25	Unknown	4.3	Oceanic	Uncertain
Diceratiidae	*Diceratias wedli*	-	Atlantic	Planktonic eggs (rafts)	25	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Chaenophryne draco*	Smooth dreamer	Atlantic	Planktonic eggs (rafts)	10	Piscivore	3.8	Oceanic	Bathypelagic
Oneirodidae	*Chaenophryne longiceps*	-	Atlantic	Planktonic eggs (rafts)	17	Piscivore	4.1	Oceanic	Bathypelagic
Oneirodidae	*Ctenochirichthys longimanus*	-	Atlantic	Planktonic eggs (rafts)	NA	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Dolopichthys allector*	-	Atlantic	Planktonic eggs (rafts)	9	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Dolopichthys danae*	-	Atlantic	Planktonic eggs (rafts)	12	Piscivore	3.6	Oceanic	Bathypelagic
Oneirodidae	*Dolopichthys jubatus*	-	Atlantic	Planktonic eggs (rafts)	9	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Dolopichthys longicornis*	-	Atlantic	Planktonic eggs (rafts)	16	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Leptacanthichthys gracilispinis*	-	Atlantic	Planktonic eggs (rafts)	NA	Piscivore	NA	Oceanic	Bathypelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Oneirodidae	*Lophodolos acanthognathus*	Whale-head dreamer	Atlantic	Planktonic eggs (rafts)	8	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Microlophichthys microlophus*	Short-rod anglerfish	Atlantic	Planktonic eggs (rafts)	12	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Oneirodes anisacanthus*	–	Atlantic	Planktonic eggs (rafts)	21	Piscivore	4.2	Oceanic	Bathypelagic
Oneirodidae	*Oneirodes carlsbergi*	–	Atlantic	Planktonic eggs (rafts)	16	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Oneirodes clarkei*	–	Atlantic	Planktonic eggs (rafts)	12	Piscivore	3.9	Oceanic	Bathypelagic
Oneirodidae	*Oneirodes eschrichtii*	Bulbous dreamer	Atlantic	Planktonic eggs (rafts)	35	Piscivore	4.4	Oceanic	Bathypelagic
Oneirodidae	*Oneirodes macronema*	–	Atlantic	Planktonic eggs (rafts)	NA	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Oneirodes macrosteus*	–	Atlantic	Planktonic eggs (rafts)	20	Piscivore	NA	Oceanic	Bathypelagic
Oneirodidae	*Oneirodes myrionemus*	–	Atlantic	Planktonic eggs (rafts)	14	Piscivore	3.9	Oceanic	Bathypelagic
Oneirodidae	*Pentherichthys venustus*	–	Atlantic	Planktonic eggs (rafts)	12	Piscivore	3.8	Oceanic	Bathypelagic
Oneirodidae	*Phyllorhinichthys micractis*	–	Atlantic	Planktonic eggs (rafts)	12	Piscivore	NA	Oceanic	Bathypelagic
Thaumatichthyidae	*Lasiognathus beebei*	–	Atlantic	Planktonic eggs (rafts)	12	Unknown	4.0	Oceanic	Uncertain
Thaumatichthyidae	*Lasiognathus saccostoma*	–	Atlantic	Planktonic eggs (rafts)	9	Piscivore	4.0	Oceanic	Bathypelagic
Centrophrynidae	*Centrophryne spinulosa*	Horned lanternfish	Atlantic	Planktonic eggs (rafts)	2	Piscivore	NA	Oceanic	Bathypelagic
Ceratiidae	*Ceratias holboelli*	Krøyer's deep-sea anglerfish	Atlantic	Planktonic eggs (rafts)	17	Piscivore	3.2	Oceanic	Bathypelagic
Ceratiidae	*Cryptopsaras couesii*	Triple-wart seadevil	Atlantic	Planktonic eggs (rafts)	44	Piscivore	4.5	Oceanic	Bathypelagic
Gigantactinidae	*Gigantactis vanhoeffeni*	–	Atlantic	Planktonic eggs (rafts)	62	Piscivore	NA	Oceanic	Bathypelagic
Linophrynidae	*Haplophryne mollis*	–	Atlantic	Planktonic eggs (rafts)	10	Piscivore	3.7	Oceanic	Bathypelagic
Linophrynidae	*Linophryne brevibarbata*	–	Atlantic	Planktonic eggs (rafts)	11	Piscivore	3.8	Oceanic	Bathypelagic
Linophrynidae	*Linophryne coronata*	–	Atlantic	Planktonic eggs (rafts)	3	Piscivore	NA	Oceanic	Bathypelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Linophrynidae	*Linophryne lucifera*	–	Atlantic	Planktonic eggs (rafts)	24	Piscivore	4.1	Oceanic	Bathypelagic
Linophrynidae	*Linophryne maderensis*	–	Atlantic	Planktonic eggs (rafts)	11	Piscivore	3.8	Oceanic	Bathypelagic
Linophrynidae	*Linophryne polypogon*	–	Atlantic	Planktonic eggs (rafts)	5	Piscivore	3.4	Oceanic	Bathypelagic
Linophrynidae	*Linophryne sexfilis*	–	Atlantic	Planktonic eggs (rafts)	11	Piscivore	3.8	Oceanic	Bathypelagic
Gobiesocidae	*Apletodon bacescui*	Small-headed clingfish	Sarmatic	Demersal eggs	4	Benthivore	3.3	Coastal	Demersal
Gobiesocidae	*Apletodon dentatus*	Small-headed clingfish	Lusitanian	Demersal eggs	4	Benthivore	3.1	Coastal	Demersal
Gobiesocidae	*Apletodon incognitus*	–	Mediterranean	Demersal eggs	3	Benthivore	3.2	Inner shelf	Demersal
Gobiesocidae	*Apletodon pellegrini*	Chubby clingfish	African	demersal eggs	5	Benthivore	3.3	Shelf	Demersal
Gobiesocidae	*Diplecogaster bimaculata*	Two-spotted clingfish	Lusitanian	Demersal eggs	4	Benthivore	3.3	Inner shelf	Demersal
Gobiesocidae	*Diplecogaster euxinica*	Two-spotted clingfish	Sarmatic	Demersal eggs	4	Benthivore	3.3	Inner shelf	Demersal
Gobiesocidae	*Diplecogaster pectoralis*	Two-spotted clingfish	Macaronesia	Demersal eggs	2	Benthivore	3.3	Inner shelf	Demersal
Gobiesocidae	*Gouania willdenowi*	Blunt-snouted clingfish	Mediterranean	Demersal eggs	5	Benthivore	3.2	Shelf	Demersal
Gobiesocidae	*Lepadogaster candollei*	Connemarra clingfish	Lusitanian	Demersal eggs	9	Benthivore	2.8	Shelf	Demersal
Gobiesocidae	*Lepadogaster lepadogaster*	Shore clingfish	Mediterranean	Demersal eggs	6.5	Benthivore	3.3	Inner shelf	Demersal
Gobiesocidae	*Lepadogaster purpurea*	Cornish sucker	Lusitanian	Demersal eggs	9	Benthivore	3.4	Inner shelf	Demersal
Gobiesocidae	*Lepadogaster zebrina*	–	Macaronesia	Demersal eggs	7	Benthivore	3.3	Inner shelf	Demersal
Gobiesocidae	*Opeatogenys gracilis*	–	Mediterranean	Demersal eggs	3	Benthivore	3.1	Shelf	Demersal
Atherinidae	*Atherina hepsetus*	Mediterranean sandsmelt	Lusitanian	Attached eggs	20	Bentho-planktivore	3.2	Coastal	Pelagic
Atherinidae	*Atherina boyeri*	Big-scale sandsmelt	Lusitanian	Attached eggs	13	Bentho-planktivore	2.3	Coastal	Pelagic
Atherinidae	*Atherina presbyter*	Sandsmelt	Lusitanian	Attached eggs	20	Bentho-planktivore	3.7	Coastal	Pelagic
Atherinidae	*Atherinomorus lacunosus*	Hardy-head silverside	Indo-Pacific	Attached eggs	25	Bentho-planktivore	3.3	Coastal	Pelagic
Cyprinodontidae	*Aphanius dispar*	–	Indo-Pacific	Demersal eggs	7	Omnivore	2.0	Coastal	Demersal
Cyprinodontidae	*Aphanius fasciatus*	–	Mediterranean	Demersal eggs	6	Omnivore	2.7	Coastal	Demersal
Cyprinodontidae	*Aphanius iberus*	Spanish toothcarp	Mediterranean	Demersal eggs	5	Omnivore	3.4	Coastal	Demersal
Scomberesocidae	*Nanichthys simulans*	Dwarf saury	Atlantic	Planktonic eggs	13	Unknown	3.4	oceanic	Epipelagic
Scomberesocidae	*Scomberesox saurus*	Saurey pike	Atlantic	Planktonic eggs	45	Planktivore	3.6	Oceanic	Epipelagic
Belonidae	*Belone belone*	Garfish	Lusitanian	Attached eggs	90	Piscivore	4.2	Shelf	Epipelagic
Belonidae	*Belone svetovidovi*	–	Lusitanian	Attached eggs	93	Piscivore	4.3	Inner shelf	Epipelagic
Belonidae	*Platybelone argalus*	Keel-tail garfish	Macaronesia	Attached eggs	52	Unknown	4.2	Inner shelf	Epipelagic

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
Belonidae	*Tylosurus acus*	Agujon needlefish	Lusitanian	Attached eggs	153	Piscivore	4.5	Inner shelf	Epipelagic
Belonidae	*Tylosurus choram*	Red Sea houndfish	Indo-Pacific	Attached eggs	120	Piscivore	4.4	Inner shelf	Epipelagic
Belonidae	*Tylosurus imperialis*	–	Lusitanian	Attached eggs	140	Piscivore	4.5	Inner shelf	Epipelagic
Hemiramphidae	*Hemiramphus far*	Black-barred halfbeak	Indo-Pacific	Attached eggs	45	Herbivore	2.9	Coastal	Epipelagic
Hemiramphidae	*Hyporhamphus picarti*	African halfbeak	African	Attached eggs	20	Herbivore	2.0	Coastal	Epipelagic
Exocoetidae	*Cheilopogon exsiliens*	Band-wing flyingfish	Atlantic	Attached eggs	30	Planktivore	3.0	Oceanic	Epipelagic
Exocoetidae	*Cheilopogon heterurus*	Atlantic flyingfish	Atlantic	Attached eggs	34	Planktivore	3.4	Oceanic	Epipelagic
Exocoetidae	*Cheilopogon pinnatibarbatus*	Bennett's flyingfish	Atlantic	Attached eggs	49	Planktivore	4.0	Oceanic	Epipelagic
Exocoetidae	*Exocoetus obtusirostris*	Oceanic two-wing flyingfish	Atlantic	Planktonic eggs	24	Planktivore	3.0	Oceanic	Epipelagic
Exocoetidae	*Exocoetus volitans*	Tropical two-wing flyingfish	Atlantic	Planktonic eggs	30	Planktivore	3.0	Oceanic	Epipelagic
Exocoetidae	*Hirundichthys rondeletii*	Black-wing flyingfish	Atlantic	Attached eggs	30	Planktivore	3.0	Oceanic	Epipelagic
Exocoetidae	*Hirundichthys speculiger*	Mirror-wing flyingfish	Atlantic	Attached eggs	30	Planktivore	3.0	Oceanic	Epipelagic
Exocoetidae	*Parexocoetus mento*	African sail-fin flyingfish	Indo-Pacific	Attached eggs	13	Planktivore	3.3	Oceanic	Epipelagic
Stephanoberycidae	*Acanthochaenus luetkenii*	Pricklefish	Atlantic	Uncertain	17	Unknown	3.5	Oceanic	Bathypelagic
Melamphaidae	*Melamphaes longivelis*	–	Atlantic	Uncertain	12	Unknown	3.9	Oceanic	Bathypelagic
Melamphaidae	*Melamphaes microps*	–	Atlantic	Uncertain	10	Unknown	3.8	Oceanic	Bathypelagic
Melamphaidae	*Melamphaes simus*	–	Atlantic	Uncertain	3	Unknown	3.0	Oceanic	Bathypelagic
Melamphaidae	*Melamphaes suborbitalis*	–	Atlantic	Uncertain	11	Unknown	3.8	Oceanic	Bathypelagic
Melamphaidae	*Melamphaes typhlops*	–	Atlantic	Uncertain	9	Unknown	3.7	Oceanic	Bathypelagic
Melamphaidae	*Poromitra capito*	–	Atlantic	Uncertain	11	Unknown	3.4	Oceanic	Bathypelagic
Melamphaidae	*Poromitra crassiceps*	Crested bigscale	Atlantic	Uncertain	22	Unknown	3.1	Oceanic	Bathypelagic
Melamphaidae	*Poromitra megalops*	–	Atlantic	Uncertain	7	Unknown	3.3	Oceanic	Bathypelagic
Melamphaidae	*Scopeloberyx opisthopterus*	–	Atlantic	Uncertain	4	Unknown	3.0	Oceanic	Bathypelagic
Melamphaidae	*Scopeloberyx robustus*	Long-jaw bigscale	Atlantic	Uncertain	8	Unknown	3.1	Oceanic	Bathypelagic
Melamphaidae	*Scopeloberyx rubriventer*	–	Atlantic	Uncertain	NA	Unknown	NA	Oceanic	Bathypelagic
Melamphaidae	*Scopelogadus beanii*	–	Atlantic	Uncertain	13	Unknown	3.8	Oceanic	Bathypelagic
Melamphaidae	*Scopelogadus mizolepis*	–	Atlantic	Uncertain	10	Unknown	3.5	Oceanic	Bathypelagic
Trachichthyidae	*Gephyroberyx darwinii*	Darwin's slimehead	Atlantic	Uncertain	60	Bentho-piscivore	3.9	Slope	Bathydemersal
Trachichthyidae	*Hoplostethus atlanticus*	Orange roughy	Atlantic	Uncertain	75	Bentho-piscivore	4.3	Slope	Bathydemersal
Trachichthyidae	*Hoplostethus cadenati*	Black slimehead	African	Uncertain	30	Bentho-piscivore	3.2	Slope	Bathydemersal
Trachichthyidae	*Hoplostethus mediterraneus*	Mediterranean slimehead	Atlantic	Uncertain	51	Bentho-piscivore	3.5	Slope	Bathydemersal
Diretmidae	*Diretmichthys parini*	Parin's spiny fin	Atlantic	Uncertain	40	Planktivore	3.5	Oceanic	Mesopelagic
Diretmidae	*Diretmoides pauciradiatus*	Long-wing spinyfin	Atlantic	Uncertain	37	Planktivore	NA	Oceanic	Mesopelagic
Diretmidae	*Diretmus argenteus*	Silver spinyfin	Atlantic	Uncertain	32	Planktivore	3.7	Oceanic	Mesopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Anoplogasteridae	*Anoplogaster cornuta*	Common fangtooth	Atlantic	Uncertain	19	Piscivore	4.0	Oceanic	Mesopelagic
Berycidae	*Beryx decadactylus*	Beryx	Atlantic	Planktonic eggs	40	Piscivore	4.1	Slope	Bathydemersal
Berycidae	*Beryx splendens*	Splendid alfonsino	Atlantic	Planktonic eggs	70	Piscivore	4.4	Slope	Bathydemersal
Holocentridae	*Sargocentron hastatus*	Red squirrelfish	African	Planktonic eggs	25	Benthivore	3.5	Coastal	Demersal
Holocentridae	*Sargocentron rubrum*	Redcoat	Indo-Pacific	Planktonic eggs	32	Benthivore	3.5	Coastal	Demersal
Mirapinnidae (Eutaeniophoridae)	*Eutaeniophorus festivus*	–	Atlantic	Uncertain	6	Planktivore	3.0	Oceanic	Pelagic
Mirapinnidae	*Mirapinna esau*	Hairyfish	Atlantic	Uncertain	5	Unknown	3.0	Oceanic	Uncertain
Mirapinnidae (Eutaeniophoridae)	*Parataeniophorus gulosus*	–	Atlantic	Uncertain	4	Planktivore	3.0	Oceanic	Pelagic
Megalomycteridae	*Ataxolepis apus*	–	Uncertain	Uncertain	5	Unknown	NA	Unknown	Uncertain
Rondeletiidae	*Rondeletia loricata*	Red-mouth whalefish	Atlantic	Uncertain	11	Planktivore	3.4	Oceanic	Bathypelagic
Cetomimidae	*Cetomimus hempeli*	Whalefish	Atlantic	Uncertain	10	Unknown	3.0	Oceanic	Bathypelagic
Cetomimidae	*Cetostoma regani*	Whalefish	Atlantic	Uncertain	30	Planktivore	3.3	Oceanic	Bathypelagic
Cetomimidae	*Ditropichthys storeri*	–	Atlantic	Uncertain	16	Unknown	3.0	Oceanic	Bathypelagic
Macrurocyttidae	*Zenion hololepis*	–	Atlantic	Uncertain	12	Unknown	3.7	Slope	Demersal
Zeidae	*Cyttopsis rosea*	Rosy dory	Lusitanian	Planktonic eggs	31	Piscivore	4.0	Outer shelf	Benthopelagic
Zeidae	*Zenopsis conchifer*	Silvery John dory	Lusitanian	Planktonic eggs	80	Piscivore	4.5	Outer shelf	Benthopelagic
Zeidae	*Zeus faber*	John dory	Lusitanian	Planktonic eggs	66	Piscivore	4.5	Shelf	Benthopelagic
Oreosomatidae	*Neocyttus helgae*	False boarfish	Atlantic	Uncertain	31	Unknown	3.5	Oceanic	Mesopelagic
Oreosomatidae	*Allocyttus verrucosus*	Warty oreo	Atlantic	Uncertain	42	Bentho-piscivore	4.2	Oceanic	Bathypelagic
Oreosomatidae	*Pseudocyttus maculatus*	Smooth oreo	Atlantic	Uncertain	68	Medusophagous	3.6	Slope	Bathydemersal
Grammicolepididae	*Grammicolepis brachiusculus*	Thorny tinselfish	Atlantic	Uncertain	64	Unknown	4.3	Slope	Benthopelagic
Caproidae	*Antigonia capros*	Deep-body boarfish	Macaronesia	Planktonic eggs	31	Benthivore	4.1	Slope	Bathydemersal
Caproidae	*Capros aper*	Boarfish	Lusitanian	Planktonic eggs	16	Planktivore	3.1	Slope	Bathydemersal
Gasterosteidae	*Gasterosteus aculeatus*	Three-spined stickleback	Boreal	Nest-forming	8	Benthivore	3.5	Coastal	Demersal
Gasterosteidae	*Pungitius platygaster*	Southern nine-spined stickleback	Sarmatic	Nest-forming	8	Benthivore	3.2	Coastal	Demersal
Gasterosteidae	*Pungitius pungitius*	Nine-spined stickleback	Boreal	Nest-forming	8	Benthivore	3.3	Coastal	Demersal
Gasterosteidae	*Spinachia spinachia*	Fifteen-spined stickleback	Boreal	Nest-forming	22	Benthivore	3.5	Coastal	Demersal
Centriscidae (Macroramphosidae)	*Macroramphosus scolopax*	Snipefish	Lusitanian	Planktonic eggs	20	Planktivore	3.5	Slope	Bathydemersal
Syngnathidae	*Entelurus aequoreus*	Snake pipefish	Lusitanian	Egg brooder	60	Planktivore	3.5	Oceanic/shelf	Pelagic
Syngnathidae	*Minyichthys sentus*	–	African	Egg brooder	6	Planktivore	3.2	Shelf	Demersal
Syngnathidae	*Nerophis lumbriciformis*	Worm pipefish	Lusitanian	Egg brooder	17	Planktivore	4.0	Coastal	Demersal
Syngnathidae	*Nerophis maculatus*	–	Lusitanian	Egg brooder	30	Planktivore	3.4	Coastal	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Syngnathidae	*Nerophis ophidion*	Straight-nosed pipefish	Lusitanian	Egg brooder	30	Planktivore	4.0	Coastal	Demersal
Syngnathidae	*Syngnathus abaster*	Black-striped pipefish	Lusitanian	Egg brooder	21	Planktivore	3.2	Coastal	Demersal
Syngnathidae	*Syngnathus acus*	Great pipefish	Lusitanian	Egg brooder	46	Planktivore	3.4	Coastal	Demersal
Syngnathidae	*Syngnathus phlegon*	-	Lusitanian	Egg brooder	20	Planktivore	3.5	Shelf	Pelagic
Syngnathidae	*Syngnathus rostellatus*	Nilsson's pipefish	Lusitanian	Egg brooder	17	Planktivore	3.7	Coastal	Demersal
Syngnathidae	*Syngnathus schmidti*	-	Sarmatic	Egg brooder	11	Planktivore	3.0	Coastal	Pelagic
Syngnathidae	*Syngnathus taenionotus*	-	Mediterranean	Egg brooder	19	Planktivore	3.3	Coastal	Demersal
Syngnathidae	*Syngnathus tenuirostris*	Narrow-snouted pipefish	Mediterranean	Egg brooder	26	Planktivore	3.3	Coastal	Demersal
Syngnathidae	*Syngnathus typhle*	Deep-snouted pipefish	Lusitanian	Egg brooder	35	Planktivore	4.3	Coastal	Demersal
Syngnathidae	*Syngnathus variegatus*	-	Sarmatic	Egg brooder	30	Planktivore	3.3	Coastal	Demersal
Syngnathidae	*Hippocampus hippocampus*	Short-snouted sea horse	Lusitanian	Egg brooder	16	Planktivore	3.2	Coastal	Demersal
Syngnathidae	*Hippocampus guttulatus*	Sea horse	Lusitanian	Egg brooder	16	Planktivore	3.5	Coastal	Demersal
Sebastidae	*Helicolenus dactylopterus*	Blue-mouth redfish	Atlantic	Planktonic eggs	44	Plankto-piscivore	3.8	Slope	Bathydemersal
Sebastidae	*Sebastes fasciatus*	Acadian redfish	Boreal	Viviparous	30	Plankto-piscivore	3.2	Slope	Demersal
Sebastidae	*Sebastes marinus*	Redfish	Boreal	Viviparous	100	Plankto-piscivore	4.0	Slope	Pelagic
Sebastidae	*Sebastes mentella*	Deep-water redfish	Boreal	Viviparous	55	Plankto-piscivore	3.7	Oceanic	Bathypelagic
Sebastidae	*Sebastes viviparus*	Norway haddock	Boreal	Viviparous	35	Piscivore	4.0	Slope	Demersal
Sebastidae	*Trachyscorpia echinata*	Spiny scorpionfish	Lusitanian	Uncertain	50	Unknown	3.4	Slope	Bathydemersal
Setarchidae	*Setarches guentheri*	Deep-water scorpionfish	African	Uncertain	25	Unknown	3.5	Slope	Demersal
Scorpaenidae	*Pontinus kuhlii*	Offshore rockfish	African	Planktonic eggs (?)	52	Unknown	4.1	Outer shelf	Demersal
Scorpaenidae	*Scorpaena azorica*	-	Macaronesia	Planktonic eggs (?)	12	Unknown	3.5	Unknown	Demersal
Scorpaenidae	*Scorpaena elongata*	Slender rockfish	African	Planktonic eggs (?)	50	Bentho-piscivore	3.9	Outer shelf	Demersal
Scorpaenidae	*Scorpaena laevis*	Senegalese rockfish	African	Planktonic eggs (?)	43	Unknown	3.8	Shelf	Demersal
Scorpaenidae	*Scorpaena loppei*	Cadenat's rockfish	Lusitanian	Planktonic eggs (?)	15	Benthivore	3.5	Outer shelf	Demersal
Scorpaenidae	*Scorpaena madurensis*	Madeira rockfish	African	Planktonic eggs (?)	14	Bentho-piscivore	4.1	Inner shelf	Demersal
Scorpaenidae	*Scorpaena notata*	Small red scorpionfish	Lusitanian	Planktonic eggs (?)	24	Bentho-piscivore	3.5	Shelf	Demersal
Scorpaenidae	*Scorpaena porcus*	Black scorpionfish	Lusitanian	Planktonic eggs	37	Bentho-piscivore	3.9	Shelf	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
				(?)					
Scorpaenidae	*Scorpaena scrofa*	Red scorpion fish	Lusitanian	Planktonic eggs (?)	50	Piscivore	4.3	Slope	Demersal
Scorpaenidae	*Scorpaenodes arenai*	Messina rockfish	Mediterranean	Planktonic eggs (?)	11	Unknown	3.5	Unknown	Demersal
Dactylopteridae	*Dactylopterus volitans*	Flying gurnard	Lusitanian	Uncertain	90	Benthivore	3.6	Shelf	Demersal
Scorpaenidae	*Sebastapistes nuchalis*	-	Indo-Pacific	Planktonic eggs (?)	10	Benthivore	NA	Inner shelf	Demersal
Triglidae	*Aspitrigla cuculus*	Red gurnard	Lusitanian	Planktonic eggs	50	Benthivore	3.8	Shelf	Demersal
Triglidae	*Aspitrigla obscurus*	Long-fin gurnard	Lusitanian	Planktonic eggs	34	Benthivore	3.4	Shelf	Demersal
Triglidae	*Eutrigla gurnardus*	Grey gurnard	Lusitanian	Planktonic eggs	50	Benthivore	3.6	Shelf	Demersal
Triglidae	*Trigla lucerna*	Tub gurnard	Lusitanian	Planktonic eggs	75	Benthivore	3.7	Shelf	Demersal
Triglidae	*Trigla lyra*	Piper	Lusitanian	Planktonic eggs	60	Benthivore	3.5	Outer shelf	Bathydemersal
Triglidae	*Trigloporus lastoviza*	Streaked gurnard	Lusitanian	Planktonic eggs	40	Benthivore	3.4	Shelf	Demersal
Triglidae	*Lepidotrigla cavillone*	Large-scaled gurnard	Lusitanian	Planktonic eggs	20	Benthivore	3.2	Shelf	Demersal
Triglidae	*Lepidotrigla dieuzeidei*	Spiny gurnard	African	Planktonic eggs	20	Benthivore	3.3	Shelf	Demersal
Peristediidae	*Peristedion cataphractum*	African armoured searobin	Lusitanian	Planktonic eggs	40	Benthivore	3.5	Outer shelf	Demersal
Platycephalidae	*Platycephalus indicus*	Bar-tail flathead	Indo-Pacific	Uncertain	100	Bentho-piscivore	3.6	Shelf	Demersal
Cottidae	*Artediellus atlanticus*	Atlantic hook-ear sculpin	Boreal	Demersal eggs	13	Benthivore	3.4	Shelf	Demersal
Cottidae	*Artediellus scaber*	Hamecon	Arctic	Demersal eggs	9	Benthivore	3.4	Shelf	Demersal
Cottidae	*Artediellus uncinatus*	Arctic hook-ear sculpin	Arctic	Demersal eggs	10	Benthivore	3.5	Shelf	Demersal
Cottidae	*Cottus gobio*	Bullhead	Boreal	Demersal eggs	18	Benthivore	3.2	Coastal	Demersal
Cottidae	*Cottus poecilopus*	Alpine bullhead	Boreal	Demersal eggs	18	Benthivore	3.0	Coastal	Demersal
Cottidae	*Gymnocanthus tricuspis*	Arctic stag-horn sculpin	Arctic	Demersal eggs	30	Benthivore	3.3	Shelf	Demersal
Cottidae	*Icelus bicornis*	Two-horn sculpin	Boreal	Demersal eggs	16	Benthivore	3.1	Shelf	Demersal
Cottidae	*Icelus spatula*	Spatulate sculpin	Arctic	Demersal eggs	21	Benthivore	3.9	Shelf	Demersal
Cottidae	*Micrenophrys lilljeborgii*	Norway bullhead	Boreal	Demersal eggs	7	Benthivore	3.8	Inner shelf	Demersal
Cottidae	*Myoxocephalus scorpioides*	Arctic sculpin	Arctic	Demersal eggs	30	Benthivore	3.4	Inner shelf	Demersal
Cottidae	*Myoxocephalus scorpius*	Bullrout	Boreal	Demersal eggs	60	Bentho-piscivore	3.9	Inner shelf	Demersal
Cottidae	*Taurulus bubalis*	Sea scorpion	Boreal	Demersal eggs	17.5	Benthivore	3.6	Inner shelf	Demersal
Cottidae	*Triglops murrayi*	Sculpin	Boreal	Demersal eggs	19	Benthivore	3.5	Outer shelf	Demersal
Cottidae	*Triglops nybelini*	Big-eye sculpin	Arctic	Demersal eggs	25	Benthivore	3.3	Slope	Demersal
Cottidae	*Triglops pingelii*	Ribbed sculpin	Arctic	Demersal eggs	25	Benthivore	3.4	Shelf	Demersal
Cottidae	*Triglopsis quadricornis*	Four-horn sculpin	Boreal	Demersal eggs	60	Benthivore	3.7	Coastal	Demersal
Psychrolutidae	*Cottunculus microps*	Polar sculpin	Boreal	Demersal eggs	37	Benthivore	3.4	Outer shelf	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Psychrolutidae	*Cottunculus sadko*	Sadko sculpin	Arctic	Demersal eggs	19	Unknown	3.4	Slope	Demersal
Psychrolutidae	*Cottunculus thomsonii*	Pallid sculpin	Atlantic	Demersal eggs	43	Benthivore	3.5	Slope	Demersal
Psychrolutidae	*Psychrolutes subspinosus*	–	Arctic	Demersal eggs	12	Unknown	NA	Slope	Bathydemersal
Agonidae	*Agonus cataphractus*	Pogge (armed bullhead)	Boreal	Demersal eggs	21	Benthivore	3.4	Inner shelf	Demersal
Agonidae	*Leptagonus decagonus*	Atlantic poacher	Arctic	Demersal eggs	21	Benthivore	3.2	Outer shelf	Demersal
Agonidae	*Ulcina olrikii*	Arctic alligatorfish	Arctic	Demersal eggs	9	Benthivore	3.3	Shelf	Demersal
Cyclopteridae	*Cyclopteropsis mcalpini*	Arctic lumpsucker	Arctic	Demersal eggs	8	Unknown	3.4	Shelf	Demersal
Cyclopteridae	*Cyclopterus lumpus*	Lumpsucker	Boreal	Demersal eggs	61	Bentho-piscivore	3.9	Shelf	Benthopelagic
Cyclopteridae	*Eumicrotremus derjugini*	Leather-fin lumpsucker	Arctic	Demersal eggs	12	Benthivore	3.3	Shelf	Demersal
Cyclopteridae	*Eumicrotremus eggvinii*	–	Arctic	Demersal eggs	9	Unknown	NA	Shelf	Demersal
Cyclopteridae	*Eumicrotremus spinosus*	Atlantic spiny lumpsucker	Arctic	Demersal eggs	13	Benthivore	3.3	Shelf	Demersal
Cyclopteridae (Liparidae)	*Careproctus aciculipunctatus*	–	Boreal	Demersal eggs	21	Benthivore	NA	Slope	Demersal
Cyclopteridae (Liparidae)	*Careproctus merretti*	Merret's snailfish	Atlantic	Demersal eggs	21	Benthivore	NA	Oceanic	Bathydemersal
Cyclopteridae (Liparidae)	*Careproctus micropus*	–	Boreal	Demersal eggs	22	Benthivore	3.3	Slope	Demersal
Cyclopteridae (Liparidae)	*Careproctus reinhardti*	Sea tadpole	Arctic	Demersal eggs	30	Benthivore	3.5	Slope	Demersal
Cyclopteridae (Liparidae)	*Liparis fabricii*	Gelatinous snailfish	Arctic	Demersal eggs	20	Benthivore	3.5	Outer shelf	Demersal
Cyclopteridae (Liparidae)	*Liparis liparis*	Seasnail	Boreal	Demersal eggs	18	Benthivore	3.6	Inner shelf	Demersal
Cyclopteridae (Liparidae)	*Liparis montagui*	Montagu's seasnail	Boreal	Demersal eggs	10	Benthivore	3.5	Inner shelf	Demersal
Cyclopteridae (Liparidae)	*Paraliparis abyssorum*	–	Atlantic	Demersal eggs	12	Benthivore	NA	Oceanic	Bathydemersal
Cyclopteridae (Liparidae)	*Paraliparis bathybius*	Black seasnail	Arctic	Demersal eggs	31	Benthivore	3.3	Slope	Bathydemersal
Cyclopteridae (Liparidae)	*Paraliparis bipolaris*	–	Atlantic	Demersal eggs	9	Benthivore	NA	Oceanic	Bathydemersal
Cyclopteridae (Liparidae)	*Paraliparis challengeri*	–	Atlantic	Demersal eggs	NA	Benthivore	NA	Oceanic	Bathydemersal
Cyclopteridae (Liparidae)	*Paraliparis edwardsi*	–	Uncertain	Demersal eggs	10	Benthivore	3.4	Unknown	Demersal
Cyclopteridae (Liparidae)	*Paraliparis hystrix*	–	Atlantic	Demersal eggs	17	Benthivore	3.3	Slope	Bathydemersal
Cyclopteridae (Liparidae)	*Paraliparis leptochirus*	–	Mediterranean	Demersal eggs	5	Benthivore	NA	Slope	Bathydemersal
Cyclopteridae (Liparidae)	*Paraliparis membranaceus*	–	Uncertain	Demersal eggs	7	Benthivore	3.2	Unknown	Uncertain
Cyclopteridae (Liparidae)	*Paraliparis murieli*	–	Mediterranean	Demersal eggs	17	Benthivore	3.3	Slope	Bathydemersal
Cyclopteridae (Liparidae)	*Psednos christinae*	European dwarf snailfish	Atlantic	Demersal eggs	NA	Benthivore	NA	Slope	Bathydemersal
Cyclopteridae (Liparidae)	*Rhodichthys regina*	Thread-fin seasnail	Arctic	Demersal eggs	38	Benthivore	3.5	oceanic	Benthopelagic
Percichthyidae	*Howella brodiei*	Pelagic basslet	Atlantic	Planktonic eggs	7	Unknown	NA	Shelf	Benthopelagic
Percichthyidae	*Howella sherborni*	–	Atlantic	Planktonic eggs	8	Unknown	3.2	Shelf	Benthopelagic
Moronidae	*Dicentrarchus labrax*	European sea bass	Lusitanian	Planktonic eggs	100	Piscivore	3.8	Shelf	Benthopelagic
Moronidae	*Dicentrarchus punctatus*	Spotted sea bass	Lusitanian	Planktonic eggs	70	Piscivore	3.9	Shelf	Benthopelagic
Polyprionidae	*Polyprion americanus*	Wreckfish	Lusitanian	Planktonic eggs	200	Piscivore	3.8	Shelf	Benthopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Serranidae	*Serranus atricauda*	Black-tail comber	Lusitanian	Planktonic eggs	43	Piscivore	4.3	Shelf	Demersal
Serranidae	*Serranus cabrilla*	Comber	Lusitanian	Planktonic eggs	40	Bentho-piscivore	3.3	Shelf	Demersal
Serranidae	*Serranus hepatus*	Brown comber	Lusitanian	Planktonic eggs	25	Bentho-piscivore	3.5	Shelf	Demersal
Serranidae	*Serranus scriba*	Painted comber	Lusitanian	Planktonic eggs	44	Bentho-piscivore	3.8	Shelf	Demersal
Serranidae	*Anthias anthias*	Swallow-tail sea perch	Lusitanian	Planktonic eggs	33	Piscivore	3.8	Shelf	Demersal
Serranidae	*Epinephelus aeneus*	White grouper	Lusitanian	Planktonic eggs	120	Piscivore	4.0	Shelf	Demersal
Serranidae	*Epinephelus caninus*	Dog-tooth grouper	Lusitanian	Planktonic eggs	157	Piscivore	3.8	Shelf	Demersal
Serranidae	*Epinephelus coioides*	Orange-spotted grouper	Indo-Pacific	Planktonic eggs	120	Bentho-piscivore	3.9	Shelf	Reef-associated
Serranidae	*Epinephelus costae*	Gold-blotch grouper	African	Planktonic eggs	171	Bentho-piscivore	3.9	Shelf	Demersal
Serranidae	*Epinephelus haifensis*	Haifa grouper	Mediterranean	Planktonic eggs	110	Unknown	4.0	Shelf	Demersal
Serranidae	*Epinephelus malabaricus*	Malabar grouper	Indo-Pacific	Planktonic eggs	234	Unknown	3.8	Shelf	Demersal
Serranidae	*Epinephelus marginatus*	Dusky grouper	Lusitanian	Planktonic eggs	150	Bentho-piscivore	3.7	Shelf	Demersal
Serranidae	*Epinephelus nigritus*	Warsaw grouper	Uncertain	Planktonic eggs	230	Bentho-piscivore	4.0	Shelf	Demersal
Serranidae	*Mycteroperca fusca*	Island grouper	Macaronesia	Planktonic eggs	80	Unknown	4.3	Shelf	Demersal
Serranidae	*Mycteroperca rubra*	Mottled grouper	Lusitanian	Planktonic eggs	144	Piscivore	4.1	Shelf	Demersal
Callanthiidae	*Callanthias ruber*	Parrot sea perch	Lusitanian	Uncertain	60	Piscivore	3.8	Shelf	Demersal
Terapontidae	*Pelates quadrilineatus*	Four-lined terapon	Indo-Pacific	Planktonic eggs	30	Benthivore	3.5	Coastal	Demersal
Terapontidae	*Terapon puta*	Small-scaled terapon	Indo-Pacific	Planktonic eggs	16	Benthivore	3.1	Coastal	Demersal
Priacanthidae	*Cookeolus japonicus*	Long-finned bullseye	Uncertain	Uncertain	68	Unknown	3.5	Shelf	Reef-associated
Priacanthidae	*Heteropriacanthus cruentatus*	Glasseye	African	Uncertain	51	Bentho-piscivore	3.8	Inner shelf	Reef-associated
Priacanthidae	*Priacanthus arenatus*	Atlantic bigeye	African	Uncertain	50	Bentho-piscivore	4.0	Inner shelf	Reef-associated
Apogonidae	*Apogon (Apogon) imberbis*	Cardinal fish	Lusitanian	Egg brooder	18	Bentho-piscivore	3.9	Shelf	Demersal
Apogonidae	*Apogon (Nectamia) taeniatus*	Two-belt cardinal	Indo-Pacific	Egg brooder	17	Unknown	3.5	Inner shelf	Demersal
Epigonidae	*Epigonus constanciae*	–	Lusitanian	Uncertain	16	Unknown	3.3	Slope	Demersal
Epigonidae	*Epigonus denticulatus*	Pencil cardinal	Lusitanian	Uncertain	20	Plankto-piscivore	3.3	Slope	Demersal
Epigonidae	*Epigonus telescopus*	Bullseye	Lusitanian	Uncertain	75	Plankto-piscivore	3.3	Slope	Demersal
Epigonidae	*Microichthys coccoi*	–	Mediterranean	Uncertain	3	Unknown	3.1	Unknown	Pelagic
Epigonidae	*Microichthys sanzoi*	–	Mediterranean	Uncertain	6	Unknown	3.2	Unknown	Pelagic
Pomatomidae	*Pomatomus saltator*	Bluefish	Atlantic	Planktonic eggs	130	Piscivore	4.5	Shelf	Pelagic
Rachycentridae	*Rachycentron canadum*	Cobia	Atlantic	Planktonic eggs	200	Piscivore	4.0	Shelf	Pelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(CM)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Echeneidae	*Echeneis naucrates*	Sharksucker	Uncertain	Planktonic eggs	110	Plankto-piscivore	3.4	Shelf	Pelagic
Echeneidae	*Phtheirichthys lineatus*	Slender suckerfish	Atlantic	Planktonic eggs	76	Plankto-piscivore	NA	Oceanic	Pelagic
Echeneidae	*Remora australis*	Whalesucker	Atlantic	Planktonic eggs	76	Plankto-piscivore	3.3	Oceanic	Pelagic
Echeneidae	*Remora brachyptera*	Spearfish remora	Atlantic	Planktonic eggs	50	Plankto-piscivore	3.3	Oceanic	Pelagic
Echeneidae	*Remora osteochir*	Marlin sucker	Atlantic	Planktonic eggs	49	Plankto-piscivore	3.5	Oceanic	Pelagic
Echeneidae	*Remora remora*	Sharksucker	Atlantic	Planktonic eggs	62	Plankto-piscivore	3.1	Oceanic	Epipelagic
Echeneidae	*Remorina albescens*	White suckerfish	Atlantic	Planktonic eggs	30	Plankto-piscivore	NA	Oceanic	Pelagic
Carangidae	*Alectis alexandrinus*	African threadfish	African	Planktonic eggs	100	Piscivore	3.6	Shelf	Pelagic
Carangidae	*Alepes djedaba*	Shrimp scad	Indo-Pacific	Planktonic eggs	40	Planktivore	3.3	Coastal	Pelagic
Carangidae	*Campogramma glaycos*	Vadigo	Lusitanian	Planktonic eggs	67	Piscivore	4.5	Inner shelf	Pelagic
Carangidae	*Caranx crysos*	Blue runner	Lusitanian	Planktonic eggs	70	Piscivore	4.4	Inner shelf	Pelagic
Carangidae	*Caranx hippos*	Crevalle jack	Lusitanian	Planktonic eggs	124	Piscivore	4.0	Shelf	Pelagic
Carangidae	*Caranx latus*	Horse-eye jack	African	Planktonic eggs	100	Piscivore	4.4	Inner shelf	Pelagic
Carangidae	*Caranx lugubris*	Black jack	African	Planktonic eggs	90	Piscivore	4.5	Shelf	Pelagic
Carangidae	*Caranx rhonchus*	False scad	African	Planktonic eggs	60	Piscivore	3.6	Inner shelf	Benthopelagic
Carangidae	*Decapterus macarellus*	Mackerel scad	African	Planktonic eggs	46	Planktivore	3.4	Shelf	Pelagic
Carangidae	*Decapterus punctatus*	Round scad	African	Planktonic eggs	37	Pisco-planktivore	4.3	Shelf	Pelagic
Carangidae	*Elagatis bipinnulata*	Rainbow runner	African	Planktonic eggs	180	Piscivore	3.6	Shelf	Pelagic
Carangidae	*Lichia amia*	Leerfish	Lusitanian	Planktonic eggs	200	Piscivore	4.5	Inner shelf	Pelagic
Carangidae	*Naucrates ductor*	Pilotfish	Atlantic	Planktonic eggs	63	Scavenger	4.0	Oceanic	Epipelagic
Carangidae	*Pseudocaranx dentex*	White trevally	Lusitanian	Planktonic eggs	122	Benthivore	3.9	Inner shelf	Demersal
Carangidae	*Selar boops*	Ox-eye scad	Tropical vagrant	Planktonic eggs	28	Planktivore	3.5	Shelf	Pelagic
Carangidae	*Selene dorsalis*	African moonfish	African	Planktonic eggs	38	Bentho-piscivore	4.1	Shelf	Benthopelagic
Carangidae	*Seriola carpenteri*	Guinean amberjack	African	Planktonic eggs	73	Piscivore	4.5	Shelf	Benthopelagic
Carangidae	*Seriola dumerili*	Greater amberjack	Lusitanian	Planktonic eggs	190	Piscivore	4.5	Shelf	Benthopelagic
Carangidae	*Seriola fasciata*	Lesser amberjack	African	Planktonic eggs	75	Piscivore	4.5	Shelf	Benthopelagic
Carangidae	*Seriola rivoliana*	Almaco jack	Lusitanian	Planktonic eggs	178	Piscivore	4.5	Shelf	Benthopelagic
Carangidae	*Trachinotus ovatus*	Derbio	Lusitanian	Planktonic eggs	70	Piscivore	3.7	Shelf	Pelagic
Carangidae	*Trachurus mediterraneus*	Mediterranean horse	Lusitanian	Planktonic eggs	67	Piscivore	3.6	Shelf	Pelagic

FAMILY	SCIENTIFIC NAME	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{max} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)
		mackerel							
Carangidae	*Trachurus picturatus*	Blue jack mackerel	Lusitanian	Planktonic eggs	60	Piscivore	3.3	Shelf	Pelagic
Carangidae	*Trachurus trachurus*	Horse mackerel	Lusitanian	Planktonic eggs	60	Piscivore	3.6	Shelf	Pelagic
Carangidae	*Trachurus trecae*	Cunene horse mackerel	African	Planktonic eggs	39	Piscivore	3.5	Shelf	Pelagic
Coryphaenidae	*Coryphaena equiselis*	Pompano dolphinfish	Atlantic	Planktonic eggs	75	Piscivore	4.5	Oceanic	Epipelagic
Coryphaenidae	*Coryphaena hippurus*	Common dolphinfish	Atlantic	planktonic eggs	210	Piscivore	4.4	Oceanic	Epipelagic
Leiognathidae	*Leiognathus klunzingeri*	Ponyfish	Indo–Pacific	Uncertain	13	Benthivore	3.5	Coastal	Demersal
Bramidae	*Brama brama*	Ray's bream	Atlantic	Planktonic eggs	70	Piscivore	4.1	Oceanic	Mesopelagic
Bramidae	*Pteraclis carolinus*	–	Atlantic	planktonic eggs	61	Unknown	4.3	Oceanic	Mesopelagic
Bramidae	*Pterycombus brama*	Silver pomfret	Atlantic	Planktonic eggs	40	Piscivore	4.0	Oceanic	Epipelagic
Bramidae	*Taractes asper*	Rough pomfret	Atlantic	Planktonic eggs	50	Piscivore	4.1	Oceanic	Epipelagic
Bramidae	*Taractes rubescens*	Pomfret	Atlantic	planktonic eggs	70	Unknown	NA	Oceanic	Epipelagic
Bramidae	*Taractichthys longipinnis*	Long-finned bream	Atlantic	Planktonic eggs	100	Piscivore	4.5	Oceanic	Epipelagic
Caristiidae	*Caristius macropus*	Manefish	Uncertain	Uncertain	32	Piscivore	4.2	Slope	Bathypelagic
Caristiidae	*Caristius maderensis*	–	Uncertain	Uncertain	30	Planktivore	NA	Unknown	Mesopelagic
Caristiidae	*Caristius opalescens*	–	Atlantic	Uncertain	19 or 60	Planktivore	NA	Oceanic	Mesopelagic
Emmelichthyidae	*Erythrocles monodi*	Atlantic rubyfish	African	Uncertain	65	Planktivore	3.4	Shelf	Pelagic
Lobotidae	*Lobotes surinamensis*	Atlantic tripletail	Lusitanian	Uncertain	110	Bentho-piscivore	4.0	Coastal	Demersal
Haemulidae	*Brachydeuterus auritus*	Big-eye grunt	African	Uncertain	30	Benthivore	3.0	Shelf	Demersal
Haemulidae	*Parapristipoma humile*	Guinean grunt	African	Uncertain	37	Benthivore	3.5	Shelf	Demersal
Haemulidae	*Parapristipoma octolineatum*	African striped grunt	African	Uncertain	61	Benthivore	3.5	Shelf	Demersal
Haemulidae	*Plectorhinchus mediterraneus*	Rubber-lip grunt	African	Uncertain	98	Benthivore	3.5	Shelf	Demersal
Haemulidae	*Pomadasys incisus*	Bastard grunt	African	Uncertain	50	Benthivore	3.8	Shelf	Demersal
Haemulidae	*Pomadasys stridens*	Striped piggy	Indo–Pacific	Uncertain	20	Benthivore	4.0	Shelf	Demersal
Sparidae	*Boops boops*	Bogue	Lusitanian	Planktonic eggs	36	Omnivore	3.0	Coastal	Benthopelagic
Sparidae	*Crenidens crenidens*	Karenteen sea bream	Indo–Pacific	Planktonic eggs	30	Omnivore	2.8	Coastal	Demersal
Sparidae	*Dentex (Cheimerius) canariensis*	Canary dentex	African	Planktonic eggs	122	Bentho-piscivore	3.6	Coastal	Demersal
Sparidae	*Dentex (Cheimerius) gibbosus*	Pink dentex	African	Planktonic eggs	118	Bentho-piscivore	4.1	Coastal	Demersal
Sparidae	*Dentex (Dentex) dentex*	Dentex	Lusitanian	Planktonic eggs	100	Piscivore	4.5	Inner shelf	Reef-associated
Sparidae	*Dentex (Polysteganus) macrophthalmus*	Large-eye dentex	African	Planktonic eggs	65	Bentho-piscivore	3.4	Inner shelf	Demersal
Sparidae	*Dentex (Polysteganus) maroccanus*	Morocco dentex	Lusitanian	Planktonic eggs	41	Piscivore	3.8	Inner shelf	Demersal
Sparidae	*Diplodus annularis*	Annular sea bream	Lusitanian	Planktonic eggs	24	Benthivore	3.4	Inner shelf	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Sparidae	*Diplodus bellottii*	Senegal sea bream	African	Planktonic eggs	37	Benthivore	3.5	Inner shelf	Demersal
Sparidae	*Diplodus cervinus*	Zebra sea bream	Lusitanian	Planktonic eggs	55	Omnivore	3.0	Inner shelf	Demersal
Sparidae	*Diplodus puntazzo*	Sharp-snout sea bream	Lusitanian	Planktonic eggs	60	Omnivore	2.9	Inner shelf	Demersal
Sparidae	*Diplodus sargus*	White sea bream	Lusitanian	Planktonic eggs	45	Omnivore	3.0	Inner shelf	Demersal
Sparidae	*Diplodus vulgaris*	Common two-banded sea bream	Lusitanian	Planktonic eggs	45	Omnivore	3.2	Inner shelf	Demersal
Sparidae	*Lithognathus mormyrus*	Striped sea bream	Lusitanian	Planktonic eggs	55	Benthivore	3.4	Inner shelf	Demersal
Sparidae	*Oblada melanura*	Saddled sea bream	Lusitanian	Planktonic eggs	34	Omnivore	3.0	Inner shelf	Demersal
Sparidae	*Pagellus acarne*	Auxiliary sea bream	Lusitanian	Planktonic eggs	36	Bentho-piscivore	3.5	Inner shelf	Demersal
Sparidae	*Pagellus bellottii*	Red pandora	African	Planktonic eggs	51	Bentho-piscivore	3.6	Shelf	Demersal
Sparidae	*Pagellus bogaraveo*	Red sea bream	Lusitanian	Planktonic eggs	70	Piscivore	3.7	Shelf	Demersal
Sparidae	*Pagellus erythrinus*	Pandora	Lusitanian	Planktonic eggs	60	Bentho-piscivore	3.4	Inner shelf	Demersal
Sparidae	*Pagrus auriga*	Red-banded sea bream	African	Planktonic eggs	98	Benthivore	3.4	Shelf	Reef-associated
Sparidae	*Pagrus caeruleostictus*	Blue-spotted sea bream	African	Planktonic eggs	110	Benthivore	3.8	Shelf	Reef-associated
Sparidae	*Pagrus pagrus*	Common sea bream	Lusitanian	Planktonic eggs	91	Benthivore	3.7	Shelf	Demersal
Sparidae	*Sarpa salpa*	Saupe	Lusitanian	Planktonic eggs	46	Herbivore	2.0	Inner shelf	Benthopelagic
Sparidae	*Sparus auratus*	Gilt-head sea bream	Lusitanian	Planktonic eggs	70	Bentho-piscivore	3.4	Inner shelf	Demersal
Sparidae	*Spondyliosoma cantharus*	Black sea bream	Lusitanian	Nest-forming	60	Benthivore	3.3	Inner shelf	Demersal
Centracanthidae	*Centracanthus cirrus*	Curled picarel	Lusitanian	Planktonic eggs	34	Unknown	3.3	Shelf	Demersal
Centracanthidae	*Spicara maena*	Blotched picarel	Lusitanian	Planktonic eggs	31	Unknown	4.2	Shelf	Demersal
Centracanthidae	*Spicara melanurus*	Black-spot picarel	African	Planktonic eggs	30	Unknown	3.5	Shelf	Demersal
Centracanthidae	*Spicara smaris*	Picarel	Lusitanian	Planktonic eggs	20	Unknown	3.0	Shelf	Demersal
Sciaenidae	*Argyrosomus regius*	Meagre	Lusitanian	Planktonic eggs	140	Piscivore	4.3	Shelf	Benthopelagic
Sciaenidae	*Pseudotolithus senegalensis*	Cassava croaker	African	Planktonic eggs	114	Bentho-piscivore	3.8	Inner shelf	Benthopelagic
Sciaenidae	*Pseudotolithus typus*	Long-neck croaker	African	Planktonic eggs	140	Bentho-piscivore	3.7	Inner shelf	Benthopelagic
Sciaenidae	*Sciaena umbra*	Brown meagre	Lusitanian	Planktonic eggs	70	Bentho-piscivore	3.7	Inner shelf	Demersal
Sciaenidae	*Umbrina canariensis*	Canary drum	Lusitanian	Planktonic eggs	80	Benthivore	3.4	Shelf	Demersal
Sciaenidae	*Umbrina cirrosa*	Shi drum	Lusitanian	Planktonic eggs	73	Benthivore	3.5	Shelf	Demersal
Sciaenidae	*Umbrina ronchus*	Fusca drum	African	Planktonic eggs	100	Benthivore	3.4	Shelf	Demersal
Polynemidae	*Galeoides decadactylus*	Lesser African threadfin	African	Planktonic eggs	50	Unknown	3.6	Inner shelf	Demersal
Mullidae	*Mullus barbatus*	Red mullet	Lusitanian	Planktonic eggs	30	Benthivore	3.2	Inner shelf	Demersal
Mullidae	*Mullus surmuletus*	Striped red mullet	Lusitanian	Planktonic eggs	40	Benthivore	3.4	Inner shelf	Demersal
Mullidae	*Pseudupeneus prayensis*	West African goatfish	African	Planktonic eggs	67	Benthivore	3.2	Inner shelf	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Mullidae	*Upeneus asymmetricus*	Golden-striped goatfish	Indo-Pacific	Planktonic eggs	30	Benthivore	3.5	Inner shelf	Demersal
Mullidae	*Upeneus moluccensis*	Gold-band goatfish	Indo-Pacific	Planktonic eggs	20	Benthivore	3.6	Inner shelf	Demersal
Kyphosidae	*Kyphosus incisor*	Yellow sea chub	African	Uncertain	90	Unknown	2.0	Shelf	Demersal
Kyphosidae	*Kyphosus sectatrix*	Bermuda sea chub	African	Uncertain	76	Unknown	2.0	Shelf	Demersal
Chaetodontidae	*Chaetodon hoefleri*	Four-banded butterfly fish	African	Uncertain	27	Benthivore	3.5	Inner shelf	Demersal
Chaetodontidae	*Chaetodon robustus*	Three-banded butterflyfish	African	Uncertain	18	Unknown	3.3	Shelf	Reef-associated
Chaetodontidae	*Prognathodes marcellae*	–	African	Uncertain	12	Unknown	3.2	Shelf	Demersal
Cepolidae	*Cepola rubescens*	Red bandfish	Lusitanian	Planktonic eggs (?)	70	Benthivore	3.1	Shelf	Demersal
Mugilidae	*Chelon labrosus*	Thick-lipped mullet	Lusitanian	Planktonic eggs	60	Detritivore	2.4	Coastal	Pelagic
Mugilidae	*Liza aurata*	Golden mullet	Lusitanian	Planktonic eggs	50	Detritivore	2.5	Coastal	Pelagic
Mugilidae	*Liza carinata*	Keeled mullet	Indo-Pacific	Planktonic eggs	18	Detritivore	2.5	Coastal	Pelagic
Mugilidae	*Liza ramada*	Thin-lipped mullet	Lusitanian	Planktonic eggs	50	Detritivore	2.2	Coastal	Pelagic
Mugilidae	*Liza saliens*	Leaping mullet	Lusitanian	Planktonic eggs	49	Detritivore	2.2	Coastal	Pelagic
Mugilidae	*Mugil capurrii*	Narrow-head grey mullet	African	Planktonic eggs	55	Detritivore	2.2	Shelf	Pelagic
Mugilidae	*Mugil cephalus*	Flat-head mullet	Lusitanian	Planktonic eggs	146	Detritivore	2.1	Coastal	Pelagic
Mugilidae	*Oedalechilus labeo*	Box-lip mullet	Mediterranean	Planktonic eggs	25	Detritivore	2.5	Coastal	Pelagic
Pomacentridae	*Abudefduf luridus*	Canary damsel	Macaronesia	Nest-forming	15	Omnivore	3.5	Coastal	Demersal
Pomacentridae	*Chromis chromis*	Damselfish	Lusitanian	Nest-forming	25	Omnivore	3.0	Coastal	Reef-associated
Pomacentridae	*Chromis limbata*	Azores chromis	African	Nest-forming	15	Unknown	3.4	Shelf	Reef-associated
Labridae	*Acantholabrus palloni*	Scale-rayed wrasse	Lusitanian	Nest-forming	25	Benthivore	3.5	Coastal	Reef-associated
Labridae	*Bodianus scrofa*	Barred hogfish	African	Uncertain	43	Unknown	3.5	Shelf	Demersal
Labridae	*Bodianus speciosus*	Blackbar hogfish	African	Uncertain	61	Unknown	3.6	Coastal	Reef-associated
Labridae	*Centrolabrus caeruleus*	–	Macaronesia	Uncertain	22	Unknown	NA	Shelf	Demersal
Labridae	*Centrolabrus exoletus*	Small-mouthed wrasse	Lusitanian	Nest-forming	15	Benthivore	3.5	Coastal	Reef-associated
Labridae	*Centrolabrus trutta*	–	Macaronesia	Uncertain	18	Unknown	3.5	Coastal	Reef-associated
Labridae	*Coris julis*	Rainbow wrasse	Lusitanian	Planktonic eggs	25	Benthivore	3.2	Coastal	Reef-associated
Labridae	*Ctenolabrus rupestris*	Goldsinny	Lusitanian	Planktonic eggs	18	Benthivore	3.3	Coastal	Reef-associated

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Labridae	*Labrus bergylta*	Ballan wrasse	Lusitanian	Nest-forming	60	Benthivore	3.1	Coastal	Reef-associated
Labridae	*Labrus bimaculatus*	Cuckoo wrasse	Lusitanian	Nest-forming	35	Bentho-piscivore	3.9	Coastal	Reef-associated
Labridae	*Labrus merula*	Brown wrasse	Lusitanian	Nest-forming	55	Benthivore	3.2	Coastal	Reef-associated
Labridae	*Labrus viridis*	Green wrasse	Lusitanian	Nest-forming	57	Bentho-piscivore	3.8	Coastal	Reef-associated
Labridae	*Lappanella fasciata*	–	Lusitanian	Nest-forming	17	Benthivore	3.3	Shelf	Demersal
Labridae	*Symphodus (Crenilabrus) bailloni*	Baillon's wrasse	Lusitanian	Nest-forming	20	Benthivore	3.3	Coastal	Reef-associated
Labridae	*Symphodus (Crenilabrus) cinereus*	Grey wrasse	Lusitanian	Nest-forming	16	Benthivore	3.3	Coastal	Demersal
Labridae	*Symphodus (Crenilabrus) doderleini*	–	Mediterranean	Nest-forming	12	Benthivore	3.4	Coastal	Demersal
Labridae	*Symphodus (Crenilabrus) mediterraneus*	Axillary wrasse	Lusitanian	Nest-forming	22	Benthivore	3.1	Coastal	Demersal
Labridae	*Symphodus (Crenilabrus) melanocercus*	–	Mediterranean	Nest-forming	14	Benthivore	3.0	Coastal	Reef-associated
Labridae	*Symphodus (Crenilabrus) melops*	Corkwing	Lusitanian	Nest-forming	28	Benthivore	3.2	Coastal	Reef-associated
Labridae	*Symphodus (Crenilabrus) ocellatus*	–	Mediterranean	Nest-forming	15	Benthivore	3.3	Coastal	Reef-associated
Labridae	*Symphodus (Crenilabrus) roissali*	Five-spotted wrasse	Lusitanian	Nest-forming	21	Benthivore	3.5	Coastal	Reef-associated
Labridae	*Symphodus (Crenilabrus) tinca*	East Atlantic peacock wrasse	Lusitanian	Nest-forming	54	Benthivore	3.1	Coastal	Reef-associated
Labridae	*Symphodus (Symphodus) rostratus*	–	Mediterranean	Nest-forming	16	Benthivore	3.5	Coastal	Reef-associated
Labridae	*Thalassoma pavo*	Ornate wrasse	Lusitanian	Planktonic eggs	31	Benthivore	3.5	Coastal	Reef-associated
Labridae	*Xyrichtys novacula*	Pearly razorfish	Lusitanian	Uncertain	38	Benthivore	3.1	Coastal	Demersal
Scaridae	*Sparisoma (Euscarus) cretense*	Parrotfish	Lusitanian	Uncertain	50	Benthivore	2.9	Coastal	Reef-associated
Zoarcidae	*Gymnelus retrodorsalis*	Aurora unernak	Arctic	Demersal eggs	19	Benthivore	3.2	Shelf	Demersal
Zoarcidae	*Gymnelus viridis*	–	Arctic	Demersal eggs	56	Benthivore	3.1	Shelf	Demersal
Zoarcidae	*Lycenchelys alba*	–	Atlantic	Demersal eggs	33	Benthivore	3.4	Slope	Bathydemersal
Zoarcidae	*Lycenchelys kolthoffi*	Checkered wolf eel	Arctic	Demersal eggs	28	Benthivore	3.1	Slope	Demersal
Zoarcidae	*Lycenchelys muraena*	–	Arctic	Demersal eggs	28	Benthivore	3.5	Slope	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Zoarcidae	*Lycenchelys platyrhina*	–	Arctic	Demersal eggs	15	Benthivore	NA	Slope	Demersal
Zoarcidae	*Lycenchelys sarsii*	Sar's eelpout	Boreal	Demersal eggs	19	Benthivore	3.2	Outer shelf	Demersal
Zoarcidae	*Lycodes adolfi*	Adolf's eelpout	Boreal	Demersal eggs	24	Benthivore	3.5	Slope	Demersal
Zoarcidae	*Lycodes esmarkii*	Esmark's eelpout	Boreal	Demersal eggs	75	Benthivore	3.4	Outer shelf	Demersal
Zoarcidae	*Lycodes eudipleurostictus*	Double-line eelpout	Boreal	Demersal eggs	54	Benthivore	3.5	Slope	Demersal
Zoarcidae	*Lycodes frigidus*	–	Arctic	Demersal eggs	69	Benthivore	3.8	Slope	Demersal
Zoarcidae	*Lycodes jugoricus*	–	Arctic	Demersal eggs	48	Benthivore	3.2	Inner shelf	Demersal
Zoarcidae	*Lycodes lavalaei*	Newfoundland eelpout	Arctic	Demersal eggs	59	Benthivore	3.9	Shelf	Demersal
Zoarcidae	*Lycodes luetkenii*	–	Boreal	Demersal eggs	43	Benthivore	3.4	Slope	Demersal
Zoarcidae	*Lycodes microcephalus*	–	Atlantic	Demersal eggs	8	Benthivore	NA	Slope	Demersal
Zoarcidae	*Lycodes pallidus*	Pale eelpout	Arctic	Demersal eggs	26	Benthivore	3.3	Shelf	Demersal
Zoarcidae	*Lycodes polaris*	Canadian eelpout	Arctic	Demersal eggs	46	Benthivore	3.3	Shelf	Demersal
Zoarcidae	*Lycodes reticulatus*	Arctic eelpout	Arctic	Demersal eggs	36	Benthivore	3.5	Shelf	Demersal
Zoarcidae	*Lycodes rossi*	Three-spot eelpout	Arctic	Demersal eggs	31	Benthivore	3.5	Shelf	Demersal
Zoarcidae	*Lycodes sagittarius*	Archer eelpout	Arctic	Demersal eggs	33	Benthivore	3.2	Slope	Demersal
Zoarcidae	*Lycodes seminudus*	Long-ear eelpout	Arctic	Demersal eggs	52	Benthivore	3.5	Slope	Demersal
Zoarcidae	*Lycodes squamiventer*	Scale-belly eelpout	Boreal	Demersal eggs	26	Benthivore	3.3	Slope	Demersal
Zoarcidae	*Lycodes terraenovae*	–	Boreal	Demersal eggs	45	Benthivore	3.5	Slope	Demersal
Zoarcidae	*Lycodes vahlii*	Vahl's eelpout	Boreal	Demersal eggs	52	Benthivore	3.4	Outer shelf	Demersal
Zoarcidae	*Lycodonus flagellicauda*	–	Arctic	Demersal eggs	24	Benthivore	3.5	Slope	Demersal
Zoarcidae	*Melanostigma atlanticum*	Atlantic soft pout	Atlantic	Demersal eggs	15	Planktivore	3.0	Slope	Bathypelagic
Zoarcidae	*Pachycara bulbiceps*	Snub-nose eelpout	Atlantic	Demersal eggs	52	Benthivore	3.4	Slope	Bathydemersal
Zoarcidae	*Pachycara crassiceps*	–	Atlantic	Demersal eggs	54	Benthivore	3.4	Slope	Bathydemersal
Zoarcidae	*Zoarces viviparus*	Eelpout	Boreal	Viviparous	52	Benthivore	3.5	Inner shelf	Demersal
Stichaeidae (Lumpenidae)	*Anisarchus medius*	Stout eel blenny	Arctic	Demersal eggs	30	Benthivore	3.2	Shelf	Demersal
Stichaeidae	*Chirolophis ascanii*	Yarrell's blenny	Boreal	Demersal eggs	25	Benthivore	3.0	Shelf	Demersal
Stichaeidae (Lumpenidae)	*Leptoclinus maculatus*	Spotted snake blenny	Boreal	Demersal eggs	20	Benthivore	3.3	Shelf	Demersal
Stichaeidae (Lumpenidae)	*Lumpenus fabricii*	Slender eel blenny	Arctic	Demersal eggs	51	Benthivore	3.3	Shelf	Demersal
Stichaeidae (Lumpenidae)	*Lumpenus lumpretaeformis*	Snake blenny	Boreal	Demersal eggs	49	Benthivore	3.6	Shelf	Demersal
Pholidae	*Pholis gunnellus*	Butterfish	Boreal	Demersal eggs	25	Benthivore	3.5	Inner shelf	Demersal
Anarhichadidae	*Anarhichas denticulatus*	Jelly cat	Boreal	Demersal eggs	138	Plankto-piscivore	3.8	Shelf	Benthopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	**L_{MAX} (cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Anarhichadidae	*Anarhichas lupus*	Wolffish	Boreal	Demersal eggs	125	Benthivore	3.2	Shelf	Demersal
Anarhichadidae	*Anarhichas minor*	Spotted catfish	Boreal	Demersal eggs	144	Benthivore	3.5	Shelf	Demersal
Chiasmodontidae	*Chiasmodon bolangeri*	–	Atlantic	Planktonic eggs	31	Unknown	3.5	Oceanic	Bathypelagic
Chiasmodontidae	*Chiasmodon niger*	Black swallower	Atlantic	Planktonic eggs	31	Unknown	4.2	Oceanic	Bathypelagic
Chiasmodontidae	*Kali macrodon*	–	Atlantic	Planktonic eggs	26	Unknown	NA	Oceanic	Bathypelagic
Chiasmodontidae	*Kali macrura*	–	Atlantic	Planktonic eggs	13	Unknown	NA	Oceanic	Bathypelagic
Chiasmodontidae	*Pseudoscopelus altipinnis*	–	Atlantic	Planktonic eggs	20	Unknown	NA	Oceanic	Bathypelagic
Ammodytidae	*Ammodytes marinus*	Sandeel	Boreal	Demersal eggs	25	Planktivore	2.7	Inner shelf	Benthopelagic
Ammodytidae	*Ammodytes tobianus*	Sandeel	Boreal	Demersal eggs	20	Planktivore	3.2	Inner shelf	Benthopelagic
Ammodytidae	*Gymnammodytes cicerelus*	Mediterranean sandeel	Mediterranean	Demersal eggs	17	Planktivore	3.4	Shelf	Benthopelagic
Ammodytidae	*Gymnammodytes semisquamatus*	Smooth sandeel	Lusitanian	Demersal eggs	28	Planktivore	2.7	Inner shelf	Benthopelagic
Ammodytidae	*Hyperoplus immaculatus*	Immaculate sandeel	Lusitanian	Demersal eggs	35	Piscivore	4.4	Inner shelf	Benthopelagic
Ammodytidae	*Hyperoplus lanceolatus*	Great sandeel	Boreal	Demersal eggs	40	Piscivore	4.2	Inner shelf	Benthopelagic
Trachinidae	*Echiichthys vipera*	Lesser weever	Lusitanian	Planktonic eggs	15	Bentho-piscivore	4.4	Inner shelf	Demersal
Trachinidae	*Trachinus araneus*	Spotted weever	Lusitanian	Planktonic eggs	55	Bentho-piscivore	4.0	Shelf	Demersal
Trachinidae	*Trachinus draco*	Greater weever	Lusitanian	Planktonic eggs	40	Bentho-piscivore	4.2	Inner shelf	Demersal
Trachinidae	*Trachinus radiatus*	Starry weever	Lusitanian	Planktonic eggs	50	Bentho-piscivore	4.0	Shelf	Demersal
Uranoscopidae	*Uranoscopus scaber*	Atlantic stargazer	Lusitanian	Planktonic eggs	40	Piscivore	4.4	Shelf	Demersal
Tripterygiidae	*Tripterygion delaisi*	Black-faced blenny	Lusitanian	Demersal eggs	9	Benthivore	3.4	Shelf	Reef-associated
Tripterygiidae	*Tripterygion melanurus*	–	Mediterranean	Demersal eggs	5	Benthivore	3.5	Shelf	Reef-associated
Tripterygiidae	*Tripterygion tripteronotus*	–	Mediterranean	Demersal eggs	8	Benthivore	3.4	Inner shelf	Reef-associated
Clinidae	*Clinitrachus argentatus*	Cline	Mediterranean	Demersal eggs	10	Benthivore	3.5	Coastal	Demersal
Blenniidae	*Aidablennius sphynx*	–	Mediterranean	Demersal eggs	8	Benthivore	2.5	Coastal	Reef-associated
Blenniidae	*Blennius ocellaris*	Butterfly blenny	Lusitanian	Demersal eggs	20	Benthivore	3.5	Shelf	Demersal
Blenniidae	*Coryphoblennius galerita*	Montagu's blenny	Lusitanian	Demersal eggs	9	Benthivore	2.2	Inner shelf	Reef-associated
Blenniidae	*Hypleurochilus bananensis*	–	Mediterranean	Demersal eggs	11	Benthivore	NA	Inner shelf	Demersal
Blenniidae	*Lipophrys adriaticus*	–	Mediterranean	Demersal eggs	4	Benthivore	2.9	Coastal	Reef-associated
Blenniidae	*Lipophrys canevae*	–	Mediterranean	Demersal eggs	8	Benthivore	2.1	Coastal	Reef-associated
Blenniidae	*Lipophrys dalmatinus*	–	Mediterranean	Demersal eggs	4	Benthivore	3.2	Coastal	Reef-

FAMILY	SCIENTIFIC NAME	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{MAX} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)
									associated
Blenniidae	*Lipophrys nigriceps*	Black-headed blenny	Mediterranean	Demersal eggs	4	Benthivore	2.7	Coastal	Reef-associated
Blenniidae	*Lipophrys pholis*	Shanny	Lusitanian	Demersal eggs	16	Benthivore	3.1	Coastal	Reef-associated
Blenniidae	*Ophioblennius atlanticus*	-	African	Demersal eggs	19	Benthivore	2.0	Inner shelf	Reef-associated
Blenniidae	*Parablennius gattorugine*	Tompot blenny	Lusitanian	Demersal eggs	30	Benthivore	2.9	Inner shelf	Reef-associated
Blenniidae	*Parablennius incognitus*	-	Lusitanian	Demersal eggs	7	Benthivore	2.4	Coastal	Reef-associated
Blenniidae	*Parablennius parvicornis*	Rock-pool blenny	African	Demersal eggs	15	Benthivore	2.0	Coastal	Reef-associated
Blenniidae	*Parablennius pilicornis*	Ringneck blenny	Lusitanian	Demersal eggs	15	Benthivore	3.2	Coastal	Reef-associated
Blenniidae	*Parablennius rouxi*	-	Mediterranean	Demersal eggs	8	Benthivore	2.6	Inner shelf	Demersal
Blenniidae	*Parablennius ruber*	Portuguese blenny	Macaronesia	Demersal eggs	14	Benthivore	2.9	Coastal	Reef-associated
Blenniidae	*Parablennius sanguinolentus*	Rusty blenny	Lusitanian	Demersal eggs	20	Benthivore	2.1	Coastal	Reef-associated
Blenniidae	*Parablennius tentacularis*	Tentacled blenny	Lusitanian	Demersal eggs	15	Benthivore	3.1	Inner shelf	Reef-associated
Blenniidae	*Parablennius zvonimiri*	-	Mediterranean	Demersal eggs	7	Benthivore	2.4	Coastal	Reef-associated
Blenniidae	*Paralipophrys trigloides*	-	Lusitanian	Demersal eggs	13	Benthivore	3.5	Coastal	Reef-associated
Blenniidae	*Salaria basiliscus*	-	Mediterranean	Demersal eggs	18	Benthivore	3.2	Coastal	Demersal
Blenniidae	*Salaria pavo*	Peacock blenny	Lusitanian	Demersal eggs	13	Benthivore	2.9	Coastal	Reef-associated
Blenniidae	*Scartella cristata*	Molly miller	Mediterranean	Demersal eggs	12	Benthivore	2.0	Coastal	Reef-associated
Callionymidae	*Callionymus fasciatus*	-	Mediterranean	Planktonic eggs	12	Benthivore	3.3	Shelf	Demersal
Callionymidae	*Callionymus filamentosus*	Blotchfin dragonet	Indo-Pacific	Planktonic eggs	20	Benthivore	3.3	Shelf	Demersal
Callionymidae	*Callionymus lyra*	Common dragonet	Lusitanian	Planktonic eggs	32	Benthivore	3.3	Shelf	Demersal
Callionymidae	*Callionymus maculatus*	Spotted dragonet	Lusitanian	Planktonic eggs	16	Benthivore	3.3	Shelf	Demersal
Callionymidae	*Callionymus pusillus*	-	Mediterranean	Planktonic eggs	14	Benthivore	3.3	Shelf	Demersal
Callionymidae	*Callionymus reticulatus*	Reticulate dragonet	Lusitanian	Planktonic eggs	11	Benthivore	3.3	Shelf	Demersal
Callionymidae	*Callionymus risso*	-	Lusitanian	Planktonic eggs	11	Benthivore	3.0	Shelf	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{MAX} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Callionymidae	*Protogrammus sousai*	-	Atlantic	Planktonic eggs	8	Benthivore	3.5	Slope	Demersal
Callionymidae	*Synchiropus phaeton*	-	Lusitanian	Planktonic eggs	18	Benthivore	3.4	Slope	Demersal
Draconettidae	*Centrodraco acanthopoma*	-	Atlantic	Planktonic eggs	10	Benthivore	3.5	Slope	Demersal
Gobiidae	*Aphia minuta*	Transparent goby	Lusitanian	Demersal eggs	6	Planktivore	3.1	Inner shelf	Pelagic
Gobiidae	*Benthophiloides brauneri*	-	Sarmatic	Demersal eggs	8	Benthivore	3.4	Coastal	Demersal
Gobiidae	*Benthophilus stellatus*	Stellate tadpole-goby	Sarmatic	Demersal eggs	14	Benthivore	3.7	Coastal	Demersal
Gobiidae	*Buenia affinis*	De Buen's goby	Mediterranean	Demersal eggs	4	Unknown	3.1	Shelf	Demersal
Gobiidae	*Buenia jeffreysii*	Jeffrey's goby	Boreal	Demersal eggs	6	Benthivore	3.6	Outer shelf	Demersal
Gobiidae	*Caspiosoma caspium*	-	Sarmatic	Demersal eggs	4	Unknown	NA	Coastal	Demersal
Gobiidae	*Chromogobius quadrivittatus*	Chestnut goby	Mediterranean	Demersal eggs	8	Benthivore	3.4	Coastal	Demersal
Gobiidae	*Chromogobius zebratus*	Kolombatovic's goby	Mediterranean	Demersal eggs	6	Unknown	3.2	Inner shelf	Demersal
Gobiidae	*Corcyrogobius liechtensteini*	Liechtenstein's goby	Mediterranean	Demersal eggs	3	Unknown	3.0	Shelf	Demersal
Gobiidae	*Coryogalops ochetica*	-	Indo-Pacific	Demersal eggs	6	Unknown	3.2	Shelf	Demersal
Gobiidae	*Crystallogobius linearis*	Crystal goby	Lusitanian	Demersal eggs	5	Planktivore	3.4	Outer shelf	Pelagic
Gobiidae	*Deltentosteus collonianus*	Toothed goby	Lusitanian	Demersal eggs	7	Unknown	3.5	Inner shelf	Demersal
Gobiidae	*Deltentosteus quadrimaculatus*	Four-spotted goby	Lusitanian	Demersal eggs	8	Unknown	3.1	Shelf	Demersal
Gobiidae	*Didogobius bentuvii*	Ben-Tuvia's goby	Mediterranean	Demersal eggs	5	Unknown	3.2	Shelf	Demersal
Gobiidae	*Gammogobius steinitzi*	Steinitz's goby	Mediterranean	Demersal eggs	5	Unknown	3.2	Shelf	Demersal
Gobiidae	*Gobius ater*	Bellotti's goby	Mediterranean	Demersal eggs	9	Unknown	3.1	Inner shelf	Demersal
Gobiidae	*Gobius auratus*	Golden goby	Lusitanian	Demersal eggs	10	Unknown	3.0	Inner shelf	Demersal
Gobiidae	*Gobius bucchichi*	Bucchich's goby	Mediterranean	Demersal eggs	10	Benthivore	3.1	Inner shelf	Demersal
Gobiidae	*Gobius cobitis*	Giant goby	Lusitanian	Demersal eggs	27	Benthivore	3	Coastal	Demersal
Gobiidae	*Gobius couchi*	Couch's goby	Lusitanian	Demersal eggs	8	Benthivore	2.9	Coastal	Demersal
Gobiidae	*Gobius cruentatus*	Red-mouthed goby	Lusitanian	Demersal eggs	18	Unknown	3.1	Inner shelf	Demersal
Gobiidae	*Gobius fallax*	Sarato's goby	Mediterranean	Demersal eggs	9	Unknown	3.3	Inner shelf	Demersal
Gobiidae	*Gobius gasteveni*	Steven's goby	Lusitanian	Demersal eggs	12	Unknown	NA	Shelf	Demersal
Gobiidae	*Gobius geniporus*	Slender goby	Mediterranean	Demersal eggs	16	Unknown	3.3	Inner shelf	Demersal
Gobiidae	*Gobius niger*	Black goby	Lusitanian	Demersal eggs	15	Benthivore	3.2	Inner shelf	Demersal
Gobiidae	*Gobius paganellus*	Rock goby	Lusitanian	Demersal eggs	12	Benthivore	3.3	Coastal	Demersal
Gobiidae	*Gobius roulei*	Roule's goby	Lusitanian	Demersal eggs	8	Unknown	3.1	Shelf	Demersal
Gobiidae	*Gobius strictus*	Schmidt's goby	Mediterranean	Demersal eggs	8	Unknown	3.1	Shelf	Demersal
Gobiidae	*Gobius vittatus*	Striped goby	Mediterranean	Demersal eggs	7	Benthivore	2.9	Shelf	Demersal
Gobiidae	*Gobius xanthocephalus*	-	Lusitanian	Demersal eggs	10	Unknown	3.1	Shelf	Demersal
Gobiidae	*Gobiusculus flavescens*	Two-spot goby	Lusitanian	Demersal eggs	6	Benthivore	3.2	Coastal	Demersal

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Gobiidae	*Knipowitschia caucasica*	–	Sarmatic	Demersal eggs	5	Benthivore	3.3	Coastal	Demersal
Gobiidae	*Knipowitschia longecaudata*	–	Sarmatic	Demersal eggs	5	Benthivore	NA	Coastal	Demersal
Gobiidae	*Knipowitschia panizzae*	–	Mediterranean	Demersal eggs	6	Benthivore	3.5	Coastal	Demersal
Gobiidae	*Lebetus guilleti*	Guillet's goby	Boreal	Demersal eggs	2.5	Benthivore	3.1	Inner shelf	Reef-associated
Gobiidae	*Lebetus scorpioides*	Diminutive goby	Boreal	Demersal eggs	4	Benthivore	3.2	Shelf	Reef-associated
Gobiidae	*Lesueurigobius friesii*	Fries's goby	Boreal	Demersal eggs	10	Benthivore	3.2	Shelf	Demersal
Gobiidae	*Lesueurigobius heterofasciatus*	–	African	Demersal eggs	4	Unknown	3.3	Outer shelf	Demersal
Gobiidae	*Lesueurigobius sanzoi*	Sanzo's goby	African	Demersal eggs	11	Unknown	3.6	Outer shelf	Demersal
Gobiidae	*Lesueurigobius suerii*	Lesueur's goby	Mediterranean	Demersal eggs	5	Unknown	3.5	Shelf	Demersal
Gobiidae	*Mauligobius maderensis*	Madeira goby	Macaronesia	Demersal eggs	15	Unknown	3.4	Coastal	Demersal
Gobiidae	*Mesogobius batrachocephalus*	Knout goby	Sarmatic	Demersal eggs	42	Piscivore	4.2	Coastal	Demersal
Gobiidae	*Millerigobius macrocephalus*	–	Mediterranean	Demersal eggs	5	Unknown	3.2	Coastal	Demersal
Gobiidae	*Neogobius cephalargoides*	–	Sarmatic	Demersal eggs	25	Unknown	NA	Coastal	Demersal
Gobiidae	*Neogobius eurycephalus*	Mushroom goby	Sarmatic	Demersal eggs	20	Unknown	3.4	Coastal	Demersal
Gobiidae	*Neogobius fluviatilis*	Monkey goby	Sarmatic	Demersal eggs	20	Benthivore	3.3	Coastal	Demersal
Gobiidae	*Neogobius gymnotrachelus*	Racer goby	Sarmatic	Demersal eggs	16	Benthivore	3.5	Coastal	Demersal
Gobiidae	*Neogobius kessleri*	Big-head goby	Sarmatic	Demersal eggs	22	Benthivore	3.5	Coastal	Demersal
Gobiidae	*Neogobius melanostomus*	Round goby	Sarmatic	Demersal eggs	25	Benthivore	3.3	Coastal	Demersal
Gobiidae	*Neogobius platyrostris*	Flat-snout goby	Sarmatic	Demersal eggs	23	Unknown	3.4	Coastal	Demersal
Gobiidae	*Neogobius ratan*	Ratan goby	Sarmatic	Demersal eggs	20	Bentho-piscivore	4.0	Coastal	Demersal
Gobiidae	*Neogobius syrman*	Syman goby	Sarmatic	Demersal eggs	25	Bentho-piscivore	3.4	Coastal	Demersal
Gobiidae	*Odondebuenia balearica*	Coralline goby	Mediterranean	Demersal eggs	3	Unknown	3.1	Shelf	Demersal
Gobiidae	*Oxyurichthys papuensis*	Frog-face goby	Indo-Pacific	Demersal eggs	24	Benthivore	3.5	Shelf	Demersal
Gobiidae	*Pomatoschistus bathi*	–	Mediterranean	Demersal eggs	3	Unknown	3.3	Inner shelf	Demersal
Gobiidae	*Pomatoschistus canestrinii*	–	Mediterranean	Demersal eggs	6	Benthivore	3.2	Coastal	Demersal
Gobiidae	*Pomatoschistus knerii*	Kner's goby	Mediterranean	Demersal eggs	7	Unknown	3.3	Coastal	Demersal
Gobiidae	*Pomatoschistus lozanoi*	Lozano's goby	Lusitanian	Demersal eggs	8	Benthivore	3.1	Inner shelf	Demersal
Gobiidae	*Pomatoschistus marmoratus*	Marbled goby	Lusitanian	Demersal eggs	8	Benthivore	3.3	Shelf	Demersal
Gobiidae	*Pomatoschistus microps*	Common goby	Lusitanian	Demersal eggs	6	Benthivore	3.3	Inner shelf	Demersal
Gobiidae	*Pomatoschistus minutus*	Sand goby	Lusitanian	Demersal eggs	9.5	Benthivore	3.2	Inner shelf	Demersal
Gobiidae	*Pomatoschistus norvegicus*	Norwegian goby	Boreal	Demersal eggs	6.5	Benthivore	3.5	Outer shelf	Demersal
Gobiidae	*Pomatoschistus pictus*	Painted goby	Lusitanian	Demersal eggs	6	Benthivore	3.1	Inner shelf	Demersal

FAMILY	SCIENTIFIC NAME	COMMON NAME	BIOGEOGRAPHICAL AFFINITY	REPRODUCTIVE MODE	L_{max} (CM)	TROPHIC GUILD	TROPHIC LEVEL	HABITAT (HORIZONTAL)	HABITAT (VERTICAL)
Gobiidae	*Pomatoschistus quagga*	Quagga goby	Mediterranean	Demersal eggs	6	Unknown	3.3	Inner shelf	Demersal
Gobiidae	*Pomatoschistus tortonesei*	Tortonese's goby	Mediterranean	Demersal eggs	7	Benthivore	3.4	Coastal	Demersal
Gobiidae	*Proterorhinus marmoratus*	Tube-nose goby	Sarmatic	Demersal eggs	12	Benthivore	3.3	Coastal	Demersal
Gobiidae	*Pseudaphya ferreri*	Ferrer's goby	Mediterranean	Demersal eggs	3	Unknown	NA	Inner shelf	Pelagic
Gobiidae	*Silhouettea aegyptia*	Red Sea goby	Indo–Pacific	Demersal eggs	5	Benthivore	3.3	Coastal	Demersal
Gobiidae	*Speleogobius trigloides*	Grotto goby	Mediterranean	Demersal eggs	2	Unknown	3.0	Inner shelf	Reef-associated
Gobiidae	*Thorogobius ephippiatus*	Leopard-spotted goby	Lusitanian	Demersal eggs	13	Benthivore	3.0	Inner shelf	Reef-associated
Gobiidae	*Thorogobius macrolepis*	Large-scaled goby	Mediterranean	Demersal eggs	7	Unknown	3.2	Shelf	Demersal
Gobiidae	*Vanneaugobius canariensis*	–	African	Demersal eggs	4	Unknown	3.2	Inner shelf	Demersal
Gobiidae	*Vanneaugobius pruvoti*	–	African	Demersal eggs	4	Unknown	3.1	Outer shelf	Demersal
Gobiidae	*Zebrus zebrus*	–	Mediterranean	Demersal eggs	6	Unknown	3.2	Coastal	Demersal
Gobiidae	*Zosterisessor ophiocephalus*	Grass goby	Mediterranean	Demersal eggs	25	Bentho-piscivore	3.1	Coastal	Demersal
Siganidae	*Siganus luridus*	Dusky spinefoot	Indo–Pacific	Uncertain	30	Herbivore	2.0	Coastal	Demersal
Siganidae	*Siganus rivulatus*	Marbled spinefoot	Indo–Pacific	Uncertain	27	Herbivore	2.0	Inner shelf	Demersal
Sillaginidae	*Sillago sihama*	Silver sillago	Indo–Pacific	Uncertain	38	Benthivore	3.4	Coastal	Demersal
Luvaridae	*Luvarus imperialis*	Luvar	Atlantic	Uncertain	180	Planktivore	4.0	Oceanic	Mesopelagic
Acanthuridae	*Acanthurus monroviae*	Monrovia doctorfish	African	Uncertain	55	Omnivore	2.5	Coastal	Demersal
Scombrolabracidae	*Scombrolabrax heterolepis*	Long-fin escolar	Atlantic	Planktonic eggs	30	Piscivore	4.0	Oceanic	Mesopelagic
Sphyraenidae	*Sphyraena chrysotaenia*	Yellow-stripe barracuda	Indo–Pacific	Planktonic eggs	30	Piscivore	4.0	Shelf	Pelagic
Sphyraenidae	*Sphyraena sphyraena*	European barracuda	Atlantic	Planktonic eggs	165	Piscivore	4.0	Shelf	Pelagic
Sphyraenidae	*Sphyraena viridensis*	Yellow-mouth barracuda	Uncertain	Planktonic eggs	142	Piscivore	4.3	Shelf	Pelagic
Gempylidae	*Diplospinus multistriatus*	Striped escolar	Atlantic	Planktonic eggs	40	Piscivore	3.5	Oceanic	Mesopelagic
Gempylidae	*Gempylus serpens*	Snake mackerel	Atlantic	Planktonic eggs	122	Piscivore	4.3	Oceanic	Mesopelagic
Gempylidae	*Lepidocybium flavobrunneum*	Escolar	Atlantic	Planktonic eggs	244	Piscivore	4.3	Oceanic	Mesopelagic
Gempylidae	*Nealotus tripes*	Black snake mackerel	Atlantic	Planktonic eggs	31	Piscivore	4.2	Oceanic	Mesopelagic
Gempylidae	*Nesiarchus nasutus*	Black gemfish	Atlantic	Planktonic eggs	159	Piscivore	4.3	Oceanic	Mesopelagic
Gempylidae	*Promethichthys prometheus*	Roudi escolar	Atlantic	Planktonic eggs	122	Piscivore	4.2	Oceanic	Mesopelagic
Gempylidae	*Ruvettus pretiosus*	Oilfish	Atlantic	Planktonic eggs	200	Piscivore	4.1	Oceanic	Mesopelagic
Trichiuridae	*Aphanopus carbo*	Black scabbardfish	Atlantic	Planktonic eggs	110	Piscivore	4.5	Slope	Benthopelagic
Trichiuridae	*Benthodesmus elongatus*	Elongate frostfish	Atlantic	Planktonic eggs	100	Piscivore	3.9	Slope	Benthopelagic
Trichiuridae	*Benthodesmus simonyi*	Simony's frostfish	Atlantic	Planktonic eggs	159	Piscivore	4.2	Slope	Benthopelagic
Trichiuridae	*Lepidopus caudatus*	Scabbard fish	Atlantic	Planktonic eggs	205	Piscivore	3.8	Slope	Benthopelagic
Trichiuridae	*Trichiurus lepturus*	Large-head hairtail	Atlantic	Planktonic eggs	234	Piscivore	4.4	Slope	Benthopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Xiphiidae	*Xiphias gladius*	Swordfish	Atlantic	Planktonic eggs	450	Piscivore	4.5	Oceanic	Epipelagic
Istiophoridae	*Istiophorus albicans*	Atlantic sailfish	Atlantic	Planktonic eggs	315	Piscivore	4.5	Oceanic	Epipelagic
Istiophoridae	*Makaira nigricans*	Atlantic blue marlin	Atlantic	Planktonic eggs	500	Piscivore	4.5	Oceanic	Epipelagic
Istiophoridae	*Tetrapturus albidus*	Atlantic white marlin	Atlantic	Planktonic eggs	300	Piscivore	4.5	Oceanic	Epipelagic
Istiophoridae	*Tetrapturus belone*	Mediterranean spearfish	Mediterranean	Planktonic eggs	240	Piscivore	4.5	Oceanic	Epipelagic
Istiophoridae	*Tetrapturus georgii*	Round-scale spearfish	Atlantic	Planktonic eggs	204	Piscivore	4.4	Oceanic	Epipelagic
Istiophoridae	*Tetrapturus pfluegeri*	Long-bill spearfish	Atlantic	Planktonic eggs	282	Piscivore	4.3	Oceanic	Epipelagic
Scombridae	*Acanthocybium solandri*	Wahoo	Atlantic	Planktonic eggs	250	Piscivore	4.4	Oceanic	Epipelagic
Scombridae	*Auxis rochei*	Frigate mackerel	Atlantic	Planktonic eggs	50	Piscivore	4.1	Oceanic	Epipelagic
Scombridae	*Auxis thazard*	Frigate tuna	Atlantic	Planktonic eggs	72	Plankto-piscivore	4.3	Oceanic	Epipelagic
Scombridae	*Euthynnus alletteratus*	Little tunny	Atlantic	Planktonic eggs	100	Piscivore	4.5	Oceanic	Epipelagic
Scombridae	*Katsuwonus pelamis*	Skipjack tuna	Atlantic	Planktonic eggs	108	Piscivore	4.3	Oceanic	Epipelagic
Scombridae	*Orcynopsis unicolor*	Plain bonito	Atlantic	Planktonic eggs	130	Piscivore	4.5	Oceanic	Epipelagic
Scombridae	*Rastrelliger kanagurta*	Indian mackerel	Indo-Pacific	Planktonic eggs	39	Planktivore	3.2	Inner shelf	Epipelagic
Scombridae	*Sarda sarda*	Bonito	Atlantic	Planktonic eggs	90	Piscivore	4.5	Oceanic	Epipelagic
Scombridae	*Scomber japonicus*	Chub mackerel	Lusitanian	Planktonic eggs	64	Planktivore	3.1	Outer shelf	Epipelagic
Scombridae	*Scomber scombrus*	Atlantic mackerel	Atlantic	Planktonic eggs	55	Piscivore	3.7	Shelf	Epipelagic
Scombridae	*Scomberomorus commerson*	Narrow-barred Spanish mackerel	Indo-Pacific	Planktonic eggs	266	Piscivore	4.5	Shelf	Epipelagic
Scombridae	*Scomberomorus tritor*	West African Spanish mackerel	African	Planktonic eggs	100	Piscivore	4.3	Shelf	Epipelagic
Scombridae	*Thunnus alalunga*	Albacore	Atlantic	Planktonic eggs	127	Piscivore	4.3	Oceanic	Epipelagic
Scombridae	*Thunnus albacares*	Yellow-fin tuna	Atlantic	Planktonic eggs	265	Piscivore	4.3	Oceanic	Epipelagic
Scombridae	*Thunnus obesus*	Big-eye tuna	Atlantic	Planktonic eggs	250	Piscivore	4.5	Oceanic	Epipelagic
Scombridae	*Thunnus thynnus*	Blue-fin tunny	Atlantic	Planktonic eggs	300	Piscivore	4.4	Oceanic	Epipelagic
Centrolophidae	*Centrolophus niger*	Blackfish	Atlantic	Planktonic eggs	150	Piscivore	4.0	Oceanic	Mesopelagic
Centrolophidae	*Hyperoglyphe perciformis*	Barrelfish	Atlantic	Planktonic eggs	91	Piscivore	4.0	Oceanic	Mesopelagic
Centrolophidae	*Schedophilus medusophagus*	Cornish blackfish	Atlantic	Planktonic eggs	50	Planktivore	4.0	Oceanic	Mesopelagic
Centrolophidae	*Schedophilus ovalis*	Imperial blackfish	Atlantic	Planktonic eggs	100	Planktivore	3.5	Oceanic	Mesopelagic
Nomeidae	*Cubiceps gracilis*	Driftfish	Atlantic	Planktonic eggs	107	Unknown	3.6	Oceanic	Mesopelagic
Nomeidae	*Nomeus gronovii*	Man-of-war fish	Atlantic	Planktonic eggs	39	Medusophagous	3.7	Oceanic	Epipelagic
Nomeidae	*Psenes maculatus*	Silver driftfish	Atlantic	Planktonic eggs	30	Unknown	NA	Oceanic	Mesopelagic
Nomeidae	*Psenes pellucidus*	Blue-fin driftfish	Atlantic	Planktonic eggs	80	planktivore	3.8	Oceanic	Mesopelagic
Stromateidae	*Pampus argenteus*	White pomfret	Indo-Pacific	Planktonic eggs	30	Planktivore	3.1	Oceanic	Epi/mesopelagic

Family	**Scientific name**	**Common name**	**Biogeographical affinity**	**Reproductive mode**	L_{max} **(cm)**	**Trophic guild**	**Trophic level**	**Habitat (horizontal)**	**Habitat (vertical)**
Stromateidae	*Stromateus fiatola*	Blue butterfish	Atlantic	Planktonic eggs	61	Plankto piscivore	3.9	Shelf	Benthopelagic
Tetragonuridae	*Tetragonurus atlanticus*	Big-eye squaretail	Atlantic	Planktonic eggs	50	Medusophagous	3.6	Oceanic	Mesopelagic
Tetragonuridae	*Tetragonurus cuvieri*	Small-eye squaretail	Atlantic	Planktonic eggs	70	Medusophagous	3.8	Oceanic	Mesopelagic
Citharidae	*Citharus linguatula*	Atlantic spotted flounder	Lusitanian	Planktonic eggs	30	Unknown	4.0	Shelf	Demersal
Scophthalmidae	*Lepidorhombus boscii*	Four-spotted megrim	Lusitanian	Planktonic eggs	40	Piscivore	3.7	Outer shelf	Demersal
Scophthalmidae	*Lepidorhombus whiffiagonis*	Megrim	Lusitanian	Planktonic eggs	59	Piscivore	4.2	Outer shelf	Demersal
Scophthalmidae	*Phrynorhombus norvegicus*	Norwegian topknot	Boreal	Planktonic eggs	12	Bentho-piscivore	4.0	Shelf	Demersal
Scophthalmidae	*Phrynorhombus regius*	Eckström's topknot	Lusitanian	Planktonic eggs	20	Benthivore	3.4	Shelf	Demersal
Scophthalmidae	*Psetta maxima*	Turbot	Lusitanian	Planktonic eggs	100	Piscivore	4.0	Shelf	Demersal
Scophthalmidae	*Scophthalmus rhombus*	Brill	Lusitanian	Planktonic eggs	75	Piscivore	3.8	Shelf	Demersal
Scophthalmidae	*Zeugopterus punctatus*	Topknot	Lusitanian	Planktonic eggs	25	Bentho-piscivore	4.0	Shelf	Demersal
Bothidae	*Arnoglossus imperialis*	Imperial scaldfish	Lusitanian	Planktonic eggs	25	Benthivore	3.8	Outer shelf	Demersal
Bothidae	*Arnoglossus kessleri*	Scaldback	Mediterranean	Planktonic eggs	10	Bentho-piscivore	4.1	Shelf	Demersal
Bothidae	*Arnoglossus laterna*	Scaldfish	Lusitanian	Planktonic eggs	20	Benthivore	3.6	Inner shelf	Demersal
Bothidae	*Arnoglossus rueppelli*	Rüppell's scaldback	African	Planktonic eggs	18	Bentho-piscivore	4.0	Slope	Demersal
Bothidae	*Arnoglossus thori*	Thor's scaldfish	Lusitanian	Planktonic eggs	22	Benthivore	3.3	Shelf	Demersal
Bothidae	*Bothus podas*	Wide-eyed flounder	African	Planktonic eggs	45	Benthivore	3.4	Shelf	Demersal
Bothidae	*Monolene microstoma*	Small-mouth moonflounder	African	Planktonic eggs	20	Unknown	NA	Shelf	Demersal
Pleuronectidae	*Glyptocephalus cynoglossus*	Witch	Boreal	Planktonic eggs	60	Benthivore	3.1	Shelf	Demersal
Pleuronectidae	*Hippoglossoides platessoides*	Long rough dab	Boreal	Planktonic eggs	50	Bentho-piscivore	3.7	Shelf	Demersal
Pleuronectidae	*Hippoglossus hippoglossus*	Halibut	Boreal	Planktonic eggs	200	Piscivore	4.5	Slope	Demersal
Pleuronectidae	*Limanda limanda*	Dab	Boreal	Planktonic eggs	40	Benthivore	3.3	Shelf	Demersal
Pleuronectidae	*Microstomus kitt*	Lemon sole	Boreal	Planktonic eggs	45	Benthivore	3.3	Shelf	Demersal
Pleuronectidae	*Platichthys flesus*	Flounder	Lusitanian	Planktonic eggs	50	Benthivore	3.2	Coastal	Demersal
Pleuronectidae	*Pleuronectes glacialis*	Arctic flounder	Arctic	Planktonic eggs	44	Benthivore	3.6	Coastal	Demersal
Pleuronectidae	*Pleuronectes platessa*	European plaice	Boreal	Planktonic eggs	100	Benthivore	3.3	Shelf	Demersal
Pleuronectidae	*Reinhardtius hippoglossoides*	Greenland halibut	Boreal	Planktonic eggs	100	Piscivore	4.5	Slope	Benthopelagic
Soleidae	*Bathysolea profundicola*	Deep-water sole	Lusitanian	Planktonic eggs	26	Benthivore	3.2	Slope	Demersal
Soleidae	*Buglossidium luteum*	Solenette	Lusitanian	Planktonic eggs	15	Benthivore	3.3	Inner shelf	Demersal
Soleidae	*Dicologlossa cuneata*	Wedge sole	Lusitanian	Planktonic eggs	37	Benthivore	3.3	Shelf	Demersal
Soleidae	*Microchirus boscanion*	Lusitanean sole	African	Planktonic eggs	20	Benthivore	NA	Shelf	Demersal
Soleidae	*Microchirus ocellatus*	Four-eyed sole	Lusitanian	Planktonic eggs	20	Benthivore	3.2	Shelf	Demersal
Soleidae	*Microchirus variegatus*	Thick-back sole	Lusitanian	Planktonic eggs	20	Benthivore	3.3	Shelf	Demersal
Soleidae	*Microchirus (Zevaia) azevia*	-	African	Planktonic eggs	49	Benthivore	3.2	Shelf	Demersal

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{max} (cm)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
Soleidae	*Microchirus (Zevaia) hexophthalmus*	Ocellated wedge sole	African	Planktonic eggs	20	Benthivore	NA	Shelf	Demersal
Soleidae	*Monochirus hispidus*	Whiskered sole	Lusitanian	Planktonic eggs	24	Benthivore	3.5	Shelf	Demersal
Soleidae	*Pegusa lascaris*	Sand sole	Lusitanian	Planktonic eggs	40	Benthivore	3.2	Inner shelf	Demersal
Soleidae	*Pegusa impar*	Adriatic sole	Mediterranean/African	Planktonic eggs	25	Benthivore	3.2	Shelf	Demersal
Soleidae	*Solea aegyptiaca*	Egyptian sole	Mediterranean	Planktonic eggs	65	Benthivore	3.2	Inner shelf	Demersal
Soleidae	*Solea senegalensis*	Senegalese sole	Lusitanian	Planktonic eggs	73	Benthivore	3.1	Shelf	Demersal
Soleidae	*Solea solea*	Sole	Lusitanian	Planktonic eggs	70	Benthivore	3.1	Inner shelf	Demersal
Soleidae	*Synaptura kleinii*	Klein's sole	African	Planktonic eggs	40	Benthivore	3.5	Shelf	Demersal
Soleidae	*Synaptura lusitanica*	Portuguese sole	African	Planktonic eggs	40	Benthivore	3.8	Inner shelf	Demersal
Cynoglossidae	*Cynoglossus browni*	Nigerian tonguesole	African	Planktonic eggs	49	Benthivore	3.4	Inner shelf	Demersal
Cynoglossidae	*Cynoglossus sinusarabici*	Red Sea tonguesole	Indo-Pacific	Planktonic eggs	12	Benthivore	3.3	Inner shelf	Demersal
Cynoglossidae	*Symphurus ligulatus*	Elongate tonguesole	African	Planktonic eggs	14	Benthivore	3.5	Slope	Demersal
Cynoglossidae	*Symphurus nigrescens*	Tonguesole	Lusitanian	Planktonic eggs	15	Benthivore	3.3	Slope	Demersal
Cynoglossidae	*Symphurus reticulatus*	–	Macaronesia	Planktonic eggs	16	Benthivore	3.3	Shelf	Demersal
Balistidae	*Balistes carolinensis*	Grey triggerfish	Lusitanian	Demersal eggs	40	Benthivore	3.5	Shelf	Reef-associated
Balistidae	*Balistes punctatus*	Blue-spotted triggerfish	Atlantic (African)	Demersal eggs	60	Benthivore	3.4	Inner shelf	Demersal
Balistidae	*Balistes vetula*	Queen triggerfish	Atlantic (African)	Demersal eggs	60	Benthivore	3.4	Shelf	Demersal
Balistidae	*Canthidermis maculata*	Spotted oceanic triggerfish	Atlantic (African)	Demersal eggs	50	Unknown	3.5	Shelf	Benthopelagic
Balistidae	*Canthidermis sufflamen*	–	Atlantic (African)	Demersal eggs	65	Planktivore	3.2	Shelf	Benthopelagic
Monacanthidae	*Aluterus monoceros*	Unicorn leatherjacket	Atlantic (African)	Uncertain	76	Benthivore	3.5	Shelf	Reef-associated
Monacanthidae	*Stephanolepis diaspros*	Reticulated leatherjacket	Indo-Pacific	Uncertain	25	Unknown	2.8	Shelf	Reef-associated
Monacanthidae	*Stephanolepis hispidus*	Plane-head filefish	Atlantic (African)	Uncertain	26	Unknown	2.2	Shelf	Reef-associated
Ostraciidae	*Acanthostracion notacanthus*	Island cowfish	African	Uncertain	50	Unknown	3.2	Shelf	Reef-associated
Tetraodontidae	*Canthigaster rostrata*	Caribbean sharp-nose puffer	Atlantic (African)	Uncertain	12	Benthivore	3.0	Shelf	Reef-associated
Tetraodontidae	*Canthigaster sanctaehelenae*	St. Helena sharp-nose pufferfish	African	Uncertain	12	Benthivore	3.0	Shelf	Demersal
Tetraodontidae	*Ephippion guttifer*	Prickly puffer	African	Uncertain	80	Benthivore	3.5	Shelf	Demersal
Tetraodontidae	*Lagocephalus lagocephalus*	Pufferfish	Atlantic	Uncertain	60	Benthivore	3.7	Shelf	Benthopelagic
Tetraodontidae	*Lagocephalus spadiceus*	Half-smooth golden pufferfish	Indo-Pacific	Uncertain	20	Benthivore	3.5	Shelf	Uncertain

Family	Scientific name	Common name	Biogeographical affinity	Reproductive mode	L_{MAX} (CM)	Trophic guild	Trophic level	Habitat (horizontal)	Habitat (vertical)
Tetraodontidae	*Sphoeroides marmoratus*	Guinean puffer	African	Uncertain	20	Benthivore	3.3	Shelf	Demersal
Tetraodontidae	*Sphoeroides pachygaster*	Blunt-head puffer	African	Uncertain	49	Benthivore	4.2	Shelf	Demersal
Tetraodontidae	*Sphoeroides spengleri*	Band-tail puffer	Atlantic (African)	Uncertain	30	Benthivore	3.2	Shelf	Demersal
Diodontidae	*Chilomycterus atringa*	Spotted burrfish	Atlantic (African)	Uncertain	60	Benthivore	3.5	Shelf	Benthopelagic
Diodontidae	*Diodon eydouxii*	Pelagic porcupinefish	Atlantic (African)	Uncertain	27	Planktivore	3.7	Shelf	Pelagic
Diodontidae	*Diodon holocanthus*	Long-finned porcupinefish	Atlantic (African)	Uncertain	50	Benthivore	3.3	Shelf	Reef-associated
Diodontidae	*Diodon hystrix*	Spot-fin porcupinefish	Atlantic (African)	Uncertain	91	Benthivore	3.4	Shelf	Benthopelagic
Molidae	*Masturus lanceolatus*	Sharp-tail mola	Atlantic	Planktonic eggs	337	Benthivore	4.2	Oceanic	Epipelagic
Molidae	*Mola mola*	Sunfish	Atlantic	Planktonic eggs	300	Planktivore	3.9	Oceanic	Epipelagic
Molidae	*Ranzania laevis*	Truncated sunfish	Atlantic	Planktonic eggs	80	Planktivore	3.7	Oceanic	Epipelagic

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