

Review of climate change impacts on marine fish and shellfish around the UK and Ireland

MICHAEL R. HEATH^{a,*}, FRANCIS C. NEAT^b, JOHN K. PINNEGAR^c, DAVID G. REID^d, DAVID W. SIMS^{e,f} and PETER J. WRIGHT^b

^a*University of Strathclyde, Department of Mathematics and Statistics, Livingstone Tower, 26 Richmond Street, Glasgow, G1 1XH, UK*

^b*Marine Scotland – Science, Marine Laboratory, Marine Laboratory, 375 Victoria Road, Aberdeen, AB11 9DB, UK*

^c*Cefas, Pakefield Road, Lowestoft, NR33 0HT, UK*

^d*Marine Institute, Rinville, Oranmore, Co. Galway, Ireland*

^e*Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK*

^f*Ocean and Earth Science, National Oceanography Centre, University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK*

ABSTRACT

1. Recent and projected future changes in the temperature and chemistry of marine waters around the UK and Ireland are having, and will in the future have, effects on the phenology, productivity and distribution of marine fish and shellfish. However, the overall consequences are still hard to predict because behaviour, genetic adaptation, habitat dependency and the impacts of fishing on species, result in complex species' responses that may be only partially explained by simple climate envelope predictions.

2. There is a broad body of evidence that climatic fluctuations are playing an important role in changing fish distributions and abundances, which is discernible against the background of trends in abundance due to fishing. During warm periods, southern species have tended to become more prominent and northern species less abundant. However, the changes in distribution are often more complicated than might be expected from a simple climate envelope approach, partly due to ocean circulation patterns which create invasion routes for southern water species into the North Sea from the south and from the north via the continental shelf west of Britain and Ireland.

3. The eventual population-scale impacts of ocean acidification on fish and shellfish are currently very difficult to predict. However, the scant evidence suggests that indirect food web effects arising from the enhanced sensitivity of calcifying planktonic organisms may be important, and the direct effect on fish sensory systems leading to subtle influences on behaviour with possible population-level implications are possible.

4. In British waters, the lesser sandeel (*Ammodytes marinus*) is identified as being at particular risk from climate change. Owing to its strict association with coarse sandy sediments it is unable to adapt its distribution to compensate for warming sea temperatures. Sandeels are a key link in the food web, linking primary and zooplankton production to top predators.

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*Correspondence to: Michael R. Heath, University of Strathclyde, Department of Mathematics and Statistics, Livingstone Tower, 26 Richmond Street, Glasgow G1 1XH, UK. E-mail: m.heath@strath.ac.uk

INTRODUCTION

Fish scales recovered from annually stratified (varved) sediments in various regions of the world (Baumgartner *et al.*, 1992; O'Connell and Tunnicliffe, 2001; Patterson *et al.*, 2005; Emeis *et al.*, 2009) indicate large fluctuations in species abundances extending back over millennia, which are most likely a consequence of climate variations. Fragmentary documentary sources for fish stocks around the UK and Ireland also indicate substantial natural variability over periods of centuries to millennia (Southward *et al.*, 1988; Alheit and Hagen, 1997). Changes in temperature, sea level and glaciation significantly altered the distribution of fish habitats during the Holocene epoch (Bigg *et al.*, 2008). Hence, there is no reason to suppose that fish will not have responded to recent (past 100 years) climate changes (Stenseth *et al.*, 2002; Chavez *et al.*, 2003), and will in the future respond to the projected changes in climate over the coming years.

Sea temperatures around the UK and Ireland have been warming at between 0.2 and 0.6 °C per decade over the past 30 years, with some of the highest observed local rates on Earth being in the shallow southern North Sea (Rayner *et al.*, 2003). Sea surface temperatures are predicted to continue rising for the foreseeable future. The carbonate chemistry of sea water is also affected by the greenhouse gases that lead to warming, and can result in acidification and de-oxygenation of sea water. Modelling studies suggest that mean surface ocean pH has decreased from 8.25 to 8.14 between the mid-18th century and 2000, but is likely to decrease to 7.85 by 2100 with projected future increases in atmospheric CO₂, representing a 2.5-fold increase in H⁺ ion concentrations since the 1750s (Jacobsen, 2005). However, understanding of the local changes in pH and carbonate saturation in sea water around the UK and Ireland, and their consequences for fish and shellfish, is currently very poor.

Geographic distributions of terrestrial taxa are estimated to be shifting to higher latitudes at an average of 16.9 km per decade and to higher altitudes at 11 m per decade (Chen *et al.*, 2011). In contrast, much larger range changes have been recorded among some marine fauna. Warm-water zooplankton communities have advanced northwards in the north-east Atlantic, and cold-water communities retreated, by more than 250 km per decade (Beaugrand *et al.*, 2002). Plankton taxa have a high potential for range shifting due to dispersal by ocean currents and similarly dispersal of the pelagic larval stages of fish might be expected to favour rapid

distributional changes in response to warming. However, with some notable exceptions, the responses of marine fish to climate change are only poorly known. This is partly because marine fish are difficult to observe and census, but also because habitat dependencies during the life cycles of many fish species complicate the sensitivity to warming and other features of marine climate change. In addition, many species, and certainly most shelf sea communities, are heavily affected by exploitation. Mortality rates on late juvenile and adult phases of major commercially exploited species are typically 3–6 times greater than natural rates due to predation, for example, which is not a situation commonly encountered among terrestrial wildlife. Fishing has certainly had a major impact on the regional abundance and diversity of many fish populations, and changed seabed habitat, fish size and age compositions as well as reproductive properties, and possibly genetic composition (Greenstreet and Rogers, 2006). Consequently it is exceedingly difficult to disentangle the effects of long-term fishing pressure from those of climate change, and to predict how these issues may interact in the future.

Key points in the life cycle where fish may be vulnerable to the physical and biological effects of climate change in the sea are: (1) the timing of spawning in relation to the seasonal production of planktonic crustaceans, especially copepods, which form the larval diet of most species; (2) the dispersal of eggs and larvae by water currents; (3) physiological effects of temperature on growth and maturation; (4) biological or physical alteration of habitat for juveniles and adults; (5) complex food web effects (changes in prey and/or predator community composition); (6) alteration of migration cues for adult fish; and (7) vulnerability of life stages to fishing gears. The variety of these factors means that deterministic modelling of the impacts of climate change on fish distributions, by piecing together all the component processes, is extremely challenging. Instead, a statistical approach is usually followed, in which spatially distributed data on environmental conditions (e.g. temperature, salinity) and the observed presence/absence or abundance of a species over its current geographic range, are used to define the statistical environmental niche or climate envelope (Dambach and Rödder, 2011). The envelope is then projected onto estimates of past or future geographic distributions of the environmental factors to hindcast or forecast the past or future distributions of the species (Cheung *et al.*, 2009). Clearly the approach

assumes that the environmental factors used to define the niche represent major constraints on a species distribution. If other factors affecting the life cycle are, or become more important, then the approach risks misleading conclusions, especially for species and communities where natural distributions have been modified by exploitation (Simpson *et al.*, 2011). Recent variants of the climate envelope approach (Cheung *et al.*, 2011) have attempted to include detailed physiological formulations such as oxygen requirements at different life stages and 'scope for growth' as outlined by Pörtner (2010) to overcome some of these difficulties.

Community responses to climate will be particularly difficult to predict (Blanchard *et al.*, 2005). However, similarities between community responses in adjacent regions in response to similar levels of sea temperature warming, even if involving different species, may help define some general patterns (Genner *et al.*, 2004). Fish species that rely on planktonic food throughout their life are most likely to exhibit rapid responses to climate change. Distributional changes are most likely to be seen in highly mobile migratory species, such as mackerel (*Scomber scombrus*), blue whiting (*Micromesistius poutassou*), and sardines (*Sardina* sp.), although such changes among migratory demersal fish have also been documented (Mieszkowska *et al.*, 2009). Conversely, the abundance of other schooling pelagic species that do not migrate, such as the lesser sandeel (*Ammodytes marinus*), may be locally affected by climate change (Frederiksen *et al.*, 2006).

We first review the aspects of life cycles and physiology which may dictate how fish and shellfish populations respond to climate change. We then discuss the mechanisms of geographic range shifting, and scope for indirect effects of climate through changes in food webs, and document evidence from a range of sources for impacts of climate change in waters around the UK and Ireland. Finally we speculate as to the possible responses of fish to projected future environmental consequences of climate change.

FACTORS AFFECTING RESPONSES TO CLIMATE CHANGE: THERMAL PHYSIOLOGY

The vast majority of marine fish species are ectothermic so temperature directly determines their vital physiological processes including acid–base regulation, resting metabolic rate, metabolic scope, growth and maturation (Jobling, 1988; Brander, 1994, 1995;

Yoneda and Wright, 2005; Graham and Harrod, 2009; Pörtner and Peck, 2010). Temperature also has indirect effects on fish behaviour, swimming performance (Videler, 1993; Peck *et al.*, 2006), food consumption (Jobling, 1988; Koskela *et al.*, 1997), and ultimately survival and reproduction. Knowledge of the thermal biology of ectothermic animals is fundamental to an understanding of their ecology and distribution (Brown *et al.*, 2004), and predicting the likelihood of change in geographic range that may occur due to climate change (Wikelski and Cooke, 2006). As each species varies in its thermal niche, tolerance, lethal limits, and optima, different species may be expected to respond differently to climate change (Pörtner and Farrell, 2008). Moreover, there are ontogenetic changes in the thermal tolerance, with eggs and larvae having a narrower window than juveniles (Pörtner and Peck, 2010). Larger individuals then become more thermally sensitive because of progressively falling oxygen supply in relation to demand. Added to this, adult spawning fish have elevated oxygen requirements to support their often large gamete masses (Pörtner and Farrell, 2008).

FACTORS AFFECTING RESPONSES TO CLIMATE CHANGE: PHYSIOLOGICAL EFFECTS OF ACIDIFICATION

Reductions in the saturation state of aragonite and calcite in sea water due to rising CO₂ concentrations and falling pH make it more difficult for calcifying marine organisms to deposit shell material (Fabry *et al.*, 2008; Vézina and Hoegh-Guldberg, 2008). Calcifying species such as corals, coccolithophorids, foraminifera, echinoderms and shelled molluscs enhance the precipitation of carbonate by means of energy-dependent ion transport enzymes (Dupont *et al.*, 2008; Rost *et al.*, 2008). Maintaining calcification at reduced environmental concentrations of aragonite and calcite is possible for such taxa but requires more energy (Pörtner, 2008; Cummings *et al.*, 2011), so acidification effects cannot be considered in isolation from nutritional status and temperature. So far, few experiments have addressed the combined effect of feeding, temperature, and acidification although new evidence indicates a physiological mechanism in coccolithophores for adaptation to lowered sea water pH (Taylor *et al.*, 2011).

Fish also face potential physiological challenges in an environment with declining aragonite and calcite saturation states since they have a need to precipitate calcium carbonate to form bone, and otoliths, the

latter being composed of aragonite. Adult fish are thought to be relatively tolerant of environmentally relevant changes in pH (Ishimatsu *et al.*, 2004, 2005), largely because active fish experience marked variability in their body CO₂ levels on a daily basis as a result of activity, but deleterious effects have been predicted for more sensitive larval stages, and for gametes released into the water (Ishimatsu *et al.*, 2008). In fact, the scant experimental evidence points to a lack of detectable effects on growth, survival, skeletal development, and otolith calcification, at least in a tropical reef fish species (*Acanthochromis polyacanthus*; Munday *et al.*, 2011) subjected to elevated CO₂ concentrations equivalent to the IPCC A2 100 year scenario. In other species, such as Pacific white sea bass (*Atractoscion nobilis*), larval fish otolith development in response to elevated CO₂ conditions showed an increased otolith size (area) compared with controls, although it was not determined whether these changes affected orientation and behaviour of young fish, or their survival (Checkley *et al.*, 2009). Similarly, Frommel *et al.* (2010) found no deleterious effects of realistic changes in pH on the motility of sperm in Atlantic cod (*Gadus morhua*) in the Baltic Sea. By contrast, Ishimatsu *et al.* (personal communication) found that high CO₂ and warm temperature together resulted in high larval mortality in the clownfish *Amphiprion ocellaris* and in the medaka (*Oryzias javanicus*). Also, at very high CO₂ concentrations, growth and gonad development were affected in *Sillago japonica*, an important food fish in east Asia.

To date, work on acidification has concentrated on physiological and biological effects and comparatively little work has considered population- and ecosystem-level effects (Le Quesne and Pinnegar, 2011). Indirect effects could potentially cause greater impacts on fish and fisheries than direct effects. The most obvious indirect effects are alteration in predator or prey abundance; however, indirect effects could also occur if acidification affects biogenic habitats that are important as fish nursery grounds, or alters nutrient recycling and benthic-pelagic coupling. Indirect impacts of acidification are hard to predict at the species level because of the complexity of ecological interactions (Le Quesne and Pinnegar, 2011).

FACTORS AFFECTING RESPONSES TO CLIMATE CHANGE: REPRODUCTIVE BIOLOGY

Temperate marine fish species exhibit a wide range of life history strategies. Most temperate marine fish are

oviparous serial spawners with high per-capita fecundity that begin investing into reproduction the year before spawning. Temperature can influence when fish become sexually mature, by determining energy intake and also directly (Tobin and Wright, 2011), by having a permissive effect on the rate of oocyte growth and development (Korsgaard *et al.*, 1986; Olin and Von der Decken, 1989; Van der Kraak and Pankhurst, 1997). Similarly, the positive effect of temperature on the rate of secondary gametogenesis can also influence the onset of spawning (Kjesbu *et al.*, 2010). For example, Pawson *et al.* (2000) found that oocyte development was aborted and full maturity did not occur in virgin female sea bass (*Dicentrarchus labrax*) unless they remained in water above 10°C during the main period of gonad development. This may partly explain the increase in sea bass numbers in the more rapidly warming southern North Sea and Channel region.

The dependence of reproduction on stored energy reserves is a key factor influencing when fish spawn, with capital breeders tending to spawn much earlier in the year than income breeders. Typically most temperate fish in northern European waters are capital breeders, spawning in the water column during the winter to spring (January–April). Egg development rate is temperature dependent, and the larvae which hatch spend between 3 and 5 months feeding mainly on planktonic crustaceans while being transported by water currents. Some notable exceptions are Atlantic herring (*Clupea harengus*) and sandeels which shed their eggs in a single batch onto the sea bed. Most herring in European waters spawn in autumn, although Atlanto-scandian herring spawn in the spring, and Celtic Sea herring in the winter, while the most abundant sandeel species (lesser sandeel) spawns in winter. Fish with an energy-income breeding strategy spawn in late spring and summer (April–June) and include species such as whiting (*Merlangius merlangus*), sole (*Solea solea*) and sprat (*Sprattus sprattus*).

At the end of the larval phase there is typically a shift in diet composition, habitat preference and swimming capability. Many pelagic species, such as herring, sardine, anchovy, become silvered and aggregate into schools. Atlantic mackerel, horse mackerel (*Trachurus trachurus*) and blue whiting, however, have definite nursery areas and habitats, particularly on shelf areas to the west of the UK and Ireland, and seem to adopt a relatively demersal habit during this phase.

Demersal species such as cod, haddock (*Melanogrammus aeglefinus*) and plaice (*Pleuronectes*

platessa) settle to the sea bed. Eggs, larvae, and settled juveniles are subject to high predation mortality, initially from invertebrate predators in the plankton and later from piscivorous fish (Temming *et al.*, 2007). Growth and maturation rates, and life expectancy vary widely between species. Short-lived, fast growing, early maturing species such as sandeel and sprat, contrast with long-lived, slow growing, late maturing species such as angler fish (*Lophius* spp.) and orange roughy (*Hoplostethus atlanticus*), and intermediate species such as cod. Species such as Atlantic mackerel, horse mackerel, blue whiting, and some stocks of herring are strongly migratory as adults, spending part of each year in feeding aggregations tracking thermal conditions and/or the development of plankton populations, and migrating to spawning regions once gonad development has been fulfilled. Others seem comparatively sedentary throughout their life. Tagging studies on, for example, cod have shown that adult fish can have a strong fidelity to given spawning sites (Robichaud and Rose, 2001, 2004; Wright *et al.*, 2006a; for review see Mieszkowska *et al.*, 2009), although this varies with region sparking some debate as to whether this reflects natal fidelity (Svedäng *et al.*, 2007). Cod have been shown to have a rich population structure with many genetically and morphologically distinguishable sub-populations (Hutchinson *et al.*, 2001) forming a metapopulation (Wright *et al.*, 2006b; Nielsen *et al.*, 2009). Other species, such as anglerfish appear to be essentially panmictic over a large region of the north-east Atlantic (Laurenson *et al.*, 2005; O'Sullivan *et al.*, 2005).

MECHANISMS OF RANGE SHIFTING

A range shift of a species along a changing environmental gradient can come about in several main ways. First, as most marine fish species are capable of extensive horizontal and vertical movements (Metcalf, 2006; Sims, 2010), they may be expected to either moderate or avoid their exposure to unfavourable climatic conditions by individual directional movements, i.e. behavioural mediation. When the changing gradient is temperature, this could either be movement to deeper waters, to different water masses or along a latitudinal gradient. There is evidence for individual based thermal preferences and niches; captive cod for example will distribute themselves along thermal gradients according to size and predicted optima for growth (Lafrance *et al.*, 2005). Juvenile plaice have been recorded to make

mass movements from estuaries if temperatures exceed a critical threshold (Berghahn *et al.*, 1993). Juvenile herring in the North Sea have been shown to change their realized temperature habitats leading to a geographic shift east into shallower water (Röckmann *et al.*, 2011).

Second, climatic conditions may force a species at one stage in its life-history in a particular direction and then sedentary behaviour at a later stage acts to reinforce this distributional shift. This is an explanation favoured by Rindorf and Lewy (2006) who suggested that North Sea cod generally remain in the areas where they settle as juveniles. Warm winters (caused by southerly winds) cause an increased northward transport of eggs and larvae, which results in a northward shift in the juvenile distribution the following year. Adult cod then remain there and are assumed to spawn there leading to a gradual abandonment of the southern spawning areas. However, their study offered no direct evidence for adult cod remaining where they settle as juveniles and later biophysical modelling evidence contradicted the idea of an increased northward transport of eggs and larvae from the southern North Sea (Heath *et al.*, 2008). Furthermore, on the northern coast of Norway, for example, coastal cod have clear spatial genetic structure, but there was no evidence of isolation-by-distance (Jorde *et al.*, 2007). In this case it was apparent that gradual adult or larval dispersal was unlikely, rather it was proposed that the spatial structure was formed through sporadic colonization waves of genetically similar individuals (Mieszkowska *et al.*, 2009).

Finally, in the longer term, a species may simply contract from unfavourable parts of its former range through lowered survival and failure to reproduce or recruit. In other words, the former extent of habitat simply no longer supports that species. Interestingly, while there are numerous accounts of northerly range extensions of Lusitanian species (e.g. sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*) and horse mackerel - Beare *et al.*, 2004c; Rijnsdorp *et al.*, 2009, 2010) or northerly shifts in distribution centres, there is less unequivocal evidence for southerly extent contractions of boreal species (Genner *et al.*, 2004; ter Hofstede *et al.*, 2010; Rijnsdorp *et al.*, 2009, 2010). This suggests, though does not prove, that fish may more readily extend their range but that contraction is a longer term process, possibly because seasonal variability means that at certain times of the year thermal conditions may still be conducive to some boreal species' persistence and survival. In this respect,

non-parametric probabilistic ecological niche models (NPPEN) provide one approach to quantifying change and likely change in distributions (Lenoir *et al.*, 2011). Lenoir *et al.* used three environmental parameters (sea surface temperature, bathymetry and sea surface salinity), to predict likely distribution changes in eight commercially exploited fish species. Most of the species showed northerly distribution shifts, mainly linked to changes at the southern end of the range. Temperate or sub-arctic species (e.g. pollack (*Pollachius pollachius*), haddock, saithe (*Pollachius virens*) and turbot (*Scophthalmus maximus*)) would be expected to be reduced in range, although sprat was projected to increase its range. Warm temperate species were projected to increase their range (particularly anchovy) or experience only slight reductions.

These mechanisms are not mutually exclusive and may all act to produce an apparent shift in the distribution of the species. With respect to global warming, thermal gradients tend to be gradual in the open sea and most fish have a larval dispersal phase and a free-swimming adult stage, consequently it is commonly assumed that fish are relatively unhindered in gradually shifting their range. Despite the compelling observations and logical basis for expecting fish to change their distribution in response to climate change, some recent studies indicate that the changes in fish distribution are not simply explained in terms of fish seeking a temperature niche.

BEHAVIOURAL CONSTRAINTS TO RANGE SHIFTING

Information on individual responses to temperature can help identify whether range shifts reflect a behavioural response to adverse conditions or population level processes affecting survival. Investigations using data storage tags attached to cod released in the southern North Sea have shown that the fish do not migrate in summer to avoid water temperatures as high as 19°C despite the availability of significantly cooler areas nearby (Neat and Righton, 2007). As the highest optima temperature for growth in laboratory studies of Atlantic cod was found to be 14.5°C (Imsland *et al.*, 2004), the southern North Sea temperature exposure appears to be well above the animal's preferred temperature. Indeed, across the distributional range of cod throughout the north-east Atlantic, data storage tags have revealed that this species has a very wide thermal range and tolerance from -1.5 to 19°C (Righton *et al.*, 2010). Individuals were recorded

moving between water masses and across thermal fronts and experiencing up to 13°C changes in temperature over one or two days. This suggests that adult cod have the behavioural and physiological plasticity that allows them to occupy the full thermal extent of the NE Atlantic ecosystem. Interestingly, however, the data suggested that at spawning time, the range of temperatures experienced was much narrower (between 1 and 8°C), although this study is likely to have overestimated this range owing to the uncertainty that all cod during the spawning period were actually spawning. Cold temperatures can inhibit oocyte development in cod (Yoneda and Wright, 2005), although this depends on local thermal adaptation. The true range suitable for spawning is probably 4–8°C. This finding fits with the notion that thermal windows are likely to be narrower for early life-history stages because of developmental constraints (Pörtner *et al.*, 2006) and with what is known about the role temperature plays in gonad maturation (Yoneda and Wright, 2005; Kjesbu *et al.*, 2010). As such there may prove to be a critical 'thermal window' for spawning for which climate change could have a much more significant impact. It is not clear to what extent this is also true of other temperate species as comparable data sets do not exist.

Species with complex behaviours such as spawning site fidelity and migration may be constrained in range shifting (West, 2010; West *et al.*, 2009). The advantages of returning to particular spawning sites, such as positive density-dependence, e.g. Allee effects (Petersen and Leviton, 2001), may override the fact that the spawning site is no longer situated in optimal environmental conditions. If the instinct to return to a particular site is ontogenetically imprinted, it may take evolutionary change to break migratory pathways and site fidelity. There is certainly good evidence from tagging studies and from anecdotal observation that cod and plaice return to highly specific sites to spawn each year (Brander, 1975; Hunter *et al.*, 2004; Neat *et al.*, 2006). Herring are also known to show considerable conservatism in both spawning site and migrations (Corten, 2002). The genetic and behavioural mechanisms, such as imprinting, underlying spawning site fidelity and migration routes are poorly understood for the majority of species and deserve greater research attention, although new methods have allowed identification of likely mechanisms in anadromous species such as salmon (*Salmo salar*) (Bandoh *et al.*, 2011; Ueda, 2011).

Those species unable to respond to climate change may be most vulnerable as it may ultimately lead to

persistent recruitment failure and continual range contraction (as opposed to range shifting). In the case of cod, while some groups and individuals show strong spawning site attachment (Neat *et al.*, 2006) and natal fidelity (Svedäng *et al.*, 2007) there is also evidence that other groups and individuals are less site attached and more vagrant (Robichaud and Rose, 2004; for review see Mieszkowska *et al.*, 2009). Thus the impact of climate change on a species will depend much on intra-specific diversity or population structure.

POPULATION STRUCTURE AND RANGE SHIFTS

There is growing evidence for fine-scale population structuring in a number of marine fish species (Graves, 1998). The extent of population differences in microsatellite allele frequencies are such that cod for example can be reliably assigned to the Baltic Sea, North Sea and the north-east Arctic Ocean on the basis of their genotypes alone (Nielsen *et al.*, 2001), therefore it seems probable that different responses to temperature variations within a species may occur between regions. In the Skaggeerrak, where population structure is evident at scales of as little as 100 km, there is apparent spatial variability in traits such as juvenile growth (Olsen *et al.*, 2008), which may lead to differential responses of a single species within a region to climatic change. Furthermore, cod from the southern North Sea appear to be reproductively isolated from those in the deep waters of the northern North Sea (Hutchinson *et al.*, 2001; Wright *et al.*, 2006a, b; Nielsen *et al.*, 2009). At the same time, fishing mortality rates on cod are probably higher in the southern North Sea than in the north (Heath *et al.*, 2003, 2008), so changes in distribution could be a consequence of fishing patterns on spatially segregated sub-stocks (Neat and Righton, 2007). Finally, there is some evidence that the general decline in cod recruitment that has occurred in the North Sea took effect earlier in the reproductively segregated sub-stock from the southern North Sea than in the deep northern area, contributing to the more rapid decline of abundance in that region (Holmes *et al.*, 2008).

While climate effects are usually considered at the stock or species level it is also important to consider locally adapted populations within stocks. For example, Atlantic cod exhibit a range of genetic polymorphisms affecting thermal tolerance. In a study of Icelandic cod, Pampoulie *et al.* (2008) demonstrated that individuals carrying the pantophysin IAA genotype were likely to display a shallow water

feeding migration while those carrying the IBB genotype preferred deeper waters and forage near cold fronts. Within these genetic constraints, a degree of thermal acclimation may also depend on the thermal environment into which the young grow up (Brix *et al.*, 2004). Similarly, different types of Atlantic cod haemoglobin have been known since 1961 (Petersen and Steffensen, 2002). The geographical distribution of Atlantic cod with the different haemoglobin types varies, with the HbI2 allele occurring at high frequency in northern regions, and the HbI1 allele dominant in warmer areas. Studies in the laboratory (Petersen and Steffensen, 2002) have revealed that HbI-2 cod typically prefer a temperature of $8.2 \pm 1.5^\circ\text{C}$ while HbI-1 cod prefer $15.4 \pm 1.1^\circ\text{C}$, and therefore that global warming may provide an advantage for HbI-1 cod in the future. Little is known about the genetic basis of local adaptation in most other marine fish species. Identifying and understanding local adaptation and the scope to acclimatize in other species is therefore an important avenue for future consideration.

INDIRECT EFFECTS OF CLIMATE CHANGE THROUGH FOOD WEB INTERACTIONS

Production of fish has traditionally been considered a function of primary production and the efficiency of transfer from lower trophic levels (Aebischer *et al.*, 1990; Schwartzlose *et al.*, 1999; Chavez *et al.*, 2003). Hence, 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. However, if the efficiency of the food web is dependent on a few key species that are vulnerable to temperature changes or acidification, then there is clear scope for indirect effects of climate change on fish. For example, the pteropod *Limacina helicina* is a key plankton species in the north Pacific (Kobayashi, 1974) which is particularly sensitive to acidification (Fabry *et al.*, 2008). The species forms dense near-surface swarms during daylight, where it is heavily predated by juvenile pink salmon (*Oncorhynchus gobuscha*). Calculations suggest that a 10% decrease in *L. helicina* production could lead to a 20% decrease in mature pink salmon body weight (Fabry *et al.*, 2008).

Comparing across ecosystems in the north-west 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. Fluctuations between bottom-up and top-down states are important signals of pressure on the food web 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.

Rijnsdorp *et al.* (2009, 2010) reviewed some of the evidence for food web linkages between climate change and fish, and showed that pelagic species exhibited clear changes in seasonal migration patterns related to climate induced changes in zooplankton productivity. Lusitanian species have increased in recent decades (sprat, anchovy, and horse mackerel), especially at the northern limit of their distribution areas, while Boreal species apparently decreased at the southern limit of their distribution range (cod and plaice), but increased at the northern limit (cod). Although the underlying mechanisms were unclear, the authors concluded that the available evidence suggested climate-related changes in recruitment success to be the key process, stemming from either higher production or survival in the pelagic egg or larval stage, or owing to changes in the quality/quantity of nursery habitats.

It is important to recognize that species will not exhibit fixed feeding preferences in the future, in response to changing prey availabilities and thus it can be very difficult to predict the likely indirect consequences of climate change and ocean acidification (Le Quesne and Pinnegar, 2011). For example, several species in the North Sea have undergone significant changes in diet in response to large changes in benthic community composition that have occurred over the last 100 years, predominantly as a result of trawling pressure but also climate change (Kröncke, 2011), illustrating the difficulties of identifying species susceptibility on the basis of current diets. Plaice switched from a diet based predominantly on calcifying organisms to one based predominantly on non-calcifying organisms without experiencing a

significant decline as a consequence (Rijnsdorp and Millner, 1996), clearly demonstrating the potential flexibility of marine food webs in the face of fundamental changes to community composition (Le Quesne and Pinnegar, 2011).

EVIDENCE OF CLIMATE RESPONSES: HISTORICAL LANDINGS DATA

Alheit and Hagen (1997) compiled data on weather conditions and commercial landings of herring and sardine at fishing ports in Brittany, Normandy, south-west England, Sweden and Norway extending back to the late-10th century. The fisheries were episodic and highly correlated with the mildness/severity of winter weather conditions. Sequences of years with large landings of herring from Swedish coastal waters, off south-west England, eastern English Channel and Bay of Biscay were characterized by cold, severe winter weather conditions in north-west Europe. In particular, herring fisheries flourished towards the southern end of their latitudinal range during sequences of cold years in the 'Little Ice Age' (1300–1850). These periods alternated with sequences of years of mild winter weather in which the Swedish, English and French herring fisheries failed, and instead large landings of herring were recorded from more northerly Norwegian coastal waters, and of sardines from south-west England and the English Channel. Such conditions occurred between the mid-12th century and the end of the 13th century ('the Medieval Warm Period') and during the late 19th to early 20th centuries. The alternation of sardine and herring off south-west England has been noted since the 16th century and has been clearly related to sea temperature and alternations between warm and cold-water plankton species (referred to as the 'Russell Cycle'; Southward *et al.*, 1988, 2005). However, when the Cycle changed from a warm water to a cold water regime between 1965 and 1979, herring failed to return to the south coast of England probably because intensive fishing during the 1920s led to a collapse of the stock (Southward, 1980).

EVIDENCE OF CLIMATE RESPONSES: RECENT LANDINGS DATA

Compilations of data on international commercial landings of fish extend back to 1903. Since this time, data from the port monitoring programmes of 33 national authorities with fleets operating in European waters have been compiled by the International

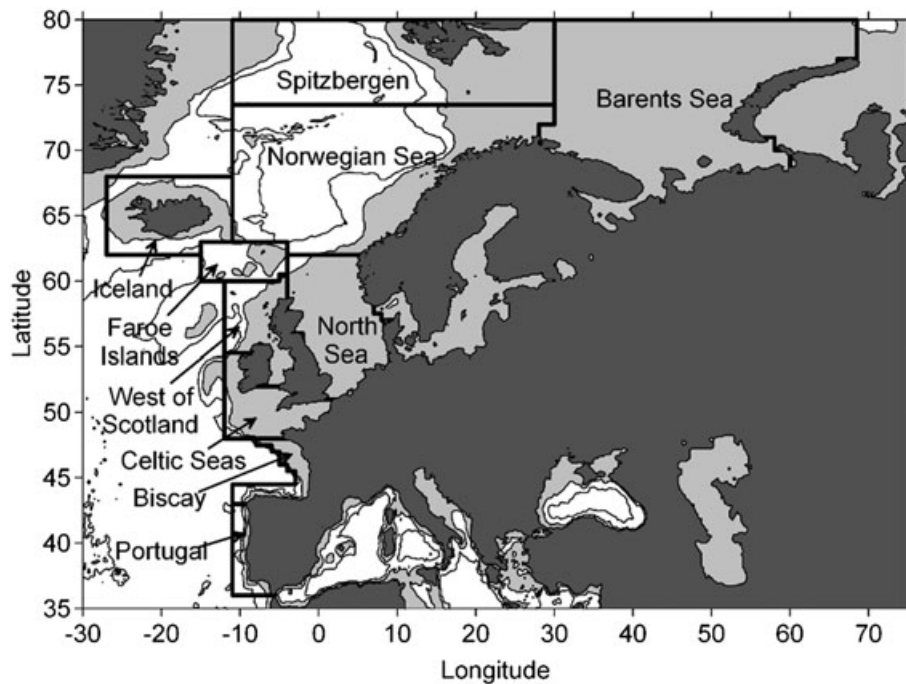


Figure 1. North-east Atlantic regions used for compiling international fishery landings data.

Council for the Exploration of the Sea (ICES) (<http://www.ices.dk/fish/statlant.asp>). During this period the catching ability of fishing fleets increased far beyond that of earlier times with the advent of steam trawlers in the early 20th century. As a result, many exploited stocks of fish suffered progressive depletion, culminating in some notable collapses during the second half of the 20th century, e.g. North Sea herring. Thereafter, restrictive catch limits were imposed on most of the major species in an effort to conserve resources. Hence, time series of abundance or landings in a given area cannot usually be interpreted solely in terms of environmental factors, although some large-scale changes can be resolved.

Annual landings of the 341 taxonomic categories of finfish recorded from the north-east Atlantic, between 35°N and 80°N, can be broadly assigned to four guilds based on dietary characteristics (Heath, 2005a, b): planktivores (average 5.96 million t y⁻¹; 61 species, e.g. Atlantic herring, sardines), benthivores (average 0.35 million t y⁻¹; 103 species, e.g. plaice, sole, gurnards *Eutrigla* spp.), demersal piscivores (average 2.84 million t y⁻¹; 118 species, e.g. cod, saithe and whiting) and pelagic piscivores (average 1.01 million t y⁻¹; 59 species, e.g. Atlantic mackerel, horse mackerel). A total of 58 species or species groups account for more than 90% of the landings (by weight) of all four categories throughout the entire latitudinal range.

For each recording region (Figure 1), the area densities of landings of each species category (t km⁻²,

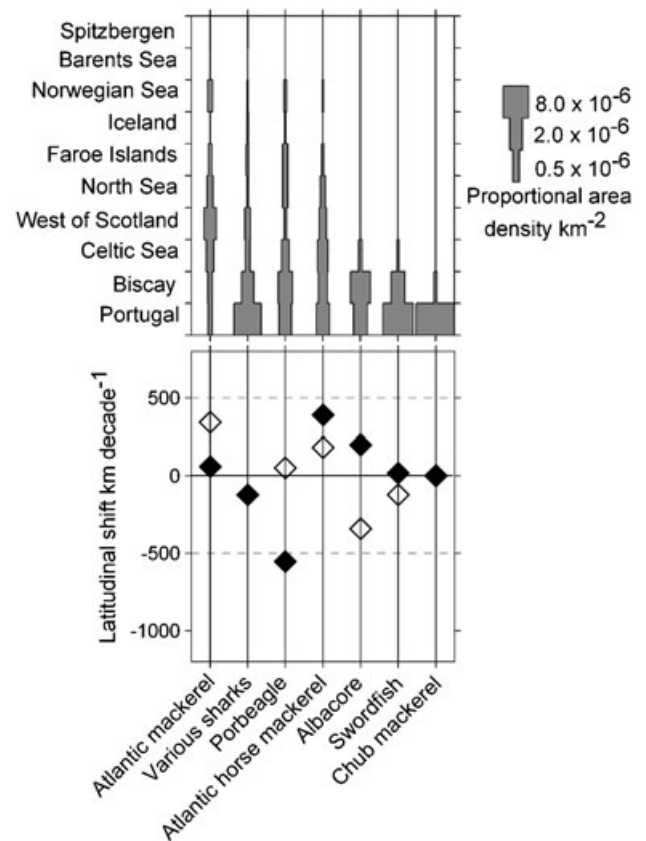


Figure 2. Latitudinal distributions of fishery landings for the pelagic piscivore feeding guild, averaged over 1973–1999. Upper panel: for each region, the width of the bar is related to the proportional area density (km⁻²) of total north-east Atlantic landings. Within each guild, species ordered by area weighted mean latitude. Lower panel: changes in the mean latitude of fishery landings for the pelagic piscivore feeding guild; open symbols between 1970s and 1980s; filled symbols between 1980s and 1990s.

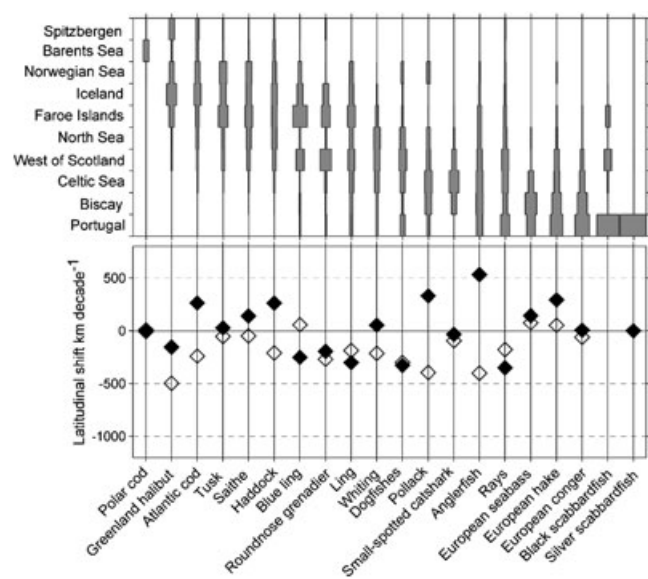


Figure 3. As Figure 2 for the demersal piscivore feeding guild.

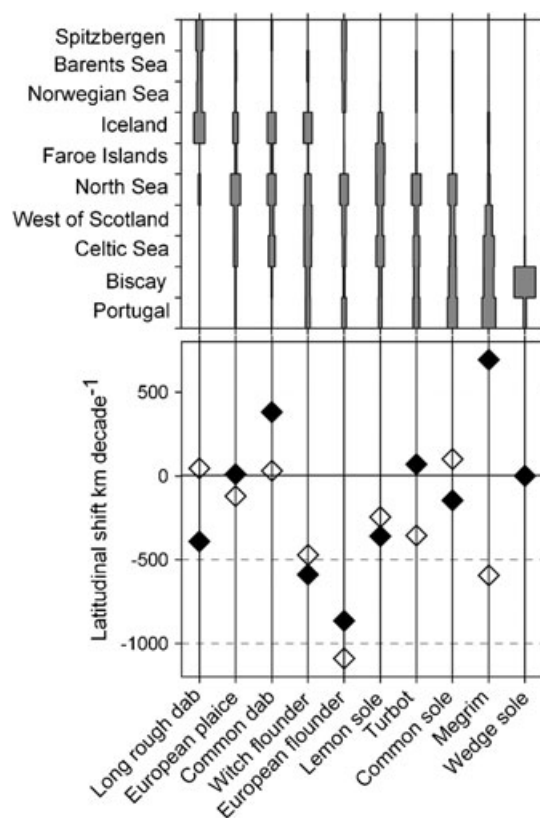


Figure 5. As Figure 2 for the benthivorous flatfish feeding guild.

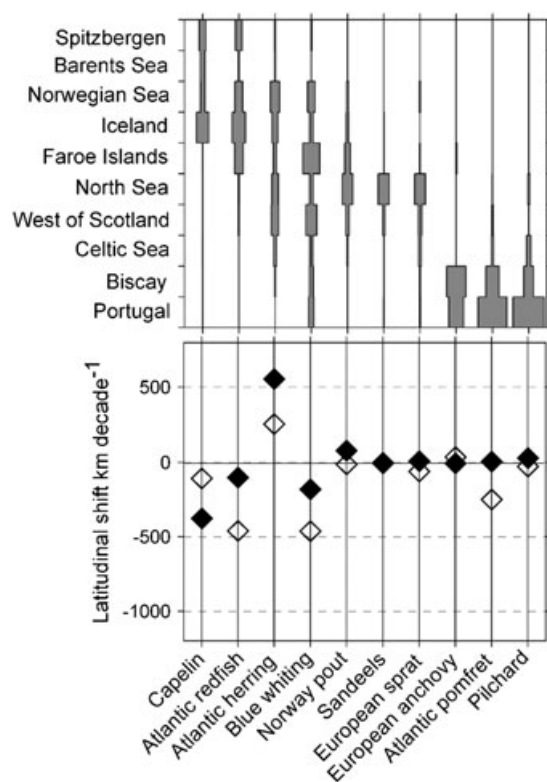


Figure 4. As Figure 2 for the planktivore feeding guild.

assuming catches were taken from an area equivalent to that of water less than 500 m depth in each region) were summed over all nations for decadal periods (1970–1979, 1980–1989 and 1990–1999), and expressed as a proportion of the total north-east Atlantic landings. The latitudinal distribution of proportional area density (km^{-2}) averaged over the entire 1970–1999 period for the 58 main species categories are shown in

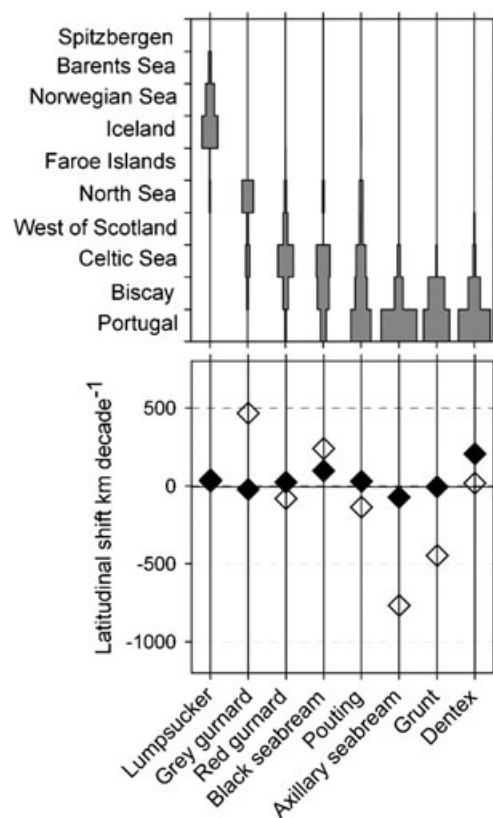


Figure 6. As Figure 2 for the benthivorous roundfish feeding guild.

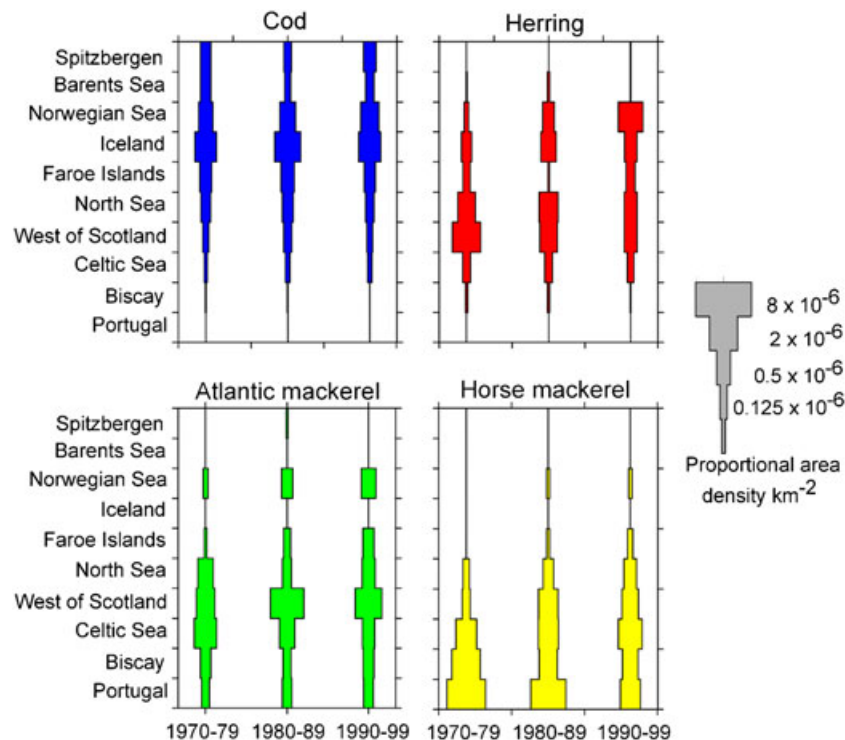


Figure 7. Latitudinal distributions of fishery landings for each of the three decades 1970–1979, 1980–1989 and 1990–1999, for cod (upper left), herring (upper right), Atlantic mackerel (lower left) and horse mackerel (lower right). The width of the bar is related to the proportional area density (km^{-2}) of total north-east Atlantic landings.

Figures 2–6 (upper panels). Changes in the density-weighted mean latitude of landings of each species (Figures 2–6, lower panels) indicated both northerly and southerly shifts between decades. More species shifted south than north between the 1970s and 1980s, and vice versa between the 1980s and 1990s. On face value this seems to parallel the inter-decadal changes in sea and air temperatures, both of which show a cooling between the 1970s and 1980s, and warming between the 1980s and 1990s at UK latitudes, in parallel with changes in the North Atlantic Oscillation (NAO) index (Hurrell, 2001; Visbek *et al.*, 2001; Hurrell *et al.*, 2003). Among the major pelagic species, the distribution of landings of herring, mackerel and horse mackerel underwent major northerly shifts during both inter-decadal periods (Figure 7). The northerly extension of horse mackerel landings reflects the well documented establishment of a fishery for this species in the North Sea during the late 1980s where commercial quantities had not previously been found (Reid PC *et al.*, 2001; Iversen *et al.*, 2002). In addition, the horse mackerel stock experienced a massive recruitment event in 1982, and this must also in part have contributed to the change in catches of this species.

A northerly shift in mackerel catches in the 1970s and later, was probably a result of migration changes

(Walsh and Martin, 1986; Walsh *et al.*, 1995). However, it was not possible to link these changes to temperature, although there is a clear temperature link to mackerel distribution (Reid DG *et al.*, 1997, 2001). It is possible therefore that the timing of fish migrations may have changed, and the fisheries altered their activity and distribution to match. There was also the developing Russian and other nations' fishery in international waters in the 1990s and beyond, that could have contributed to changes in the catch distribution. Furthermore, there was also a substantial Bay of Biscay fishery in the earlier period. Hence, the changing patterns in catches are probably as much about the choices of the fishing fleets as about changes in fish distribution. Analysis of mackerel egg survey data suggests that there has been a slight northerly shift in the centre of gravity of the spawning. Mackerel appear to spawn within a 2°C temperature interval, and show an approximately 60 km northward movement for each degree increase in temperature (ICES, 2008).

The northerly shift in herring landings was a consequence of the resurgence of the Atlanto-Scandian herring stock centred in the Norwegian Sea, which collapsed due to overfishing around 1970 (Alheit and Hagen, 1997; Toresen and Østvedt, 2000). This is a separate stock of fish from the herring found further

south in the North Sea and south-west of the UK. The North Sea herring stock also recovered during the 1990s, having collapsed and been closed to fishing during most of the 1980s. Hence, the recent latitudinal changes in herring landings, which parallels the historical pattern established from analysis of data back to the 10th century, should not be interpreted as reflecting any northward movement of fish *per se*. Rather, it reflects a change in the pattern of production across the latitudinal range. In part, this might be due to climatic factors, but must also be considered in relation to management actions to regulate fishing mortality on distinctly separate stocks of the species.

Large southerly shifts in the landings distribution of some species (e.g. European flounder) with a temperate distributional range, are hard to explain in terms of either climate or fisheries activity. However, it seems certain that economic factors and market forces have had a large impact on the distribution of the fishery for angler-fish, for example, since fishing fleets began to actively target this species during the 1990s as catching opportunities for more traditional species such as cod and haddock declined (Hislop *et al.*, 2001). The major demersal species (Atlantic cod (Figure 7), saithe, haddock, European hake *Merluccius merluccius*, and seabass) all showed small rates of northerly movement in landings distribution between the 1970s and 1990s (25–50 km decade⁻¹), although it is difficult to interpret these given the high level of management intervention in these fisheries.

Recent analyses of Scottish and English commercial catch data in the North Sea spanning the period 1913–2007, by Engelhard *et al.* (2011b) have revealed that the locations where peak catches of target species such as cod, haddock, plaice, and sole are obtained, have all shifted throughout the 20th century. High sole catches seem to have retreated away from the Dutch coast, southwards towards the eastern Channel. High plaice catches have moved steadily north-westwards, while cod catches seem to have shifted north-eastward, towards deeper water in the North Sea over the past 9 decades. Haddock catches have moved very little in terms of their centre of distribution, but their southern boundary has shifted northwards by approximately 130 km over the past 80–90 years. These movements in a number of different directions illustrate the fact that climate change and its influence on fish stocks is not a straightforward issue.

For the period 1913–1980, data were obtained from 'statistical charts' (catalogued in Engelhard, 2005) that were produced by the UK Ministry of Agriculture,

Fisheries and Food (now Defra). For the period 1968–2007, data on trawler landings into Scotland were obtained from the Fisheries Management Database (FMD) of Marine Scotland. Landings into England and Wales were obtained from the Fisheries Activity Database (FAD) of Defra/Cefas. Using the much longer time series of fish distribution data collated here, covering both warming and cooling periods, and including periods of contrasting levels of fishing effort, it was possible to tease out the relative impacts. Accordingly it was possible to attribute the observed shift in plaice distribution to climate rather than to fishing (although other factors may have played an important role). For sole, both climate and fishing pressure/mortality seem to have been important (Engelhard *et al.*, 2011b).

Fishery landings are not the only source of information on the spatial distributions of finfish – there are also extensive data from scientific surveys (see following section). However, survey data spanning geographic ranges are lacking for most exploited invertebrate species, and landings data are often the only coherent source of information. The latitudinal range for landing of one of the main invertebrate fishery species in the north-east Atlantic, Norway lobster (*Nephrops norvegicus*), extends from the Portuguese coast to Iceland. Overall landings increased 5-fold between 1955 and 1990 and then stabilized, but since the 1980s, the proportion taken from the southern portion of the geographic range has declined, while the proportion from the northern part has increased (Engelhard and Pinnegar, 2010). The changes are consistent with a poleward shift in distribution of the species, but at least three other hypotheses have been proposed to explain the observed pattern, including: (a) regional differences in the historical patterns of fishing, (b) changes in the distribution of fishing effort, and (c) indirect food web effects resulting from the decline of predator abundances. Time series analysis of landings and fishing effort data from 13 Norway lobster populations around northern and central Europe failed to find any coherent trends related to climatic drivers including the North Atlantic Oscillation Index (NAO) or sea surface temperatures (Zuur *et al.*, 2003). In the case of brown shrimp (*Crangon crangon*), landings from the North Sea have increased since the 1970s and a fishery for the species has developed at Iceland (Hufnagl and Temming, 2010). However, it is not clear whether these changes have any relation to warming. There are suggestions that the species may have been introduced to Icelandic waters via ships'

ballast (Gunnarson *et al.*, 2007), and that changes in yield and distribution in the North Sea are largely due to declining predator abundances and changes in fishing patterns.

In summary, while the landings data provide a useful gross summary of the latitudinal ranges of commercially exploited fish and invertebrate species, shifts in the latitudinal distribution of landings are, with a few exceptions, difficult to interpret. Nevertheless, ratios of commercial species landings, in particular the ratio of sole landings to the sum of sole and plaice landings (Brander *et al.*, 2003), has been adopted as an indicator of distributional change in marine species by the European Environment Agency (<http://www.eea.europa.eu/data-and-maps/indicators/northward-movement-of-marine-species/northward-movement-of-marine-species>).

EVIDENCE OF CLIMATE RESPONSES: SCIENTIFIC SURVEY DATA

Perry *et al.* (2005) analysed data on the abundance and distribution of both exploited and non-exploited fish species caught during annual scientific trawl surveys of the North Sea. Nearly two-thirds of species exhibited northerly shifts in mean latitude (e.g. Atlantic cod and anglerfish) and/or movements into deeper water (e.g. plaice and cuckoo ray, *Leucoraja naevus*) over a 25 year period. For species with northerly or southerly range margins in the North Sea, half showed boundary shifts, and all but one shifted northward. Species with northward shifting distributions had faster life cycles and smaller body sizes than non-shifting species. The shifts in latitude or into deeper water were correlated with variations in temperature estimated from measurements carried out during the same surveys and implied that shifting species remained within a constant temperature range. Similarly, Hedger *et al.* (2004) analysed the survey distributions of cod in the North Sea and showed that fish were found in deeper water during 1990–1999 compared with 1980–1989, but that their distribution with respect to temperature was largely unchanged.

Engelhard *et al.* (2011a) used bottom trawl survey data to show an increase in Lusitanian, small bodied and low to mid-trophic level species in the North Sea, while Boreal, large bodied, and high trophic level species decreased or showed only marginal increases. Distribution and abundance of John dory (*Zeus faber*) and incidences of other warm-favouring Lusitanian species have also increased in the Irish and Celtic Seas

(Briggs *et al.*, 2008; ter Hofstede *et al.*, 2010). However, no corresponding decrease in the number of cold-favouring Boreal species was detected. In the southern North Sea, warming periods were correlated with relatively higher richness of Lusitanian species compared with Boreal (Hiddink and ter Hofstede, 2008), and lower mean body size in the demersal fish community as a whole regardless of fishing intensity (ter Hofstede and Rijnsdorp, 2011). Poulard and Blanchard (2005), and Desaunay *et al.* (2006) have similarly reported analyses of scientific trawl survey data series from the shelf waters of the Bay of Biscay. These studies also show a northerly advance in the distribution of southern sub-tropical species such as wedge sole *Dicologlossa cuneata* along the shelf, and a decline in abundance of species with a northerly distribution, such as European plaice. The authors found that the changes in abundance of northern and southern species were correlated with sea temperature and hence inferred that the changes detected are related to climate. However, unlike in the North Sea, the possibility of other explanations such as fishing patterns remains unresolved.

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 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, 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 north-eastern 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 cooled to less than 1°C. For example, sole tend to overwinter in deeper, warmer waters, in order to avoid the lethally cold winter temperatures before returning to the shallows in spring (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, 1964).

Off the south-west of Britain, in the English Channel and Bristol Channel, Genner *et al.* (2004) showed from analysis of long time series of scientific trawl survey data that climate-linked temperature shifts and fishing together have substantially altered the species abundances and composition of the community over the last century. Responses of some species fitted well with 'climate envelope' predictions. For example, non-commercial species such as dragonet (*Callionymus lyra*), poor cod, thickback sole (*Microchirus variegatus*), greater pipefish (*Syngnathus acus*), butterfly blenny (*Blennius ocellaris*) and redband fish (*Cepola macrophthalma*) responded positively to warming episodes during the last 90 years, with the largest increases in abundance occurring since 1986. These changes reflected the patterns of sea surface temperature change in the western English Channel since 1900. However, commercially important warm-water species such as skates, rays (*Raja* spp.), and brill (*Scophthalmus rhombus*) declined steadily over the same period, despite the potentially positive effects of warming. The implication was that these species were unable to respond to sea temperature increases because of fisheries exploitation (Genner *et al.*, 2010b).

Changes in abundance of Boreal species due to climatic variations should be most apparent in the western English Channel which is a major biogeographic boundary for a wide range of fauna. However, many Boreal fish species show little or no trend in abundance in this region. For example, cod and other species abundances showed no trend in the

Bristol Channel between 1981 and 2002 despite significant sea temperature warming since 1985 (Genner *et al.*, 2004). These results are taken to indicate that natural species responses may be poorly, or perhaps only partially predicted by climate envelope modelling approaches that typically predict declining abundances of northern Boreal species at the southern edge of their ranges in response to warming (Genner *et al.*, 2004). A more recent analysis of scientific survey data from this region collected between 1911 and 2007 showed a dichotomous size-dependent response of species to long-term climate change and commercial fishing, with small-bodied, generally Lusitanian, species (e.g. solenette, red mullet *Mullus surmuletus*) increasing in abundance with warming, while larger species (both Lusitanian and Boreal, e.g. ling *Molva molva*, turbot *Scophthalmus maximus*, rays) declined in abundance and size, reflecting expectations from sustained size-selective harvesting (Genner *et al.*, 2010b). This demonstrates the importance of accounting for both climate and fishing effects when interpreting how fishes have responded to climate change.

In the Celtic Sea, analyses of the catch data from the Irish Ground Fish Survey indicate that Lusitanian fish have been increasing on the shelf to the north and west of Ireland while the Boreal community has been declining to the south (Lynam *et al.*, 2010). But again, some of these effects may be compounded by changes in fishing pressure and stock status as much as climate change. Non-commercially exploited species such as pilchard and anchovy may have increased to the north and west, respectively, due to immigration, while sea bass (to the south-east) and bib (to the west) would have already been present but may have flourished in the warmer conditions. Nolan *et al.* (2009) suggested that largely unexploited Lusitanian species such as poor cod and lesser spotted dogfish *Scyliorhinus canicula* could be useful indicator species for climate change (Genner *et al.*, 2004, 2010b; McHugh *et al.*, 2011), and the latter species in particular since they survive well after discarding by the fishery (Revill *et al.*, 2005) and hence fishing effects on trends may be limited, compared with those due to climate responses. Both species have increased in abundance (g m⁻², swept area) in survey catches to the north and north-west of Ireland, and decreased in the shelf waters south of Ireland.

Further north, in the shelf waters west of Scotland, trends in fish species richness have been distinctly different from those in the North Sea and Celtic Sea. While overall richness increased between 1999 and

2008 with time and with temperature in the North and Celtic Seas, species numbers have decreased off the west of Scotland (ter Hofstede *et al.*, 2010). Elsewhere, increasing richness has been mainly driven by rising incidence of warm-water Lusitanian species, with no significant trends in cold-water Boreal species, but off the west of Scotland the decreasing richness has been due mainly to losses of Boreal species with no significant trend in Lusitanian ones. However, the analysis in question (ter Hofstede *et al.*, 2010) also illustrates the dangers of interpreting trends solely on the basis of bivariate correlations, since overall richness was also found to be inversely related to fishing mortality in the North Sea, but positively related off the west of Scotland, indicating the likelihood of more complicated explanations for the observed trends than simple climate envelope responses. Also, while the shelf-wide trend in species richness off the west of Scotland was found to be decreasing with time between 1999 and 2008, this was not replicated at smaller spatial scales. Richness was found to be stable over an 80 year period (1927–2009) in the semi-enclosed Firth of Clyde despite an intense boom and bust cycle of fishing, and increasing between 1960 and 2009 off the north coast of Ireland in the southern shelf part of the west of Scotland region (Heath and Speirs, 2012).

EVIDENCE OF CLIMATE RESPONSES: RARE SPECIES RECORDS

There are many reports in the recent literature indicating northerly expansion of the geographic ranges of fish species along the north-east Atlantic margin. Stebbing *et al.* (2002) analysed the incidence of new species in Cornish waters between 1960 and 2001 from records in a regional environmental database. For the first 18 years of the scheme no new species of fish were encountered. From 1979 onwards, the cumulative number of new species increased steadily in parallel with rising sea temperatures. The new species were predominantly of southern, warm water origin.

From 1995 onwards, Beare *et al.* (2004a, b) and Mamie *et al.* (2007) reported dramatic increases in catches of red mullet, European anchovy, sardine and bluemouth (*Helicolenus dactylopterus* D.) during scientific trawl surveys in the north-western North Sea. These species had been almost absent from the area throughout the preceding 70 years (only 19 individual red mullet were recorded between 1925 and 1995). All of the red mullet, and most of the sardines and

anchovy recorded since 1995, were caught during surveys in January–March despite equivalent sampling activity at other times of the year, particularly in July–September. The time series of sardine and anchovy catches were correlated with sea temperature. In the case of the red mullet, the authors postulated that the fish found in the northern North Sea were in reality part of an increasing southern North Sea population that migrated northwards during the winter seeking warmer waters. Winter sea temperatures are significantly colder in the southern North Sea than in the north due mainly to the shallower depths.

Bluemouth appeared in the northern North Sea in 1991 as a distinct cohort, with total lengths ranging between 6 and 8 cm. Before this time there were hardly any records of bluemouth in the North Sea (Heessen, 1994; Heessen *et al.*, 1996). Bluemouth abundance increased during the 1990s along the continental shelf west of the UK, and their appearance in the North Sea in 1991 coincided with a period of exceptional inflow of warm saline water from the continental slope current into the North Sea (Heath *et al.*, 1991). It is likely that the bluemouth were carried into the northern North Sea with this water mass as larvae or juveniles. Since 1991, there appear to have been no further immigrations of bluemouth, and the fish from 1991 formed a distinct cohort which could be tracked over a period of years (Mamie *et al.*, 2007).

In 2003, snake pipefish (*Entelurus aequoreus*) began to appear in trawl catches in the North Sea and west of the UK and Ireland, and their abundance increased rapidly (Harris *et al.*, 2007; van Damme and Couperus, 2008). The snake pipefish is the most oceanic of the species in the pipefish family, and is typically distributed in the open ocean between the Azores and Iceland. The species was previously rare in shelf waters. Particularly large numbers were caught in 2006, and foraging seabirds brought them to their nests and attempted (unsuccessfully) to feed them to their young (Harris *et al.*, 2007). Concurrently, since 2003 the CPR surveys across the Atlantic have encountered increasing numbers of juvenile snake pipefish in the samples as far west as the Mid-Atlantic Ridge (Kirby *et al.*, 2006). Since 2007, however, numbers have fallen back to normal levels (Marine Scotland unpublished trawl survey data; total number in catches: 2006, 9755; 2007, 5486; 2008, 241; 2009, 160; 2010, 6), indicating that while warm temperatures may have contributed to triggering this population explosion, it was only a temporary phenomenon

probably caused by some combination of environmental factors. From what is known of the reproductive biology of a closely related species, the increased abundance may be linked to temperature through effects on the sex ratio, reproductive rate and onset of breeding in this sex role-reversed fish (Kirby *et al.*, 2006).

Other species that have recently appeared in the North Sea for the first time (or have reoccurred after a very long absence) include the violet stingray (*Pteroplatytrygon violacea*), blue butterflyfish (*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). Similarly, sightings of bluefin tuna (*Thunnus thynnus*), triggerfish (*Balistes capris*), thresher shark, blue shark (*Prionace glauca*), stingray (*Pteroplatytrygon violacea*), and turtles are all becoming more commonplace off south-west Britain (Stebbing *et al.*, 2002), as are ocean sunfish (*Mola mola*; Houghton *et al.*, 2006), although mechanisms and consequences are poorly understood. For ocean sunfish, increased occurrence off SW Britain may be related to higher numbers of seasonal migrants arriving from overwintering areas off North Africa and the Gulf of Cadiz (Sims *et al.*, 2009a, b), perhaps in relation to abundances of gelatinous zooplankton, on which they feed, that may also be increasing due to climate change (Richardson *et al.*, 2009). 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 UK and Ireland at a rate of 60 km decade⁻¹. Similarly, Quero *et al.* (1998) documented a northerly advance of sailfin dory and rosy dory (*Cyttopsis roseus*) along the shelf edge between 1963 and 1996 which was correlated with rising temperatures.

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 Vandermeersch, 2005) and offshore seamounts (Fock *et al.*, 2002). In the past, boarfish outbreaks have been linked to storms and variability in offshore climate (Cooper, 1952). Boarfish are now being landed by Irish, Danish and

Scottish fishing boats and converted to fishmeal for aquaculture; in excess of 110 000 t were landed in 2010 (Marine Institute, 2010).

On the Rockall plateau, an isolated offshore bank in the north-east Atlantic, a recent study (Neat and Campbell, 2011) based on a trawl survey times series from 1986–2008 suggested that Ray's sea bream (*Brama brama*) and whiting have colonized the Bank in recent years. Ray's sea bream which was first recorded in surveys in 2006 is an oceanic and traditionally southern species for which northerly range expansion is commensurate with climate change, whereas whiting, which was first recorded in 1993 is a more northerly shelf-sea species which may simply be expanding its range irrespective of climate change. It is important to bear in mind that given the climatic fluctuations in the NE Atlantic since the last glaciation some species distributions may still be changing and that communities may be in a state of dynamic equilibrium of extinction and colonization.

The effects of climate change on elasmobranch fish (rays, skates, and sharks) are less well known than for most 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). It has been well documented that the abundance of the small-bodied catshark, the lesser spotted dogfish, has increased off SW Britain in line with increases in sea temperature since 1911 (Genner *et al.*, 2004, 2010b), with similar trends in both shallow inshore and deeper offshore habitats (McHugh *et al.*, 2011). However, the responses of pelagic species are poorly known by comparison. Cotton *et al.* (2005) demonstrated that a major component of the inter-annual variation in relative abundance of basking sharks (*Cetorhinus maximus*) off south-west Britain was positively correlated with fluctuations in SST and the NAO index. Results of this study indicate that climatic forcing of the copepod *Calanus 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 and Merrett, 1997; Sims and Quayle, 1998; Sims, 1999), with sea surface temperature being less important (Sims *et al.*, 2003). However, at larger scales (10–1000 km), sea surface temperature correlated significantly with basking shark distribution and movement patterns (Sims and

Quayle, 1998; Sims *et al.*, 2000; Cotton *et al.*, 2005). 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).

Overall therefore there is little doubt that many fish distributions have changed in recent years and that in many cases the most parsimonious explanation is climate change. In other cases it is also clear that climate change is almost certainly not the sole cause of any distributional change observed. Disentangling climatic effects from other factors, such as fishing in particular, is critically important as the advice for fisheries managers will be very different if it is one or the other, or as is most likely, some combination of both (Genner *et al.*, 2010b). To understand why some species and not others may respond to climate change, it is necessary to consider aspects of their behaviour, life-history and population structure.

EVIDENCE OF CLIMATE RESPONSES: PHENOLOGICAL CHANGES IN FISH AND SHELLFISH

Climate-related phenological properties (the timing of life-history events) of fish can be difficult to identify clearly due to the confounding effects of ontogenetic variations. For example, there are clear differences in spawning time and duration between age classes of many species (Wright and Trippel, 2009). Since there is clear evidence that fishing has led to truncation of the age range of fish in many exploited populations, trends in phenology would be expected regardless of any effects due to climate. Nevertheless, low temperature has been correlated with delayed spawning in temperate species such as Atlantic cod and capelin (*Mallotus villosus*) (Hutchings and Myers, 1994; Carscadden *et al.*, 1997), and higher temperature with earlier spawning of North Sea mackerel (Jansen and Gislason, 2011).

Invertebrate species may have more scope for phenological adaptation to warming sea temperatures by increasing the number of spawning cycles per annum. For example, Kuipers and Dapper (1984) demonstrated that brown shrimp achieved only a single reproductive cycle in the northern North Sea, but produced two in the warmer conditions of the shallow southern North

Sea. However, the increased reproductive output required substantially higher food intake. Similarly, the phenology of seasonal peak in abundance of veined squid (*Loligo* spp.) in the north-east Atlantic as a consequence of migration to feeding areas was shown to be closely linked to temperature changes mediated by climatic fluctuations associated with the North Atlantic Oscillation (NAO) (Sims *et al.*, 2001). Timing of temperature-dependent squid movement was 120–150 days earlier in the warmest years compared with the coldest.

Temperature in the spring appears to influence movements of some migratory temperate marine fish species to spawning grounds. Higher sea-surface temperatures are associated with earlier migration in Pacific herring (*Clupea harengus pallasii*, Clupeidae), capelin (Ware and Tanasichuk, 1989; Carscadden *et al.*, 1997) and North Sea mackerel (Jansen and Gislason, 2011). Temperature has also been shown to affect western mackerel migration onset, path and velocity (Walsh *et al.*, 1995; Reid *et al.*, 1997, 2001). Exceptionally, Sims *et al.* (2004) found that flounder (*Platichthys flesus*) off south-west Britain migrated from their estuarine habitat to open sea spawning grounds 1–2 months earlier in years that were up to 2 °C cooler. Fish arrived on the spawning grounds over a shorter time period when colder-than-normal conditions prevailed in the estuary, compared with warmer years, suggesting that they were responding to low temperatures by exhibiting a more synchronous, population-level early migration.

Despite some demonstrated links between fish migration phenology and climatic change, surprisingly few studies have investigated how the timing of events within the planktonic larval fish assemblage may be related to environmental variability even though appearance of larvae would be expected to follow successful spawning after migration. One study in the western English Channel showed that the timing of appearance in the plankton of spring spawning species (e.g. dab, lemon sole *Microstomus kitt*, ling) was dependent on sea temperatures during the previous November and December, with earlier appearance in cooler years (Genner *et al.*, 2010a). It was hypothesized that this may be due to colder winter temperatures triggering earlier winter migration of adults from cooler inshore habitat to warmer offshore grounds, in turn resulting in earlier gonad maturation and spawning. In contrast, summer spawners' (e.g. mackerel, horse mackerel) timings of appearance in the plankton were dependent on previous March temperatures, with earlier spawning during warmer years, presumably due to effects on gonad maturation rates (Genner *et al.*, 2010a). These trends indicate a

potentially important indirect effect of climate on recruitment success through the possibility of inappropriate timing of larval fish appearance in relation to seasonal trophic resources (the so-called match–mismatch hypothesis) (see section on Indirect Effects). A clear seasonal shift to earlier appearance of fish larvae has also been described for southern North Sea cod and many other commercial and non-commercial species (Greve *et al.*, 2005).

Pilling *et al.* (2007) examined annulus formation in the otolith (ear bone) of North Sea cod. The authors reported a change in the timing of annulus formation during warm versus cold periods (1985–1986 contrasted with 1994–1995). This study confirmed that southern North Sea cod do experience increased thermal stress during warmer years and that this manifests itself in slower growth rates. In warm years, translucent bands were laid down in the otolith, up to 22 days earlier than in colder periods (Millner *et al.*, 2011).

EVIDENCE OF CLIMATE RESPONSES: INTERACTIONS BETWEEN CLIMATE CHANGE AND FISHING

Fishery landings over the past millennium show changes occurring in concert with major climate signals. However, identifying the causes of recent decadal timescale changes in fish populations is complicated by the impact of fisheries which, since the late 19th and early 20th centuries (Sims and Southward, 2006), have had impacts at least as large as those due to climate fluctuations.

The preceding examples of changes in fish distribution fall broadly into two categories. First, those that involve changes in distributional limits through colonization of previously unoccupied areas (e.g. red mullet). In most cases these observations can be reasonably reliably linked to warming or other aspects of recent climate change, although the possible role of competitor release allowing colonization of newly available habitats by migratory species, perhaps due to removal of resident fish species by human exploitation, cannot be ignored. Second, changes in distribution within existing species ranges. These could be due to movement, or changes in spatial patterns of production and/or mortality in different sub-stocks of the species. In these cases it is much more difficult to disentangle the roles of climate and fishing in the observed response. Examples of the latter category are the recent changes in distribution of herring landings across the latitudinal range, and distributional changes of cod.

A key aspect of the productivity of fish stocks, including cod, is the rate of recruitment to the populations. Recruitment, also referred to as the ‘year-class strength’, is defined as the number of juvenile fish of a given age surviving from the annual egg production in a given year. Population dynamics theory predicts some form of saturating relationship between the number of recruits and the number of eggs produced, governed by an ecosystem carrying capacity for juveniles. Once egg production is sufficient to saturate the carrying capacity with surviving juveniles, further increases in egg production will, on average, produce no increase in recruitment.

Stock–recruitment relationships for individual fish stocks are routinely parameterized from historical time series of population demography derived from stock assessments. Typically, there is a high degree of variability in recruitment around any fitted relationship. However, provided this variability is stationary over time the fit can be used, together with data on growth and maturation rates, to estimate the long-term level of per-capita fishing mortality that can be sustained by the stock. In the case of North Sea cod, there is a well established relationship between deviations of recruitment from the stock–recruitment relationship fitted to historical data, and sea temperature and/or zooplankton abundance (O’Brien *et al.*, 2000; Beaugrand *et al.*, 2003; Clarke *et al.*, 2003; Olsen *et al.*, 2011). Warmer conditions lead to negative deviations in recruitment and vice versa. During the late 1960s and early 1970s, cold conditions associated with low values of NAO index were correlated with a sequence of positive recruitment deviations (Brander and Mohn, 2004), which led to the so called ‘gadoid outburst’ in the North Sea (Heath and Brander, 2001) during which stocks of cod and other major groundfish species increased to levels unprecedented in the 20th century. However, in a warming climate, such as has prevailed since the 1980s, the level of fishing mortality that can be sustained should decline. In fact, contrary to scientific advice (Cook *et al.*, 1997), fishing mortality rates for North Sea cod increased steadily from the 1970s to the early 2000s throughout a period of warming; the net result has been a progressive decline in the stock abundance (Cook and Heath, 2005). Nevertheless, calculations show that the North Sea cod stock could still support a sustainable fishery under a warmer climate but only at lower levels of fishing mortality (Cook and Heath, 2005).

Planque and Fredou (1999) analysed the response of cod recruitment deviations to temperature in different

stocks spanning the geographic range, showing positive responses at the northern limits (Barents Sea), and negative responses at the southern limits (North Sea). Planque and Fox (1998) also showed strong negative responses in the Irish Sea cod. Thus, there have been systematic changes in the productivity of cod across the latitudinal range of the species which, over time, should lead to a northwards shift in distribution without any active movement of fish, subject to regional patterns of fishing mortality. In addition, it is clear that the response of any species to temperature at a given location will depend critically on position relative to the latitudinal range. Hence, while recruitment deviations of cod in the North Sea have shown a negative correlation with temperature, deviations in saithe recruitment have shown positive deviations (Cook and Heath, 2005).

Although there has been a demonstrable correlation between recruitment deviations and temperature, this does not necessarily imply that temperature *per se* is the causative factor. Other aspects of the ecosystems inhabited by cod have changed in concert with temperature and these could be primarily responsible. In particular, the composition of the plankton on which cod larvae feed in each system has changed as the biogeographic boundary between the sub-polar and sub-tropical plankton communities in the north-east Atlantic have moved northwards by approximately 1000 km since 1960, in parallel with the warming of sea surface temperature (Beaugrand *et al.*, 2002; Beaugrand, 2003; Heath and Lough, 2007).

Further afield in the North Atlantic, Rose (2004) developed a surplus production model for the northern cod stock of Newfoundland which suffered a dramatic and well publicized collapse in the late 1980s. The model showed that the history of landing from the stock over approximately 500 years between 1505 and 2004, could not be explained solely in terms of either fishing or climate alone. However, a model incorporating both factors mimicked the observed landings history. The main features were (i) a climate-driven decline in production during the Little Ice Age (1300–1880), (ii) stock collapse in the 1960s due to overfishing, (iii) secondary collapse in the late 1980s due to the combined effects of fishing and climate, and (iv) subsequent failure to recover due to compensatory effects of very low abundances.

Fisheries are also postulated to have been involved in the northerly contraction of the spawning grounds of north-east Arctic cod (Opdal, 2010). In this case

the effect has been an indirect consequence of the truncation of the size and age structure of the population. Larger fish migrate greater distances and their selective removal over the past century has caused a reduced migratory capacity of the stock and gradual disappearance of southerly spawning areas. Again the shift has been in a direction that is parsimonious with climate change and while this explanation cannot be ruled out (Sundby and Nakken, 2008), the study of Opdal (2010) clearly suggests that fishing has played a role.

Notwithstanding the complex interactions described above, there is evidence for a widespread change in recruitment linked with temperature rises and climate change (Brunel and Boucher, 2007). This study looked at populations of cod, haddock, herring, Norway pout, plaice, saithe, sole, sprat, and whiting from the Arctic to the Celtic Sea. While many other factors had an effect, e.g. fishing pressure, results indicated that increased temperature was a significant driver.

EVIDENCE OF CLIMATE RESPONSES: CHANGES IN FISH FOOD WEBS

At the level of functional groups of species, the pelagic food web in the North Sea appeared to be under bottom-up control during the period 1973–2000, with significant positive correlations between zooplankton and planktivorous fish production, and between planktivorous and pelagic piscivorous fish production (Heath, 2005a). Similarly, Frederiksen *et al.* (2006) demonstrated that, off the Scottish east coast in the north-western North Sea, the food web 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 versus top-down control for shelf ecosystems around the North Atlantic. However, at the same time, the evidence suggested that the benthic food web was probably under top-down control, with a highly significant negative correlation between the consumption of macrobenthos by demersal fish and the production of macrobenthos carnivores (Heath, 2005a). Thus, within the same geographic domain, different branches of the food web displayed fundamentally different control mechanisms and hence potential responses to climate change. Increases in the abundance and fishery landings of, in particular, Norway lobster and brown shrimp since the 1970s are

attributed to the reduction in top-down predation by cod and whiting as a result of the combined fishing and climate effects on these fish species (Engelhard and Pinnegar, 2010; Hufnagel and Temming, 2010).

A key factor that may dictate whether a system is prone to top-down or bottom-up control may be species redundancy, 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 (2005a) noted that sprat, herring, sandeels, and Norway pout (*Trisopterus esmarkii*) 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 and possibly sandeel production expanded to fill the food web niche vacated by herring, but reversed in the 1980s as herring stocks recovered (Cushing, 1980).

Elsewhere, reversibly alternating control of fish food webs has been demonstrated in the north Pacific. Control of the food web along the shelf south of the Alaska Peninsula which was bottom-up in the early 1970s (as indicated by positive correlations between prey, mainly shrimp and capelin, and predators, mainly Pacific cod (*Gadus macrocephalus*)), shifted to top-down control during the late 1970s, coincident with a rise in temperature, and then reverted to bottom-up control (Litzow and Ciannelli, 2007). The oscillation between control processes coincided with a change in state of the ecosystem: 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 Pacific 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 Pacific cod.

The lesser sandeel is a key component of the food web in waters around northern Britain, linking primary and zooplankton production to top predators including piscivorous fish, birds, and mammals. Changes in sandeel abundance can therefore precipitate effects throughout the food web. Sandeel

recruitment in the southern North Sea has been negatively correlated with high winter sea temperature (Arnott and Ruxton, 2002) although the exact mechanism through which temperature might affect sandeel recruitment remains unclear. Apart from a direct effect of temperature on some aspect of the sandeel life history, regulation through changes in the abundance of zooplankton is also a plausible explanation. Sandeels feed mainly on zooplankton, and there has been a marked decline in the growth rate of sandeels in the north-western North Sea, with consequential delayed maturation (Wanless *et al.*, 2004; Boulcott *et al.*, 2007; Boulcott and Wright, 2008). Other possibilities include predation control by fish that consume sandeel larvae (Frederiksen *et al.*, 2007). Still further possible mechanisms involve changes in the dispersal patterns of larvae from spawning sites to settlement sites for juveniles which have a direct effect on survival and recruitment (Proctor *et al.*, 1998; Christensen *et al.*, 2008), and changes in seasonal behavioural patterns of sandeels, in particular the time they spend buried in sediments, in relation to temperature and the timing of the spring plankton bloom, both of which are subject to climate trends (Greenstreet *et al.*, 2006; Scott *et al.*, 2006).

PREDICTING THE IMPACT OF FUTURE CLIMATE CHANGE ON FISH AND SHELLFISH

The consensus of coupled global ocean-atmosphere models is for rising sea temperatures and acidity over the coming 50 years, under a wide range of plausible greenhouse gas emission scenarios. The models that deliver these predictions are essentially based on fundamental principles of physics and chemistry rather than empirical relationships. However, there is currently no equivalent understanding of biological and biochemical processes that permits us to build models to predict future patterns and abundances of fish and shellfish communities in response to climate change, though this may be possible for certain key species. In general, predictions must be founded on empirical or statistical relationships derived from observations of recent distributions.

General expectations for the impact of climate change on marine fauna stem from the observed global scale decrease in species richness with increasing latitude in both hemispheres. Inevitably, this means that spatial observations of species richness correlate with annual average temperature on a global basis even if this is not necessarily a cause and effect

relationship, and climate envelope models based on spatial data predict a poleward shift in levels of species richness with warming, i.e. increasing species richness at high latitudes. In some localities, recent rises in fish species richness over time seem to bear out this interpretation (e.g. southern North Sea (Hiddink and ter Hofstede, 2008) and Celtic Sea (ter Hofstede *et al.*, 2010). During warmer periods, southern species have tended to become more prominent and northern species less abundant in European waters, and vice versa. However, as this review has shown there are also many instances where this is not the case owing to a range of other factors, with differences between regions reflecting the ocean circulation patterns, availability of essential fish habitat, exploitation, and biogeographic history before and since the last glaciation. Nevertheless, with additional constraints imposed by statistical associations between species and habitats (e.g. bathymetry, coral, sea-ice cover), the approach has been used to predict global spatial redistributions of species richness that may be anticipated as a result of changes in sea temperature estimated by ocean–atmosphere models under greenhouse gas emission scenarios (Cheung *et al.*, 2008, 2009).

Climate envelope interpretations of redistributions of fish species richness have not been formally tested at global, regional or local scales by comparing hindcasts with observations. This review suggests that at regional and local scales we might expect mixed or low success rates in such tests because richness is not necessarily a fundamental property of a community, rather the dynamic outcome of adaptations and responses of individual species to the combination of exploitation patterns and environmental conditions (Simpson *et al.*, 2011). At these scales, a more fruitful approach may be to develop models of the spatial population dynamics of key species from groups that show similar biological characteristics and hence may respond in similar ways to environmental change. Ellis *et al.* (2010) collated an inventory of all fish species recorded in north-east Atlantic trawl surveys and classified them according to biogeographic affinity (Mediterranean, Boreal (northern, cold water), Lusitanian (southern, warm water), Atlantic), reproductive strategy, maximum body length, trophic level, and habitat, referring to the resulting groupings as ‘ecotypes’ (Table 1). Such models might be developed either as stand-alone single species, or networks of species in food web models (Speirs *et al.*, 2010).

Several authors have attempted climate predictions for individual species by linking particle tracking

models forced with the outputs from Global Climate Models, to biological sub-routines which replicate the behaviour/characteristics of eggs, larvae, juveniles or adults, and are parameterized using the piecemeal laboratory data that does exist. One example of this approach is the study of Peck *et al.* (2009), which used outputs from the biophysical circulation model HAMSOM, connected to detailed routines aimed at simulating the drift, distribution and development of fish eggs and larvae in the North Sea. For cod in the North Sea, Peck *et al.* (2009) found that negative NAO years were associated with relatively low sea temperatures and relatively large egg/larvae distribution areas (+400% of the initial spawning area). By contrast, the most positive NAO years (which were also the warmest) were characterized by particle retention in a relatively small ellipse area around the spawning site. Similarly in sprat, years with a high NAO index (>1.5) had the smallest distribution ellipse (~145% initial release area) but these years were not necessarily the warmest. The authors argue that future climate change will probably inhibit the dispersal of fish eggs and larvae throughout the North Sea, and this could have significant implications for larval survival if insufficient planktonic food resources are available to support the further development of these animals. Hufnagl and Peck (2011) used the same methodology to look at climate-driven constraints on larval survivorship and development in Atlantic herring. This study suggested that climate-driven changes in bottom-up factors will affect spring- and autumn-spawned larvae in different ways. It is unlikely that autumn-spawning herring will be able to avoid unfavourable conditions by delaying their spawning time or by utilizing more northern spawning grounds because of limitations in day-length to larval growth and survival. Conversely, earlier spawning in spring, or later, midsummer spawning will be tightly constrained by match–mismatch dynamics between larvae and zooplankton production.

The above species-specific modelling approaches focus on early life history stages, but for a complete assessment of the responses of fish to climate change, models need to represent the whole life cycle. This means that they need to simulate the active migration behaviours and habitat preferences of juvenile and adult fish, as well as the passive dispersal of eggs and larvae. So far, few spatial models of population dynamics have achieved this (Andrews *et al.*, 2006; Heath *et al.*, 2008). Key missing information is a clear understanding of the factors determining fish migrations. However, recent studies using data-storage

Table 1. Examples of ecotypes of North Sea fish (adapted from Ellis *et al.*, 2010)

Biogeographic affinity: Atlantic			
Horizontal habitat	Vertical habitat	Trophic guild	Example species
Oceanic (occasional or periodic vagrants)	Epipelagic	Planktivores	Saurey pike, sunfish
		Scavenger	Pilotfishdh
Slope	Mesopelagic	Piscivores	Dealfish, Ray's bream
		Planktivores	Orafish, louver
	Bathydemersal	Large piscivores	Six-gill shark, kitefin shark
		Large benthivores	Rabbitfish
Shelf	Bethopelagic	Piscivores	Black scabbardfish
		Planktivores	Blue whiting
	Bathypelagic	Planktivore	Pearlside
	Demersal	Scavenger	Hagfish
Coastal	Benthopelagic	Benthivore	Pufferfish
	Pelagic	Planktivore	Basking shark
		Piscivore	Porbeagle, Atlantic mackerel
	Demersal	Bentho-piscivore	European eel
Biogeographic affinity: Boreal			
Horizontal habitat	Vertical habitat	Trophic guild	Example species
Slope	Demersal	Piscivore	Norwegian skate, ling, halibut
	Benthopelagic	Piscivore	Greenland shark
Shelf		Planktivore	Greater argentine
	Pelagic	Plankto-piscivore	Redfish
	Demersal	Piscivore	Starry ray, saithe
		Ectoparasite	Sea lamprey
Coastal		Bentho-piscivore	Bullrout, long-rough dab
		Benthivore	Haddock, pogge, Norwegian goby, plaice, witch
	Reef associated	Benthivore	Guillet's goby, diminutive goby
	Bentho-pelagic	Piscivore	Spurdog
		Bentho-piscivore	Lumpsucker
		Plankto-benthivore	Norway pout
		Plankto-piscivore	Jellycat
		Planktivore	Herring, lesser sandeel
	Demersal	Piscivore/ectoparasite	River lamprey
		Benthivore	Three-spined stickleback
		Planktivore	Whitefish
	(Bentho) Pelagic	Piscivore	Char
		Benthivore	Smelt
Biogeographic affinity: Lusitanian			
Horizontal habitat	Vertical habitat	Trophic guild	Example species
Slope	Demersal	Bentho-piscivore	Black-mouth dogfish
		Planktivore	Boarfish
Shelf	Pelagic	Planktivore	Silvery pout
	Demersal	Piscivore	Angel shark, cuckoo ray, whiting, turbot
		Bentho-piscivore	Thornback ray, greater forkbeard, lesser weeverfish
		Benthivore	Smoothhounds, grey gurnard, dragonets, sole
	Reef-associated	Piscivore	Greater spotted dogfish, conger eel
		Benthivore	Tompot blenny, triggerfish
	Benthopelagic	Piscivore	Tope, John dory, seabass
		Benthivore	Eagle ray
Coastal		Planktivore	Lesser argentine
		Herbivore	Saupe
	Pelagic	Piscivore	Garfish, horse mackerel
		Planktivore	Sprat, anchovy, shad, crystal goby
	Demersal	Benthivore	Rock goby, flounder
		Planktivore	Sea-horse, greater pipefish
	Reef-associated	Piscivore	Moray eel
		Benthi-piscivore	Cuckoo wrasse
		Benthivore	Ballan wrasse
	(Bentho) Pelagic	Benthivore	Sand smelt
		Omnivore	Bogue
		Detritivore	Grey mullet

tags, genetics, and analyses of otolith microstructure and chemistry (Hutchinson *et al.*, 2001; Wright *et al.*, 2006b; Elsdon *et al.*, 2008; Righton *et al.*, 2010), have begun to unravel the behavioural and physiological processes that dictate the distribution and production

of fish species. These types of study seem to offer the most promising way of determining the reactions of fish to changing climate conditions in sufficient detail for us to incorporate these processes into species-specific models and more accurately predict future responses.

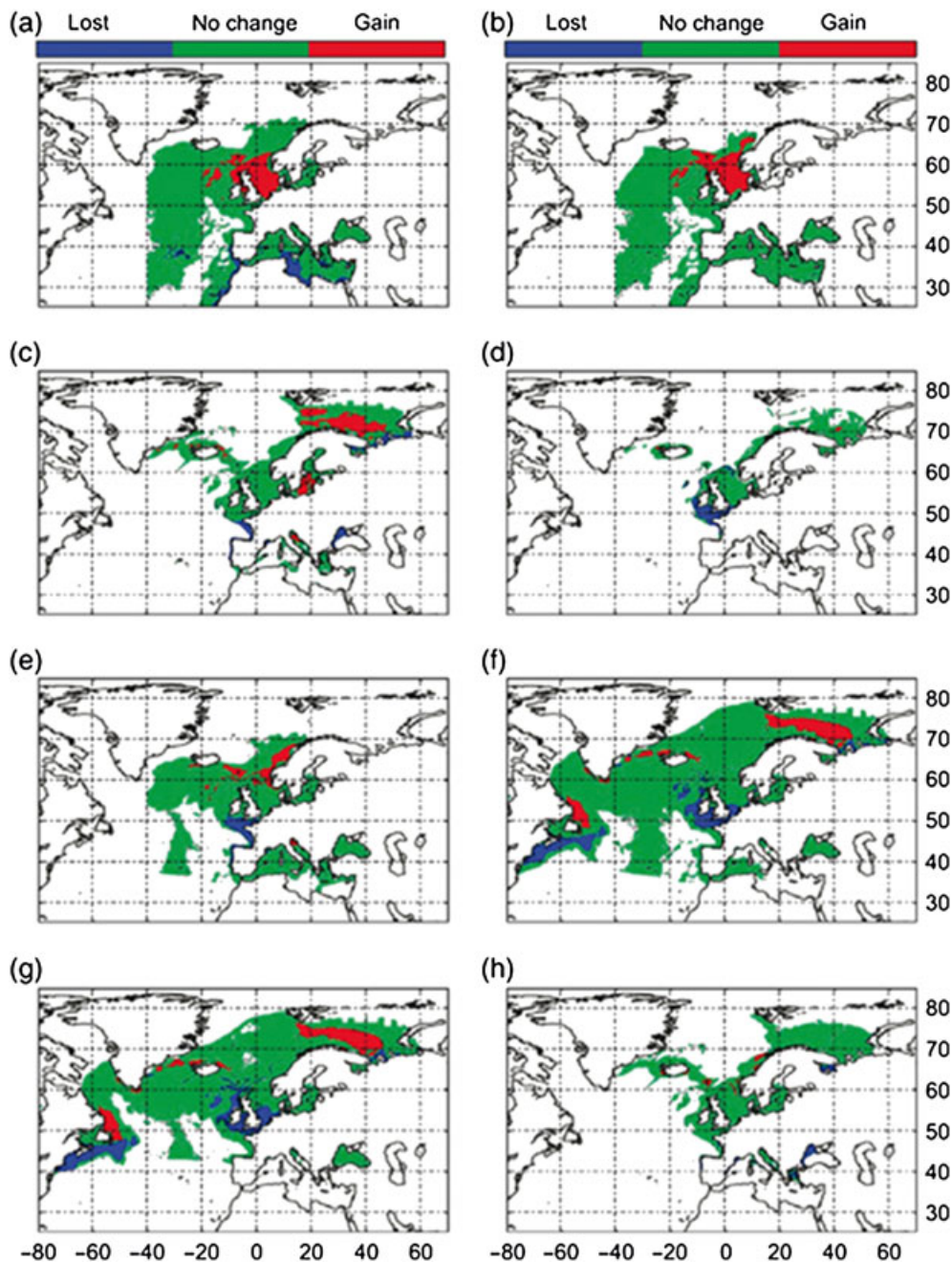


Figure 8. Reproduced from Lenoir *et al.* (2011). Maps showing areas where a substantial increase (in red) or decrease (in blue) in the probability of occurrence (changes >0.2) is expected between the 2090s and the 1960s. Green areas denote no substantial change or changes <0.2 . (a) Atlantic horse mackerel, (b) European anchovy, (c) European sprat, (d) pollack, (e) common sole, (f) haddock, (g) saithe and (h) turbot.

PROGNOSIS FOR IMPACTS OF CLIMATE CHANGE ON FISH IN BRITISH WATERS

Aside from global-scale climate envelope forecasts of marine species richness under future elevated sea temperature conditions (Cheung *et al.*, 2008, 2009), only one quantitative forecast of changes in fish species distributions or community characteristics resulting from ocean–atmosphere model predictions of marine environmental conditions under greenhouse gas emission scenarios has been published that covers

British waters (Lenoir *et al.*, 2011). The authors applied a non-parametric probabilistic ecological niche model (NPPEN) with multiple explanatory variables (sea surface temperature and salinity, and bathymetry) to predict the 2090s distributions of eight fish species in the north-east Atlantic. The forecast (Figure 8) was that by the 2090s horse mackerel and anchovy should show an increased probability of occurrence in northern British waters compared with the 1960s, pollack, sole, haddock, and saithe should show a decrease in southern British waters, and turbot and

sprat should show no significant change in probability ($-0.2 - +0.2$) anywhere in British waters. This example represents the most sophisticated effort to date to predict future fish distributions, but still does not incorporate any representation of the documented shift of demersal taxa into deeper water since it does not include near seabed temperatures, nor of the scope for fishing intensity or food web effects to modify the impacts of climate change. In addition, there is currently no basis on which to assess the role of acidification in future fish distributions. So, conclusions on likely future consequences of climate change for fish and shellfish in general can only be qualitative at this stage.

As we have demonstrated, fish species have exhibited a range of distributional changes in the waters around the UK and Ireland, which in some cases can be traced back over centuries. For seabed-living demersal fish the depth ranges over which Boreal species have been distributed, at least since the 1980s, have deepened by around 10 m per decade, roughly tracking a deepening of the seasonal isotherms. However, at the scale of UK and Irish waters, deepening does not necessarily equate to poleward shifts in distribution owing to the complex bathymetry. If the recent responses of fish represent a precedent for the future, then we would expect to see a continuation of the colonization of the rapidly warming southern North Sea and Celtic Sea regions by Lusitanian demersal species (e.g. sea bass), and a retreat of Boreal species into the deeper parts of UK waters in the northern North Sea, since average near-seabed temperatures are predicted to increase by more than 2.5°C in the southern North Sea by 2080, and by $1\text{--}2^{\circ}\text{C}$ in the northern North Sea. It is not possible to be more specific because of variations in habitat preferences and sensitivities to prey and environmental conditions of individual species, the possible role of food web effects, and particularly the extent of future fisheries.

Distributions of some pelagic fish have shown the most pronounced latitudinal responses to seasonal sea temperatures in the historical records from the north-east Atlantic (e.g. cycles of herring and sardine abundance related to temperature). Hence we might expect clearer latitudinal shifts in pelagic fish distribution over the coming century than for demersal fish. The poleward flowing shelf edge currents which carry warm water into high latitudes are particularly important in this respect and have enabled southern species (e.g. anchovy, horse mackerel) to appear in both the English Channel at the southern entrance to

the North Sea, and off the north of Scotland at the open northern boundary, leading to more complicated distributional changes than might be expected simply from a latitudinal range shift.

We should be especially concerned with identifying species that appear to be unable to respond to warming by adapting their distributions due to strict habitat association, because it is likely it is they that will suffer the most significant impacts and threat of local extinction. In British waters, the most critical of these is the lesser sandeel, which is a key link in the food web. Unlike many other fish species, sandeels are not free to move into deeper waters in response to warming sea temperatures because they are tightly associated with coarse sandy sediments (Holland *et al.*, 2005). The pattern of declining recruitment to sandeel populations all around northern Britain since 2002, which is inversely correlated with temperature, suggests that the productivity and hence the capacity to sustain exploitation and support predator populations is likely to decline in the future with a warming climate.

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