Journal of Fish Biology (2009) **74,** 1143–1205
doi:10.1111/j.1095-8649.2009.02180.x, available online at http://www.blackwell-synergy.com

REVIEW PAPER

Implications of climate change for the fishes of the British Isles

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(Received 6 May 2008, Accepted 2 November 2008)

Recent climatic change has been recorded across the globe. Although environmental change is a characteristic feature of life on Earth and has played a major role in the evolution and global distribution of biodiversity, predicted future rates of climatic change, especially in temperature, are such that they will exceed any that has occurred over recent geological time. Climate change is considered as a key threat to biodiversity and to the structure and function of ecosystems that may already be subject to significant anthropogenic stress. The current understanding of climate change and its likely consequences for the fishes of Britain and Ireland and the surrounding seas are reviewed through a series of case studies detailing the likely response of several marine, diadromous and freshwater fishes to climate change. Changes in climate, and in particular, temperature have and will continue to affect fish at all levels of biological organization: cellular, individual, population, species, community and ecosystem, influencing physiological and ecological processes in a number of direct, indirect and complex ways. The response of fishes and of other aquatic taxa will vary according to their tolerances and life stage and are complex and difficult to predict. Fishes may respond directly to climate-change-related shifts in environmental processes or indirectly to other influences, such as community-level interactions with other taxa. However, the ability to adapt to the predicted changes in climate will vary between species and between habitats and there will be winners and losers. In marine habitats, recent changes in fish community structure will continue as fishes shift their distributions relative to their temperature preferences. This may lead to the loss of some economically important cold-adapted species such as *Gadus morhua* and *Clupea harengus* from some areas around Britain and Ireland, and the establishment of some new, warm-adapted species. Increased temperatures are likely to favour cool-adapted (*e.g. Perca fluviatilis*) and warm-adapted freshwater fishes (*e.g.* roach *Rutilus rutilus* and other cyprinids) whose distribution and reproductive success may currently be constrained by temperature rather than by cold-adapted species (*e.g.* salmonids). Species that occur in Britain and Ireland that are at the edge of their distribution will be most affected, both negatively and positively. Populations of conservation importance (*e.g. Salvelinus alpinus* and *Coregonus* spp.) may decline irreversibly. However, changes in food-web dynamics and physiological adaptation, for example because of climate change, may obscure or alter predicted responses. The residual inertia in climate systems is such that even a complete cessation in emissions would still leave fishes exposed to continued climate change for at least half a century. Hence, regardless of the success or failure of programmes aimed at curbing climate change, major changes in fish communities can be expected over the next 50 years with a concomitant need to adapt management strategies accordingly.

Key words: biogeographical shifts; climate change; ecological change; estuarine; fresh water; marine.

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INTRODUCTION

Climate change is considered to be one of the principal threats to biodiversity and to the structure and functioning of ecosystems (McCarthy *et al.*, 2001). Although the causes and likely effects are subject to debate (Sharp, 2003), the scientific consensus is that climate change is real (Houghton *et al.*, 2001; Walther *et al.*, 2005) and will affect the British Isles (Hulme *et al.*, 2002; Sweeney *et al.*, 2003). Average global temperatures have increased by *c.* 0·6° C over the past century (Houghton *et al.*, 2001; Hulme *et al.*, 2002). During this period, both marine (Levitus *et al.*, 2000) and freshwater systems (Winder & Schindler, 2004) have warmed. Over geological time, climate has varied (Crowley, 1983), influencing the distribution and suitability of habitats, which in turn have influenced the distribution and dispersal of species (Cox & Moore, 1993). It is therefore realistic to expect that further climate change will have a strong controlling effect on habitats, communities, species and individual organisms in the future (Levitus *et al.*, 2000; Parmesan & Yohe, 2003; Root *et al.*, 2003).

Britain and Ireland have a temperate marine climate, which because of the strong influence of the North Atlantic Drift prevent the climatic extremes more typical of the latitudes (49–61° N) in which these islands are located (Barrow & Hulme, 1997). The marine, freshwater and estuarine ecosystems of Britain and Ireland vary considerably with regard to physical form, chemistry and biology (Ladle & Westlake, 1995; Reynolds, 1998; Hughes *et al.*, 2004). The seas surrounding Britain and Ireland are diverse in terms of bathymetry (Lee & Ramster, 1981), *e.g.* maximum depths are only *c.* 50 m in the southern North Sea (Zijlstra, 1988) but 300 m to the south-west of England and >1000 m deep to the west and north of Scotland where the continental shelf drops away into the abyssal plain of the north-east Atlantic (Lee & Ramster, 1981).

Britain and Ireland have a temperate, wet maritime climate (Hulme & Barrow, 1997), and as such, freshwater habitats are a characteristic feature of the often-heterogeneous landscape (Ladle & Westlake, 1995; Reynolds, 1998). Many freshwater and brackish systems have undergone human modification and have been degraded from natural conditions including hydrological alterations (Ladle & Westlake, 1995) and pollution (Haygarth & Jarvis, 2002). The seas around Britain and Ireland have also been subject to human disturbances, including overfishing (Hutchings, 2000; Cushing, 2003) and significant inputs of anthropogenic pollutants, including nutrients and other contaminants (Stapleton *et al.*, 2000; Matthiessen & Law, 2002). Although fish and other marine biota were affected by anthropogenic pollution (Stapleton *et al.*, 2000), recent studies indicate that conditions in the seas around Britain and Ireland have improved following changes in industrial activity (Matthiessen & Law, 2002).

Global climate change represents a further stress on fish that are already subject to a series of natural and anthropogenic stressors (Allan & Flecker, 1993): species introductions (Winfield, 1992; Youngson & Verspoor, 1998), pathogens and disease (Bakke & Harris, 1998; Marcogliese, 2001), predation (Birkeland & Dayton, 2005); poor catchment management (Allan, 2004), prey availability in both freshwater and marine environments (Vander Zanden *et al.*, 1999; Heath, 2005), intensive aquaculture (Gross, 1998), overfishing (Hutchings, 2000), river obstacles such as dams and weirs (Crisp, 1993), pollution (Alabaster & Lloyd, 1980), drought (Magoulick & Kobza, 2003) and water extraction (Collares-Pereira *et al.*, 2000). Often, these factors work in concert to affect a fish population (Parrish *et al.*, 1998). Accelerating climate change will probably further compound adverse anthropogenic effects on fish populations (Schindler, 2001), as it is another stress agent.

The biogeographical location of Britain and Ireland (Ekman, 1953; Maitland & Campbell, 1992) may lead to further complications in predicting the response of fishes to climate change. For instance, populations located at extremes of a species' distribution can display increased interannual variation in abundance when compared with populations found at the centre of their distribution (Myers, 1998; but see Sagarin *et al.*, 2006). Britain and Ireland represent the western extreme of the distribution of many freshwater fishes, and these species may therefore show unpredictable responses to climate change. Shifts in the distribution of fish species may lead to significant disruption for resident fish communities. For instance, invasion by non-native fishes might lead to native species becoming extirpated or affected directly through predation (Kaufman, 1992) or indirectly following ecological shifts, *e.g.* in food webs (Vander Zanden *et al.*, 1999) or following the introduction of novel parasites or pathogens (Marcogliese, 2001; Gozlan *et al.*, 2005), which may be more harmful to fishes stressed following environmental change (Lafferty & Kuris, 1999).

CLIMATE CHANGE

Although climate can change because of natural phenomena, there is now convincing evidence for a growing human influence on global climate. The predicted rate of climatic change, especially in temperature, is such that it will exceed any that has occurred over recent geological time. The International Panel on Climate Change (IPCC) bases its prediction on a series of different climate change models (Houghton *et al.*, 2001). The climate change scenarios reported by Hulme *et al.* (2002) were generated by the Hadley Centre Coupled Model, version 3 (HadCM3) climate model, which generates results at a regional scale of 50 km across the British Isles, which compares favourably with spatial resolution of 250–500 km of other global models. The improved spatial resolution results in more credible representations of changes in extreme weather than in previous models (Hulme *et al.*, 2002). Recent changes in several major components of climate in the British Isles and future predictions are detailed in Table I. It is important to note that since climate change over this period has already been determined by past and current emissions differences (Hulme *et al.*, 2002), differences between emission scenarios have relatively little effect on the climate that will be experienced over the next 30–40 years.

THE ECOLOGICAL EFFECTS OF CLIMATE CHANGE

Fish, as individuals, populations or communities, experience climate through temperature, winds, currents and precipitation (Ottersen *et al.*, 2001, 2004). The present ichthyofauna of Britain and Ireland and the surrounding seas reflect the effects of climate change experienced in the past (Wheeler, 1969, 1977). Understanding how climate change will affect the planet is a key issue

TABLE I. Recorded and predicted climate change in Britain and Ireland (Hulme *et al.*, 2002)

	Recorded climatic change	Predicted climatic change
Temperature	Temperature in central England 0·5° C warmer in the 1990s compared with the 1961–1990 average Thermal growing season is longer at present than at any time since records began in 1772 (328 days in Central England in 2000)	A north-west to south-east gradient in the magnitude of the average climate warming across Britain and Ireland (H*). Temperature increases greater in summer and autumn than in winter (L) and spring (L). Temperature in the south-east of Britain will rise in excess of 4° C by the 2080s (H). The thermal growing season is predicted to lengthen significantly (H), and it is likely that occasional years with year-round terrestrial thermal growing seasons will occur before the 2080s
Precipitation	Winters have become wetter and summers drier Intensity of short-duration precipitation increased in winter and decreased in summer Despite an increase in winter precipitation over high ground, less is falling as snow because of increase in temperature	Significant seasonal shift in precipitation pattern forecast. Winter precipitation anticipated to increase by 5–30% (H) with up to 50% less rain in summers (M). There is a south-east to north-west gradient in the magnitude of this average precipitation change. Snowfall will decline in all regions but particularly in the north of Britain and Ireland (H)
Wind circulation patterns and gales	Increasing positive NAO† resulting in more westerly winds and therefore milder and wetter weather	Areas off the south and east coast of England will experience the greatest wind speed increases in winter and spring (2–8%). In summer and autumn, wind speed expected to decrease especially in the Irish Sea and Atlantic coast of Ireland
Marine climate	No long-term trends in salinity 0·6° C rise in sea temperature in the past 70–100 years. Summer temperatures in the relatively shallow North Sea, however, warmed by 1·5° C since 1985, 3× the global warming rate expected in the 21st century, with summer temperatures rising significantly faster than other seasons (Mackenzie & Schiedek, 2007)	All coastal waters will warm, especially shallower areas such as the North Sea and English Channel, with temperatures rising by up to 3° C by the 2080s (H). Average sea surface temperatures in these areas will exceed the current mid-August to mid-September maximum for a 5 month period from mid-June to mid-November

TABLE I. Continued

	Recorded climatic change	Predicted climatic change
Sea level	Sea level rose on average around Britain and Ireland by 1 mm during the 20th century	Sea levels will rise from 23 to 36 cm by the 2080s but increase will be greatest in the south compared with the north. This is because of natural land movements and regional variations in the rate of climate-induced sea level rises
Wave height	Large temporal and spatial variation but has generally increased	Storm surges to increase around Britain and Ireland with the greatest increases off south-east England
North Atlantic Drift	Overall Atlantic circulation system may be weakening (but see Hansen *et al.*, 2001, 2004; Bryden *et al.*, 2005 for further details)	May weaken slightly (Bryden *et al.*, 2005), but this is unlikely to lead to cooling as increased greenhouse gas heating exceeds the cooling effect (M–H)

*This relates to the relative confidence levels assigned by the UKCIP02 authors to each prediction: H, high; M, medium and L, low.

†Many aspects of U.K. winter climate are strongly influenced by the North Atlantic Oscillation (NAO) (Hulme *et al.*, 2002) as it is the dominant mode of atmospheric behaviour in the North Atlantic (Hurrell, 1995) and is considered a proxy for a variety of climatic processes (Ottersen *et al.*, 2001; Brander & Mohn, 2004). The NAO is an alteration in the pressure difference between the subtropical atmospheric high-pressure zone centred over the Azores and the atmospheric low-pressure zone over Iceland (Hurrell, 1995; Ottersen *et al.*, 2001). In years when the NAO is positive, the airflow across Britain and Ireland is more westerly and therefore winters are windier and wetter but also milder with cold winters in Canada and Greenland (Hulme & Barrow, 1997). When the NAO is negative, winds weaken, resulting in drier, less windy and colder weather (Hurrell, 1995; Hulme & Barrow, 1997). Understandably, variation in the NAO is linked to variation in many biological systems. The NAO index is predicted to become more positive (L), with considerable year-to-year variability, and the increase in the NAO index is predicted to become significant (*i.e.* larger than natural variability), by the 2050s. This will, on the basis of the present day relationship between winter weather in Britain and Ireland and the NAO, result in milder, windier and wetter weather, which is consistent with the other predictions described above (Hulme *et al.*, 2002). The thermal growing season (which does not take account of day length or water availability) is predicted to lengthen substantially (H), increasing on a south-east to north-west gradient, and it is likely that occasional years with year-round terrestrial thermal growing seasons will occur before the 2080s (Hulme *et al.*, 2002).

worldwide (Houghton *et al.*, 2001; McCarthy *et al.*, 2001; Hays *et al.*, 2005). Although species have encountered and responded to climatic changes throughout their evolutionary history (Crowley, 1983; Cox & Moore, 1993), a primary concern for wild species and their ecosystems is the rate of climate change (Root *et al.*, 2003) with the rate of temperature increase predicted for the future to exceed any seen in the past 10 000 years (Houghton *et al.*, 2001).

Climate profoundly influences ecological processes in a number of direct, indirect and complex ways (Friedland *et al.*, 2000; Ottersen *et al.*, 2001, 2004). A number of complementary processes may be acting on a fish population or aquatic ecosystem (Ottersen *et al.*, 2004), *e.g.* exploitation and climate change (Beaugrand *et al.*, 2003; Heath, 2005). Furthermore, climate-induced changes may act on several aspects of the ecology of fish (Friedland *et al.*, 2000; Clark *et al.*, 2003) and their interactions with biotic and abiotic environments [see Schiedek *et al.* (2007) for a review of interactions between climate change and contaminants]. Consequently, predicting the outcomes of environmental change on fish populations is complex (Planque & Frédou, 1999).

Climate change will affect aquatic taxa at all levels of biological organization: molecular, cellular, individual, population, species, community and ecosystem level. The response of fishes, and other aquatic taxa, will vary according to their individual tolerances and life stage and are complex and difficult to predict (Fig. 1). Fishes may respond directly to climate-change-related shifts in environmental processes or indirectly to other influences, *e.g.* changes in land-use (Conlan *et al.*, 2005) or community level interactions with other taxa, including predators, prey, parasites and competitors (Marcogliese, 2001; Ottersen *et al.*, 2001; Harvell *et al.*, 2002). The combined effect of these proximate responses leads to emergent ecological responses, including shifts in community structure and distributional changes, which, if significant, could lead to changes in ecosystem function.

FISH AND CLIMATE

Temperature has long been recognized as a major influence on the ecology and physiology of fish (Fry, 1947, 1971; Magnuson *et al.*, 1979). Temperature directly controls metabolic processes and, besides food availability, is the single most important factor that determines growth rates in fish (Fry, 1971; Brett, 1979; Elliott, 1994). As temperature decreases, metabolic processes get slower and maximum food intake will decrease, regardless of prey availability (Michalsen *et al.*, 1998). As temperature increases, metabolism and energy demands increase and may increase to a point where energetic inputs from food are insufficient and fish have to utilize stored energy reserves (Fry, 1971; Otterlei *et al.*, 1999). If food supply is limited, growth rates may be higher at lower temperatures than in warmer areas because of reduced metabolic costs (Elliott, 1994). Activity is strongly linked with ambient temperatures (Neuman *et al.*, 1996), which can further influence foraging behaviour and efficiency, and changes in water temperature may affect interspecific interactions, *e.g.* predation and competition (Persson, 1986). Fishes have evolved to fit distinct thermal niches where they are able to optimize physiological, ecological and reproductive performance (Coutant, 1987*b*; Magnuson & Destasio, 1997).

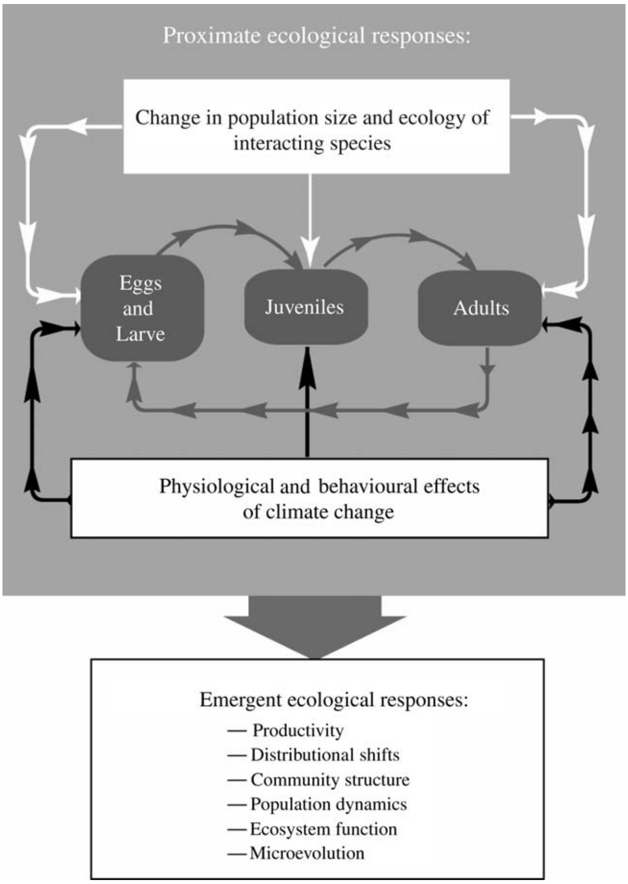

FIG. 1. Conceptual diagram detailing potential ecological responses to climate change of a typical fish. Abiotic changes will lead to physiological and behavioural shifts in individual fish, which will influence their performance in community and population-level interactions. Hence, climate change will potentially influence the ecology of individuals, populations and communities, and these combined effects could result in emergent responses, *e.g.* changes in ecosystem function, community structure and the overall productivity of aquatic systems [redrawn from Harley *et al.* (2006), reproduced with permission from John Wiley & Sons].

Temperature, however, can affect fish at multiple levels. Enzymatic rates are strongly temperature dependent in fish; hence, temperature is a key determinant of an individual's physiological and biochemical (vital) rates (Fry, 1971; Coutant, 1987*b*; Regier *et al.*, 1990) and influences behaviour (Sims *et al.*, 2006). Temperature variation influences almost all aspects of fish physiology and ecology, *e.g.* hatching and development of eggs and larvae (Guma'a, 1978), activity (Koch & Wieser, 1983), oxygen demand (Clarke & Johnston, 1999), swimming performance (DiMichele & Powers, 1982), distribution (Coutant, 1987*b*), growth (Brander, 1995), maturation (Svedäng *et al.*, 1996), immune function (Le Morvan *et al.*, 1998), the phenology of migration (Sims *et al.*, 2004), foraging rate (Elliott & Leggett, 1996; van Dijk *et al.*, 2002), production (Schlesinger & Regier, 1982), reproductive success (Planque & Frédou, 1999), availability of prey (Heath, 2005), predation risk (Elliott & Leggett, 1996) and mortality (Fry, 1971; Griffiths & Harrod, 2007).

Understandably, temperature is considered as a fundamental component of the niche of fishes (Magnuson *et al.*, 1979; Magnuson & Destasio, 1997). Some fishes are capable of detecting and responding to extremely small temperature variations, with estimates as low as 0·001° C (Brown, 2003), and fish tend to select thermal habitats that maximize their growth rate (Magnuson *et al.*, 1979). Clearly, with such an important influence on the individual biology of fish, temperature often has a strong effect on fishes at population (Mills & Mann, 1985) and community levels (Persson, 1986; Southward *et al.*, 1988). Predicting the effects of temperature change on fish is difficult because of the huge variation in possible responses that individuals can exhibit, and the potentially confounding influence of many other physiological or environmental factors (Fry, 1971; Burton, 1979).

Although the bulk of research on the likely effects of climate change on fish has rightly concentrated on the role of temperature, temperature is only one of a complex assemblage of climatic variables that individually or together will drive future ecological change in aquatic ecosystems (Harley *et al.*, 2006). For instance, the solubility of oxygen in water is strongly temperature dependent (Weiss, 1970) and increases in water temperature following climate change will be paralleled by reductions in dissolved oxygen concentrations and therefore the carrying capacity of aquatic systems. Fishes vary considerably in their dissolved oxygen requirements, both between species and different life stages (Alabaster & Lloyd, 1980), but oxygen demands increase as metabolic rates rise with temperature (Pörtner, 2001). Reductions in oxygen concentrations following increases in temperature forced by climate change will influence many aspects of the ecology of fish, *e.g.* habitat use and behaviour (Coutant, 1987*b*), reproductive success (Coutant, 1987*a*), capacity for growth (Brett, 1979), activity (Domenici *et al.*, 2000) and predation risk (Headrick & Carline, 1992).

Other facets of climate change will influence many environmental factors with the potential to affect fish, *e.g.* cloud cover, ultraviolet (UV) radiation, sea and lake levels, storm surges, hydrographic regimes in estuaries, precipitation, runoff, wind intensity and patterns, evaporation, river and stream discharge (Fig. 2). Changes in temperature and other abiotic factors are likely to result in changes in interspecific interactions (*e.g.* predation, competition and parasitism), which will further influence the response of fish and other taxa to climatic change (Davis *et al.*, 1998) and greatly complicates the process of making reliable predictions.

Aquatic ecosystems by definition require water (Hughes & Morley, 2000), but the quantity and quality of available water resources can vary spatially and temporally. Recent droughts in Britain demonstrated that freshwater resources are under significant pressure and that currently supplies have to fulfil the demands of multiple end users (*e.g.* agriculture, industry and household supplies) as well as natural ecosystems (Arnell, 1998; Hughes & Morley, 2000). Climate change predictions for Britain and Ireland (Table I) suggest changes in abundance and frequency of precipitation (Hulme *et al.*, 2002), including an increased frequency in droughts, and these changes will undoubtedly affect fishes, both in fresh water and in habitats receiving freshwater

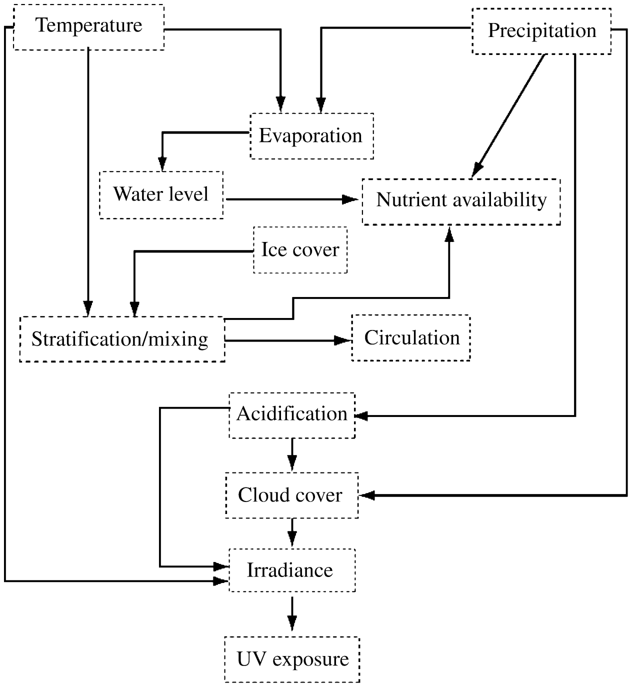

FIG. 2. Conceptual diagram detailing the range of environmental factors likely to affect aquatic systems predicted from climate change scenarios [redrawn from Marcogliese (2001), reproduced with permission from NRC Canada]. UV, ultraviolet.

discharge, *e.g.* estuaries (Struyf *et al.*, 2004). Those habitats most sensitive to reduced flow, *e.g.* streams, ditches, small lakes or ponds, are likely to be most affected. Predicted drought conditions will lead to a loss of sensitive habitats through reduced availability of water, and a reduction in habitat quality in other systems because of increased water temperatures, decreased dilution of pollutants (and therefore increased toxicity) and reduced availability of oxygen (Elliott *et al.*, 1997; Magoulick & Kobza, 2003). Conversely, increased river and stream discharge following winter flooding could be detrimental to stream and river fishes (Schlosser, 1991; Natsumeda, 2003).

Lakes and standing waters

The water temperature of aquatic habitats in Britain and Ireland is largely a function of air temperature (Arnell, 1998), but as elsewhere, other drivers can influence water temperatures, *e.g.* groundwater inputs, precipitation, riparian cover and industrial effluents (Poole & Berman, 2001). Lake primary productivity is closely linked to mean air temperature and the length of the growing season (Brylinsky & Mann, 1973), and lacustrine fish production is positively correlated with mean annual air temperature (Schlesinger & Regier, 1982). In the North American Great Lakes, Meisner *et al.* (1987) suggested that an increase in mean air temperatures by just 2° C could lead to an increase in fisheries yield of *c.* 25%. However, such increases in potential fish production following climate change may be limited by a greater probability of hypolimnetic oxygen depletion in productive lakes (Carpenter *et al.*, 1992). The timing and intensity of lake stratification is likely to change (De Stasio *et al.*, 1996), with implications for lake fishes (Lehtonen, 1996), their parasites (Marcogliese, 2001) and their prey (Winder & Schindler, 2004). Recent modelling studies suggest that the negative effects of nutrient enrichment on lake algal dynamics may become increasingly problematic as temperatures increase (Elliott *et al.*, 2006). Fishes found in shallow habitats or habitats with restricted water exchange, *e.g.* shallow lakes and ponds, will be affected by increased water temperatures following climate warming and in extreme cases, loss of habitat or death if these systems dry out. Some systems may become ephemeral following future climate change and become fish-free or only partly utilized by fish. Increased lake levels following winter precipitation will improve access to additional spawning or feeding habitats for some species (Ross & Baker, 1983), *e.g.* pike (*Esox lucius* L.) (Billard, 1996). There are a number of detailed reviews of the effects of climatic variation and the predicted consequences of climate change on the ecology of lakes (De Stasio *et al.*, 1996; Straile *et al.*, 2003; George *et al.*, 2004).

Running waters

Apart from increases in water temperature, climate change is likely to affect riverine systems following shifts in precipitation patterns. Residence times, import and export of organic matter, dilution of pollutants, primary production and dissolved oxygen concentrations are all likely to be altered (Carpenter *et al.*, 1992; Arnell, 1998; Mohseni *et al.*, 2003). Riverine fishes display a complex array of environmental requirements (Crisp, 1996; Mann, 1996), and major changes in seasonal flow patterns are likely to have significant consequences (Arnell, 1998). Migratory species have evolved to utilize predictable floods for migrations (Crisp, 1996), and changes in the frequency or intensity of floods may affect the ability of adult fishes to successfully reach spawning areas. Climate change scenarios predict significant increases in extreme precipitation events (Hulme *et al.*, 2002), where flood intolerant species or sensitive life stages, *e.g.* eggs or larvae, could become displaced or killed (Mann, 1996; Jager *et al.*, 1999; Poff, 2002). However, in some river systems, fishes have proved to be remarkably resilient to flooding (Heggenes, 1988; Lobón-Cerviá, 1996), and increased winter flooding may prove beneficial to certain species, providing additional feeding or spawning opportunities (Ross & Baker, 1983; Masters *et al.*, 2002). If hydrological regimes shift, *e.g.* reduced surface or groundwater flows during periods of drought, hydrologically marginal habitats such as floodplains or wetlands may become disconnected from the main river channel, with subsequent effects on habitat availability for fish, and their production and diversity (Robinson *et al.*, 2002). A series of reviews have examined the likely ecological and hydrological effects of climate change on riverine habitats in the U.K. and elsewhere (Carpenter *et al.*, 1992; Eaton & Scheller, 1996; Arnell, 1998; Mohseni *et al.*, 2003).

Estuaries

Estuaries represent the interface between marine, freshwater and terrestrial environments and are extremely complex ecosystems where salinity, temperature and oxygen fluctuate according to tidal stage and season (Ketchum, 1983). Estuarine communities, including fishes (Haedrich, 1983), are often structured according to salinity resistance and are well adapted to fluctuations in salinity, temperature and oxygen (Vernberg, 1983). Estuarine habitats are likely to experience very different hydrological regimes under future climate conditions (Struyf *et al.*, 2004), and the effects of climate change on estuaries are likely to be complex (Scavia *et al.*, 2002). Decreased summer precipitation will affect freshwater inputs, which will increase residence times and the time taken to flush nutrients and pollutants from the system (Struyf *et al.*, 2004), and lead to increased intrusion by saline waters (Roessig *et al.*, 2004). Although there is considerable variation in nutrient load between regions (Nedwell *et al.*, 2002), some estuaries in Britain and Ireland have undergone eutrophication (Mathieson & Atkins, 1995). The risk and frequency of estuarine algal blooms may increase in nutrient-rich estuaries following climate change. Reduced freshwater inputs during hot dry summer months could increase residence times and reduce the dilution of dissolved nutrients. This combined with increased summer temperatures might lead to increased phytoplankton production and the risk of low oxygen conditions. Several authors have reviewed the effects of climate change on estuarine fishes (Scavia *et al.*, 2002; Roessig *et al.*, 2004).

Marine and coastal habitats

The seas around Britain and Ireland are predicted to continue to warm in the future following continued climate change (Hulme *et al.*, 2002). However, the likely effects of climate change on marine ecosystems extend beyond increased water temperature (Scavia *et al.*, 2002; Harley *et al.*, 2006) and include changes in oceanic circulation (Scavia *et al.*, 2002), sea level rise (Hulme *et al.*, 2002), increasing frequency of storm surges (Hulme *et al.*, 2002), changes in chemistry including acidification (Royal Society, 2005) and nutrient availability (Scavia *et al.*, 2002). The likely ecological consequence of these changes to fish and marine ecosystems are understandably diverse but include changes in the phenology of species that form the base of marine food webs (Heath, 2005), *e.g.* phytoplankton and zooplankton (Hays *et al.*, 2005; Steingrund & Gaard, 2005), with clear implications for fishes and other taxa (Edwards & Richardson, 2004). If changes in the biotic (*e.g.* seasonal availability of food) and abiotic (*e.g.* water temperature, salinity and circulation) environments of marine fishes are significant, it is likely that interactions between individuals and species will be modified, influencing population and community dynamics and leading to shifts in the structure of marine fish assemblages (Attrill & Power, 2002; Genner *et al.*, 2004; Perry *et al.*, 2005; Hiddink & ter Hofstede, 2008).

Harley *et al.* (2006) suggest that changes in the chemistry of marine waters may be more important than changes in temperature. For instance, the oceans have absorbed large volumes of CO_2 that has led to significant acidification of sea waters (Royal Society, 2005). If global emissions of CO_2 continue, it is feared that the average pH of the oceans could fall by 0·5 pH units (equivalent to a three-fold increase in H^+ ions) by 2100 (Royal Society, 2005). Although the effect of such acidification is likely to be less extreme in the seas around Britain and Ireland than in the tropical or southern seas, it has clear potential to affect ecologically important calciferous organisms, such as molluscs, cold-water corals, echinoderms, foraminifera and coccolithophores (Royal Society, 2005). Increased concentrations of dissolved CO_2 also have the potential to affect the physiology and reproductive success of aquatic organisms including larger invertebrates and fishes (Ishimatsu *et al.*, 2004; Pörtner *et al.*, 2004). Increases in sea level around Britain and Ireland because of thermal expansion of sea water (Hulme *et al.*, 2002) and the melting of polar ice (Overpeck *et al.*, 2006) may reduce the area of inter-tidal habitats as coastal waters encroach, especially if coastal defences are present (Galbraith *et al.*, 2002). As might be expected, there have been a series of major reviews examining the role of climate on marine systems and the likely biotic and abiotic consequences of climate change to marine habitats (Edwards *et al.*, 2002; Scavia *et al.*, 2002; Soto, 2002; Sharp, 2003; Ottersen *et al.*, 2004; Stenseth *et al.*, 2004; Hays *et al.*, 2005; Harley *et al.*, 2006).

CLIMATE CHANGE AND THE FISHES OF BRITAIN AND IRELAND

The potential effects of climate change on fish (and their responses) are likely to be diverse, and there is an extensive literature examining the influence of climate (especially temperature) on many of the fishes of Britain and Ireland. This review focuses on well-studied species that are important for ecological, trophic and socio-economic reasons, including examples of typical cold, cool and warm-water fishes (Hokanson, 1977; Magnuson *et al.*, 1979).

MARINE FISHES

North Atlantic cod Gadus morhua

The Atlantic cod *Gadus morhua* L. represents a key North Atlantic fish resource (Brander, 1997; Planque & Frédou, 1999) and has been studied more than any other marine fish (Brander, 1997), including detailed stock assessments since the 1960s (Heath, 2005). *Gadus morhua* has a boreal distribution and is a typical inhabitant of the continental shelf (Pörtner *et al.*, 2001). *Gadus morhua* stocks are found around the North Atlantic margin from North Carolina to west of Greenland and from the Celtic Sea to the Barents Sea in the eastern North Atlantic (Planque & Frédou, 1999; Ottersen *et al.*, 2004).

At present, exploitation is regulated *via* quotas generated from annual stock assessments that use models jointly derived from catch and fisheries research data. The historical relationship between recruitment and spawning stock biomass (SSB) is used to generate medium-term projections (5–10 years) of the likely trends in the stocks under different exploitation scenarios (Brander, 2003; Clark *et al.*, 2003; Planque *et al.*, 2003). Understanding the relationship between spawning stock and recruitment is the most important issue in fisheries biology and assessment (Myers, 2001), but environmental variation is not typically included as a model input (Clark *et al.*, 2003).

Gadus morhua abundance has changed markedly around Britain and Ireland over the last century, particularly in the North Sea (ICES, 2001; Clark *et al.*, 2003). Until the 1960s, the North Sea *G. morhua* stock was estimated at *c.* 100 000 t (ICES, 2001). However, between the early 1960s to the mid-1980s, during what is known as the gadoid outburst (ICES, 2001; Brander & Mohn, 2004), the stock increased four-fold, following greatly increased recruitment (ICES, 2001; Beaugrand *et al.*, 2003). This resulted in increased stock size, fishing effort and catches (ICES, 2001; Clark *et al.*, 2003). However, following overexploitation (Beaugrand *et al.*, 2003), the SSB of these stocks are now at an historic low (Brander, 2005), and today, north-east Atlantic *G. morhua* stocks are still considered at risk of total collapse (Cook *et al.*, 1997), although recruitment has recently improved slightly in some areas around the British Isles (ICES, 2007).

Gadus morhua *and climatic variation*

Brander (1995) studied 17 stocks of *G. morhua* across the North Atlantic and found that most (>90%) of the variability in growth was associated with variation in mean ambient temperature (2–11° C). He demonstrated that stocks at higher ambient temperatures (Celtic Sea: 11° C) achieved a mean mass at age 4 of 7·3 kg compared with 0·6 kg at 2° C (Labrador, Canada). *Gadus morhua* stocks from the relatively warm waters of Britain and Ireland are more than four times as productive as stocks from colder, more northerly regions (Dutil & Brander, 2003). Temperature not only accounts for differences in growth between stocks but also interannual variation within a stock (Ottersen *et al.*, 2004). Growth performance of *G. morhua* was optimized at temperatures close to 9° C, regardless of the population investigated along a latitudinal cline (Pörtner *et al.*, 2001). Optimum temperature for growth and food conversion in *G. morhua* fed to satiation ranged between 16° C and 7° C for 2 and 2000 g *G. morhua*, respectively (Björnsson *et al.*, 2001), an observation also made by Lafrance *et al.* (2005). Under natural conditions, where the food resources may be limited or less predictable, optimal temperatures for growth are likely to be reduced (Despatie *et al.*, 2001); however, Neat & Righton (2007) have recently demonstrated that some North Sea *G. morhua* utilize habitats with water temperatures above those considered optimal for growth.

The spatial distribution (*e.g.* depth) of *G. morhua* has been associated with temperature variation in a series of studies. Comparison of the spatial distribution of mature Icelandic *G. morhua* with several environmental variables, including temperature, indicated they migrated between depths to actively maintain optimum temperatures (Begg & Martinesdottir, 2002). However, data gathered at the level of individual fish using electronic data storage tags, an approach that better demonstrates the large degree of temperature variability experienced by individuals, has revealed that *G. morhua* can show high variability in migratory behaviour, both between stocks and individuals. Pálsson & Thorsteinsson (2003) demonstrated that the depth and temperature conditions encountered by *G. morhua* off Iceland contrasted greatly, and fish could be classified as following one of two alternative strategies: residing and feeding in deep or shallow water. Temperature conditions encountered by shallow-water *G. morhua* followed that of the seasonal trend in the shelf region (highest in summer and autumn and coolest in the winter months), but deep-water *G. morhua* were found in deeper and cooler waters during summer months and encountered warmer water in winter months. North-east Arctic *G. morhua* migrate into the Barents Sea during warm years, but *G. morhua* migrate in cold years only as a result of high densities (Ottersen *et al.*, 1998). Castonguay *et al.* (1999) found that *G. morhua* in the northern Gulf of St Lawrence did not appear to be exposed to colder temperatures during a period of oceanic cooling but modified their spatial distribution to remain within a range of preferred temperatures. Gødo & Michalsen (2000) described a similar situation in the Barents Sea. Pálsson & Thorsteinsson (2003) suggested that the use of deeper and colder waters in the summer and autumn permitted large-bodied *G. morhua* to minimize maintenance costs under conditions of reduced food availability.

Temperature affects the developmental rate of fish eggs, with higher temperatures resulting in faster development and hatching (Nissling, 2004). Laboratory experiments have demonstrated that the development rate of *G. morhua* eggs is positively correlated with temperature and that egg survival is unaffected at temperatures between 3–9° C (Nissling, 2004) and 2–10° C (Laurence & Rogers, 1976). However, above these temperatures, egg survival was significantly reduced. Laboratory studies show that the growth of larval *G. morhua* is also positively correlated with temperature, with growth increasing from 4–10° C (Laurence, 1978) and 4–14° C (Otterlei *et al.*, 1999). Yin & Blaxter (1987) estimated that larval cod have an upper lethal temperature of 15·5° C.

Gadus morhua productivity, like all fish stocks, is dependent on recruitment, and variability in recruitment is the principal cause of fluctuations in fish stocks (Garrod, 1983). Understanding what regulates recruitment variability has been a primary objective of fisheries science since the early 20th Century (Beverton, 1998; Ottersen *et al.*, 2004). As soon as eggs are laid, they and the resulting offspring are subject to different mortality rates at different life stages of the fish. As a rule, natural mortality is most intense during early life stages and declines as age and size increases (Anderson, 1988; Sogard, 1997). Early life stages are considered to be the principal determinants of year-class strength (YCS) and recruitment success (Myers, 2001) and hence survival in the early life stages of fish is of extreme importance (Anderson, 1988; Cushing & Horwood, 1994) and strong cohorts (or year classes) remaining large in subsequent years (Myers, 2001). Variation in survival of early life-history stages is considered to be the principal determinant of YCS (Garrod, 1983; Myers, 1998).

A series of studies have demonstrated an effect of climatic variation on the recruitment of cod, and in a meta-analysis, Planque & Frédou (1999) demonstrated consistent correlations between water temperature and recruitment of stocks at the edge of their geographical range (*i.e.* positive in cold-water stocks and negative in warm-water stocks). Laboratory studies suggest that the optimal temperature for hatchery-reared larval *G. morhua* was 8·5–8·8° C (Steinarsson & Björnsson, 1999). Interannual variability of temperature affects the survival and recruitment of *G. morhua*, with positive effects in cold regions of the species range, negative effects in warm regions and with no significant relationship for stocks located in intermediate areas (Planque & Frédou, 1999). In the Irish Sea, *G. morhua* are situated towards their southern distributional limit and display a strong negative connection between recruitment and recent temperature increases (Planque & Fox, 1998). O'Brien *et al.* (2000) noted that spring temperatures >8° C had a detrimental effect on recruitment of North Sea *G. morhua*, whereas in the north-east Arctic, Ottersen *et al.* (1998) reported a positive relationship between temperature and recruitment. When Planque *et al.* (2003) incorporated sea surface temperature into a North Sea *G. morhua* stock recruitment model, it accounted for 46% of the variance in past recruitment compared with 17% obtained when SSB alone was modelled. They concluded that although long-term trends in recruitment were related to SSB, year-to-year variability was mostly driven by fluctuations in the environment.

It has proved difficult to determine which processes consistently exert a major influence on recruitment and at what stage during early life they occur and the appropriate season at which environmental factors such as temperature should be measured (Brander & Mohn, 2004). Such problems are alleviated *via* the use of a climatic indicator, *e.g.* North Atlantic Oscillation (NAO) as it does not have local values and can be considered a proxy for temperature, wind and precipitation (Ottersen *et al.*, 2001; Brander & Mohn, 2004). The NAO has significant effects on the recruitment of *G. morhua* throughout the North Atlantic: Brander & Mohn (2004) demonstrated that recruitment was independent of SSB and negatively correlated with the NAO in some areas (*e.g.* Irish Sea, North Sea, Baltic Sea and west of Scotland) and positively correlated with the NAO in others (*e.g.* Iceland, north-east Arctic and Faroes). These findings are consistent with the effects of temperature on growth of *G. morhua* discussed above. However, it should be noted that temperature is not the only process acting in each area (Brander & Mohn, 2004). Further analysis on *G. morhua* stocks demonstrating negative correlations between recruitment and the NAO suggested that the NAO only significantly affects recruitment when spawning biomass is low (Brander, 2005). He concluded that long-term recruitment prospects for low biomass stocks are not favourable, as the NAO has followed a positive trend in recent decades (Ottersen *et al.*, 2001; Brander, 2005), and is predicted to continue this pattern. The NAO probably affects all *G. morhua* stocks in the North Atlantic, but the degree and sign of the effect vary as the influence of the NAO is not geographically uniform (Brander & Mohn, 2004). Fromentin *et al.* (1998) were unable to demonstrate a relationship between the NAO and the interannual variability in *G. morhua* recruitment along the Norwegian Skagerrak coast. They hypothesized that this was because of this population being located close to the centre of the latitudinal distribution of Atlantic *G. morhua* and that climate variability was more likely to affect species at the edge of their range than in the centre of their range, such as the waters surrounding Britain and Ireland. These results follow a growing consensus that stock–recruitment models require environmental inputs to better forecast future recruitment and therefore permit improved stock management (Clark *et al.*, 2003; Planque *et al.*, 2003). This is likely to be particularly important for stocks at the edge of their geographical range (Planque *et al.*, 2003). Although it is not known whether temperature is acting directly or as a proxy for other drivers, the effect of sea temperature on *G. morhua* recruitment appears to be a robust statistical observation (Planque *et al.*, 2003). However, including data from all main North Atlantic stocks in one analysis, Stige *et al.* (2006) concluded that the affect of the NAO on recruitment in *G. morhua*, through local environmental variables, shows significant, stock-specific trends with a specific geographic pattern and that this climatic effect is non-stationary. Their results support those of Brander & Mohn (2004) in that the effect of the NAO is felt greatest at the extreme edges of the species distribution.

Critical periods, match–mismatch theory and trophic cascades: Gadus morhua *as an example*

During early life stages, fish typically encounter extremely high mortality rates, and hence, this period is considered critical for survival of young fishes. When fish larvae hatch, they depend on their yolk sac for nutrition (Braum, 1978). However, they must feed soon after yolk exhaustion or risk reaching a point of irreversible starvation when they are too weak to feed (Craig, 2000). The time taken to reach the latter point depends on water temperature and larval size and hence egg size (Elliott, 1994). Following absorption of the yolk sac, juvenile fishes must grow as quickly as possible to minimize mortality risk (Sogard, 1997). If food is scarce, juvenile fish may be vulnerable to predation for a longer period and also struggle to reach a certain size by the end of the first summer resulting in starvation and mortality during the winter period (Griffiths & Kirkwood, 1995; Lappalainen *et al.*, 2000). The SSB of *G. morhua* in the seas around Britain and Ireland has been below safe biological limits for some time (Cook *et al.*, 1997; Brander, 2005), and this may further limit the likelihood of the formation of a strong year class (Garrod, 1983).

Food availability for rapidly growing *G. morhua* larvae affects their survival in many if not all areas (Brander & Mohn, 2004) and food quantity and quality are essential (Munk, 1997). The survival of larval *G. morhua* depends on four key biological variables of prey: mean size, seasonal availability, food quality and abundance. These factors may be the driving force behind variation in cod recruitment, and recent increases in temperature have modified the plankton ecosystem in such a way as to affect the survival of juvenile *G. morhua* (Beaugrand *et al.*, 2003). Detailed analysis of zooplankton data has revealed that the gadoid outburst that occurred between the late 1960s and the early 1980s (ICES, 2001) corresponded with a change in the dominant species of copepods in the North Sea, *e.g.* years of good recruitment occurred in parallel with positive anomalies in the plankton community. Larger bodied copepods replaced smaller species, while the abundance of certain important species increased at the time of year when juvenile *G. morhua* were developing, and this is believed to have increased gadoid recruitment (Beaugrand *et al.*, 2003). Unfavourable shifts in the plankton community occurred in the years following the gadoid outburst, and these were associated with poor recruitment of *G. morhua* (Beaugrand *et al.*, 2003). These unfavourable shifts included a decrease in the average size of calanoid copepods by a factor of two and mechanisms involving the match–mismatch hypothesis. According to this hypothesis, the survival of fish larvae depends on their ability to encounter and consume a sufficient quantity of suitable prey to avoid starvation and grow (Brander *et al.*, 2001). *Calanus* spp. (from eggs to adults) are an important source of food for larval and juvenile *G. morhua* until July to August (Munk, 1997), and the progressive substitution of *Calanus finmarchicus* by *Calanus helgolandicus* (Hays *et al.*, 2005) has delayed the timing of occurrence of *Calanus* prey in the North Sea from spring to late summer, when juvenile *G. morhua* feed more on euphausiids and other fish larvae (Beaugrand *et al.*, 2003). Euphausiids represent an important, high-energy source of food for juvenile *G. morhua*, and a long-term decrease in euphausiids is significantly related to these plankton anomalies. Such plankton anomalies are more significantly correlated with sea surface temperature (SST) than *G. morhua* recruitment changes in the North Sea (Beaugrand *et al.*, 2003). This implies a multiple negative impact of increasing temperature on *G. morhua* recruitment: increasing temperatures increase *G. morhua* metabolism and energy costs (Otterlei *et al.*, 1999), which subsequently hasten exhaustion of yolk-sac energy reserves. Furthermore, if food availability is reduced (Beaugrand *et al.*, 2003), the optimal temperature for growth decreases, further compounding the effects of increased temperatures (Michalsen *et al.*, 1998).

On the Faroe Shelf, the stocks of *G. morhua* and other major demersal fishes declined in the early 1990s (Steingrund & Gaard, 2005). Prior to the collapse, fishing mortality was high and recruitment and growth had been poor for several years. However, by 1995, the SSB recovered following strong recruitment in 1992 and 1993 because of an increased scope for growth in pre-recruits, even though SSB was small (Steingrund *et al.*, 2003). No correlation between temperature and recruitment was apparent, but the collapse and recovery of the *G. morhua* stocks were closely linked to phytoplankton production. Years of low phytoplankton production resulted in low *G. morhua* recruitment through limitation of food for both larval (zooplankton prey) and post-settlement cod (sandeel prey) (Steingrund & Gaard, 2005).

Effects of climate change on primary and secondary production – phenology

Sea surface warming in the north-east Atlantic has been associated with increased and decreased phytoplankton abundance in cooler and warmer regions, respectively (Richardson & Schoeman, 2004). This effect can propagate up through food webs *via* herbivorous and carnivorous zooplankton. Effects on higher trophic levels seem inevitable, and it is likely that fish and other top predators will have to adapt to a changing spatial distribution of primary and secondary production within marine pelagic ecosystems following climate change (Richardson & Schoeman, 2004). Results from continuous plankton recorder (CPR) surveys have shown that south of 59° N in the north-east Atlantic (*e.g.* in the seas around Britain and Ireland), phytoplankton has shown a significant response to climate change, with increased abundance and a marked extension of the growing season (Reid *et al.*, 1998).

As detailed above, the phenology of major oceanic trophic events such as spring blooms, seasonal peaks in zooplankton abundance and the timing of hatching of fish eggs can be of central importance to fish stocks. Variation in pelagic food webs can be driven by fluctuations in plankton production, and effects of climate change on plankton dynamics are transmitted to upper trophic levels (*e.g.* fishes). Temperate marine environments may be particularly vulnerable to changes in phenology because the level of response to climate change may vary across functional groups and trophic levels. This is important because recruitment success of higher trophic levels is highly dependent on synchronization with pulsed planktonic production (see above and Edwards & Richardson, 2004). There is widespread evidence of climate change affecting the phenology and structure of plankton communities around Britain and Ireland (Reid *et al.*, 1998; Hays *et al.*, 2005), leading to trophic mismatch (Beaugrand *et al.*, 2003; Edwards & Richardson, 2004). Indeed, Greve *et al.* (2005) showed that the timing of fish larvae abundance for a significant number of fish species in the North Sea is negatively correlated with the mean annual winter sea surface temperatures.

The copepod *C. finmarchicus* is of key trophic importance in the north-east Atlantic but is in pronounced decline. It is being gradually replaced by its warm-temperate congener *C. helgolandicus* with negative effects on fish recruitment in some species including *G. morhua* (Beare *et al.*, 2002; Beaugrand *et al.*, 2003). In the North Sea, *C. finmarchicus* has shown a rapid and almost complete collapse and an increasing overall prevalence of temperate Atlantic and neritic taxa (Beare *et al.*, 2002; Edwards & Richardson, 2004). Atlantic inflow into the North Sea is increasingly thought to be the main regulator of long-term abundance of *C. finmarchicus* in the North Sea (Planque & Taylor, 1998; Heath *et al.*, 1999). Unlike temperate Atlantic taxa such as *C. helgolandicus*, *C. finmarchicus* cannot overwinter in large numbers in the North Sea because it is too shallow and cold and must therefore migrate to deeper overwintering areas (*e.g.* the Faroe–Shetland Channel) (Heath & Jonasdottir, 1999).

The decline of *C. finmarchicus* and its progressive substitution by *C. helgolandicus* has been associated with the influence of an increasingly positive NAO on oceanic currents around Britain and Ireland and temperatures in the North Sea (Fromentin & Planque, 1996; Planque & Reid, 1998; Planque & Taylor, 1998; Beare *et al.*, 2002), changes in west wind stress, and effects on primary production (Fromentin & Planque, 1996). A reduction in the Atlantic inflow into the northern North Sea, which transports *C. finmarchicus* from overwintering habitats, coupled with an increase in inflow through the English Channel of presumably temperate Atlantic species is thought to be the driving mechanism for the decline. Rising temperatures would result in increased winter survival of temperate neritic species in the North Sea. However, two ecological features clearly differentiate these two species of calanoid copepod: their temperature preferences and overwintering strategies (Planque & Taylor, 1998). Recent work by Helaouët & Beaugrand (2007) suggests that the most important variable that influences the abundance and spatial distribution of these two species is temperature and changes in temperature alone could have triggered the substantial and rapid changes in the zooplankton dynamics in the North Atlantic ecosystem.

Future predictions for Gadus morhua

Pörtner *et al.* (2001) modelled the likely effects of future climate on *G. morhua* populations and predicted a northerly distribution shift, with increased growth rates and fecundity of *G. morhua* in northern stocks consistent with some observations (Laurence, 1978; Yin & Blaxter, 1987). If other temperature-related factors (*e.g.* zooplankton production) do not restrict recruitment, the predicted increases in temperature in the northern range of *G. morhua* distribution might increase recruitment in these areas and decrease recruitment in what becomes the new southern distribution of *G. morhua* (Planque & Frédou, 1999; O'Brien *et al.*, 2000). However, it should be noted that these observations reflect estimates of optimal temperatures from laboratory studies and noisy temperature–recruitment relationships and therefore represent anticipated changes rather than firm predictions. It should also be noted that to date, water temperatures have not yet reached levels that have resulted in a general northwards shift in the distribution of *G. morhua* across its southern distribution (Perry *et al.*, 2005). However, during the prolonged warming period off Greenland from 1925 to 1935, *G. morhua* rapidly extended their distribution northwards by >1000 km in <20 years giving rise to a substantial fishery (Jensen, 1939 cited in Brander, 2007).

Clark *et al.* (2003) modelled the likely future effects of climate change on North Sea *G. morhua* using projections of sea surface temperatures for the period 2000–2050. At present fishing mortality, and with no climate change, they predicted a steady decrease in SSB over the next 50 years, but the inclusion of temperature rise had a dramatic effect, accelerating the decline in SSB and recruitment and led to a predicted collapse of the stock (Clark *et al.*, 2003). Their model indicated that changes in temperature would affect population dynamics through recruitment rather than adult growth. In a follow-up study, Kell *et al.* (2005) indicated that a 50% reduction of fishing mortality from current levels would permit the recovery and persistence of North Sea *G. morhua* even under climate scenarios similar to those used by Clark *et al.* (2003).

The long adult life span of *G. morhua* buffers occasional recruitment failures, but overfishing has truncated the age structure of *G. morhua* stocks. Increased fishing mortality reduces SSB, the average size and age of spawners and therefore the number of older, larger fish that make a greater contribution to reproduction (Martinesdottir & Thorarinsson, 1998). Larger eggs produced by larger, more fecund females may produce larvae that have a better survival rate than small eggs (Moodie *et al.*, 1989). At the onset of spawning, larger, older *G. morhua* spawn earlier than smaller, younger *G. morhua* (Begg & Martinesdottir, 2002). The spatial distribution of spawning *G. morhua* also varies according to age and size, with larger *G. morhua* spawning closer to the coast than smaller or younger individuals that spawned in deeper water (Martinesdottir *et al.*, 2000). Therefore, the decreasing fraction of older, earlier spawning females and the increasing proportion of younger, first-time spawners, a phenomenon exacerbated by overfishing, is likely to result in delayed spawning (Wieland *et al.*, 2000). This may have implications for trophic mismatch with food resources if *G. morhua* eggs hatch later. Furthermore, the intensity and the extent of spawning covary with the size of individual *G. morhua* (Kjesbu *et al.*, 1996). The resultant spawning populations may therefore have a reduced spawning season, smaller eggs with a lower survival rate, a smaller range in the specific gravity of eggs and a reduced spawning area, all which combine to limit the viability of the critical early life stages and confer increased vulnerability to environmental fluctuations. Myers (2001) noted that recruitment variability decreased with age for marine demersal fish but increased with lowering SSB.

Although sea temperatures around Britain and Ireland have warmed in recent years, and some authors suggest that the geographical distribution of *G. morhua* has shifted north (Beare *et al.*, 2004; Perry *et al.*, 2005), it seems that even the warmer waters of the southern North Sea are still suitable for the continued existence of adult *G. morhua* (Neat & Righton, 2007), assuming that they are not removed through fishing (Blanchard *et al.*, 2005). However, sea temperatures are predicted to continue to warm (Hulme *et al.*, 2002; Clark *et al.*, 2003), and this heavily exploited fish faces an uncertain future in the seas around Britain and Ireland with changing climate acting on many facets of the biology and ecology of this species.

Herring Clupea harengus *and Pilchard* Sardina pilchardus

The seas surrounding Britain and Ireland support several distinct stocks of herring *Clupea harengus* L. including the Celtic Sea, West of Ireland (winter–spring spawners) and West of Scotland, Irish Sea and the North Sea (summer–autumn spawners) (Heath *et al.*, 1997). Exploitation of *C. harengus* has occurred over many centuries (Cushing, 2003), and during this period, major fluctuations in abundance have been a characteristic of all stocks. In the North Sea, a major collapse resulted in a ban on *C. harengus* fishing from 1977 to 1983. Since then exploitation has been subject to a total allowable catch regulation for the international fleet, which has resulted in biomass rising to an estimated 1·5 million t in the early 1990s (Heath *et al.*, 1997). The ability of *C. harengus* stocks to recover rapidly from exploitation is unusual in collapsed fish stocks (Hutchings, 2000) and reflects the biological characteristics of clupeids, such as young age at maturation and high fecundity, combined with exploitation methods that use highly selective gears that minimize by-catch.

Clupea harengus is highly mobile, relies on short, plankton-based food chains, is highly fecund and shows plasticity in growth, survival and other life-history traits. These biological characteristics make it sensitive to environmental forcing and highly variable in their abundance (Alheit & Hagen, 1997) and hence sensitive to recruitment fluctuations (Axenrot & Hansson, 2003). Nash & Dickey-Collas (2005) reported a positive relationship between abundance of *C. harengus* early larvae and winter bottom temperature in the North Sea. They concluded that the relationship probably reflected a direct physiological effect of temperature on growth and development rates, as the youngest larvae are mostly still in the yolk-sac development stage as the stock are autumn spawners, and larvae do not metamorphose until the spring following spawning (Heath & Richardson, 1989). However, higher abundance of juvenile *C. harengus* was associated with colder temperatures, possibly reflecting higher *Calanus* abundance, which was itself inversely correlated with winter bottom temperatures (Nash & Dickey-Collas, 2005).

Long-term variation in the SSB of the Norwegian spring-spawning *C. harengus*, situated towards the northern extreme of the species distribution, is positively correlated with mean annual temperature (Toresen & Østvedt, 2000). Recruitment of this stock is positively correlated with average winter water temperature in the Barents Sea (Toresen & Østvedt, 2000; Sætre *et al.*, 2002). In years with warmer waters and high wind speeds during April, recruitment and the mean size of recruits increases, which subsequently gives rise to stronger year classes (Sætre *et al.*, 2002). Ottersen & Loeng (2000) suggest that these higher than average temperatures allow juvenile *C. harengus* to attain increased growth and survival rates in the vulnerable larval and juvenile stages. In warm years, the spawning season begins earlier as does the development of phytoplankton and zooplankton. This results in the *C. harengus* feeding earlier and attaining maximal lipid concentrations by June to July as opposed to August to September when the water is cooler and plankton growth slower.

Axenrot & Hansson (2003) attempted to relate Baltic Sea *C. harengus* recruitment with the density of young-of-the-year (YOY) fish, SSB and climate (NAO). All factors were positively (if weakly) correlated with YCS, but when combined, there was a strong positive relationship with YCS (adjusted $R^2 = 0{\cdot}93$), and the authors stressed the significance of climate change to recruitment in this stock.

The English Channel represents the approximate geographical boundary between the distribution of the cold-water *C. harengus* and the warm-water pilchard *Sardina pilchardus* (Walbaum) (Southward *et al.*, 1988, 1995). Both species have been captured in the sea off southern England since the 16th century (Southward *et al.*, 1988). The geographical boundary between the two species has shifted northwards and southwards on a decadal scale in relation to changing temperature. During very warm periods, the *S. pilchardus* has extended its range as to occur in all coastal waters around Britain and Ireland, and as far north as southern Norway. During cold periods, *C. harengus* even dominated in areas off the south coast of England and *S. pilchardus* retreated (Southward *et al.*, 1988, 1995). Southward *et al.* (1995) reported that during warmer periods, the density of *S. pilchardus* eggs increased (by up to a factor of three) and the plankton community structure shifted. During cooler periods, plankton were characterized by an abundance of large diatoms in spring, a profusion of *Calanus* in the summer, and the presence of intermediate trophic level zooplankters such as euphausiids. The warm-water plankton community consisted of smaller diatoms and flagellates in spring, while dinoflagellates dominated the summer plankton.

In the North Sea during the summers of 1988–1990, the northern extent of *C. harengus* was greater and some of the stock may have left the North Sea and migrated to the Faroe Plateau, a shift that appears to reflect a response to short-term climatic variation (Corten, 2001). This period was characterized by a combination of high winter temperatures and low abundance of *C. finmarchicus*, the principal food of the stock, which itself was probably related to high water temperatures. Apart from the 1988–1990 anomaly, a long-term shift of catches occurred from 1960 to 1990, coinciding with a gradual increase in winter temperature and a sustained decline in *C. finmarchicus*. If the recent climatic trend towards higher winter temperatures continues, the anomalous winter distribution of *C. harengus* in 1988–1990 could become the normal pattern in future years (Corten, 2001). Recently, *S. pilchardus*, and another typical warm-water pelagic species, the anchovy *Engraulis encrasicolus* (L.), have become increasingly frequent in research trawls from the north-western North Sea, a pattern associated by Beare *et al.* (2004) with marked ecological change in the area.

From their analyses of historical catch records of *S. pilchardus* and *C. harengus*, Alheit & Hagen (1997) demonstrated that the intensity of fishing varied from very high to an apparent absence of exploitation, which may have been linked to the strength of the NAO. During negative phases of the NAO, which corresponded with severe winters with cold-water temperatures and a reduction of westerly winds, *C. harengus* fisheries off the west coast of Sweden (Bohuslän) and southern England showed abundant fish and high catches. In contrast, the Norwegian spring-spawning *C. harengus* and *S. pilchardus* fishery off the south coast of England was negatively affected. The situation was reversed during positive phases of the NAO, which corresponded with intensified westerly winds and relatively warm water in the English Channel, North Sea and Skagerrak (off Sweden) (Alheit & Hagen, 1997). However, it should be noted that it has been >90 years since *C. harengus* were recorded in large numbers off the Bohuslän coast.

Sinclair & Tremblay (1984) noted that although different herring stocks spawn throughout the year across the North Atlantic, larval metamorphosis is restricted to a 5 month period (April to August). The authors hypothesized that for each stock, the timing of spawning is adapted to the growth conditions along the drift trajectory of the larvae to ensure arrival at the correct size for metamorphosis at the most appropriate time of year. This suggests that herring may be particularly sensitive to the effects of climate change, as recruitment occurs throughout the year, and for certain stocks (*i.e.* autumn spawners), the larval stage extends through the winter period when growth is slow and the larvae are exposed to high predation for a prolonged period (Sinclair & Tremblay, 1984).

Sandeels, the Ammodytidae

Sandeels (Ammodytidae) represent an abundant and important component of North Atlantic food webs (Lewy *et al.*, 2004) and play a central role in the North Sea ecosystem (Frederiksen *et al.*, 2006) as prey for several commercially significant fish species (Pedersen, 1999) as well as for seabirds (Wright, 1996) and marine mammals (Harwood & Croxall, 1988). Although five species of sandeels are found around Britain and Ireland (Wheeler, 1969), the lesser sandeel *Ammodytes marinus* Raitt is the most abundant, comprising >90% of sandeel fishery catches (Pedersen *et al.*, 1999). Although limited to suitable shallow-water habitats, where it can be locally extremely abundant, sandeels are distributed throughout the seas surrounding Britain and Ireland, with the English Channel representing the southern extreme of the *A. marinus* range (Reay, 1970). Sandeels form large aggregations and support the largest single-species fishery in the North Sea, and annual landings in the 1990s reached levels of 1 million t (ICES, 1997). However, only an estimated 0·36 million t were landed in 2004 (ICES, 2005), and recently, the abundance of North Sea sandeels has decreased, and the status of the stock and associated fishery is uncertain (ICES, 2005).

Changes within sandeel stocks are heavily dependent on YCS, particularly in exploited stocks, where fish under 3 years old predominate (Wright, 1996). Assessments of North Sea sandeels have been conducted since 1983 on the assumption that populations were part of a single stock, but it is likely that several distinct aggregations exist with limited movements taking place between them (Pedersen *et al.*, 1999). One such aggregation, on the Wee Bankie and associated banks off the entrance to the Firth of Forth (56°10′ N; 2°33′ W), south-east Scotland, has supported an industrial fishery since 1990 (Wanless *et al.*, 2004). This aggregation includes fish that are relatively slow growing, are around half the mean mass at age of other North Sea populations and tend to mature at a greater age and smaller size (Wright & Bailey, 1996; Boulcott *et al.*, 2007).

Wanless *et al.* (2004) showed that the slow growth recorded from the Wee Bankie aggregation was part of a long-term decline in size over a 30 year period that began before the fishery commenced and does not seem to be reflected at the wider scale of the North Sea. Wanless *et al.* (*op cit.*) tentatively suggested that climate change may be the mechanism behind these observations. As the duration of embryonic development of juvenile sandeels is inversely related to sea temperature, warm years result in earlier hatching and providing food is abundant, rapid growth. However, unusually early hatching can result in poor synchrony with food availability and therefore a trophic mismatch (Wright & Bailey, 1996). Conversely, late hatching results in rapid growth but over a reduced growing period, limiting first-year growth (Wanless *et al.*, 2004). The observed decline in mean size at age of Wee Bankie sandeels could potentially increase the risk of stock collapse because of a reduced reproductive capacity. The maturity at age key used by ICES assumes 100% maturity at age 2, but a decline in size at age of this sandeel population may have led to a marked reduction in the numbers of fish maturing at age 2, resulting in an elevated spawning stock assessment (and therefore catch quotas), compounding the effects of climate change (Boulcott *et al.*, 2007).

The SSB of North Sea sandeel is, by itself, a poor indicator of recruitment (Pedersen *et al.*, 1999; ICES, 2005), possibly because of the marked population substructuring exhibited by sandeels (Pedersen *et al.*, 1999). Arnott & Ruxton (2002) suggested an additional and interacting role of environmental variation and the demographic structure of the population. Recruitment of sandeels is negatively related to the abundance of 1+ sandeels, which typically comprises between 40 and 80% of biomass. This density-dependent process may act through the disturbance of sandeel eggs as older fish burrow in the sediment and, or *via* cannibalism when larvae hatch. Recruitment is positively related to feeding conditions (*Calanus* nauplii abundance) during the larval stage of development (Arnott & Ruxton, 2002). However, the same authors report a negative relationship between the NAO index and the sandeel recruitment in the North Sea and suggest that this is because of temperature effects operating predominantly upon the egg and, or larval stages. Arnott & Ruxton (2002) also suggest that the negative correlation between water temperature and sandeel recruitment is strongest in the southern part of the North Sea and its strength decreases in a northerly direction, as one would expect with populations located at the southern edge of a species' distribution. However, their conclusions may have been influenced by their measures of recruitment. In the northern area of the North Sea, they used the number of 0+ sandeels in July as an estimate of recruitment in the north of the North Sea, while in the south, they considered the abundance of 1 year-old fish in the following January as a proxy for recruitment in the previous year. Arnott & Ruxton (2002) suggest that long-term increases in SST are likely to shift the distribution of the *A. marinus* northwards, assuming of course that suitable habitats are available to the north (Reay, 1970). The availability of thermal refugia close to some populations in the southern North Sea (*e.g.* Dogger Bank) may limit the influence of sea warming and allow their continued survival.

Basking shark Cetorhinus maximus

The effects of climate change on elasmobranch fishes are poorly understood, and contrast with what is known about many important teleost fishes. Some elasmobranch fishes are extremely sensitive to temperature variation (*e.g.* as low as 0·001° C; Brown, 2003). Although it is currently unclear how important this sensitivity to temperature affects their ecology, many elasmobranchs demonstrate complex behavioural trade-offs that are often associated with temperature (Sims, 2003).

The planktivorous basking shark *Cetorhinus maximus* (Gunnerus) is the world's second largest fish species, with a circumglobal distribution in warm-temperate to boreal seas (Cotton *et al.*, 2005). It has been exploited for at least 200 years in the north-east Atlantic, and concerns about its status have led to its listing as 'vulnerable' by the IUCN (2002) and in appendix II of CITES (UNEP-WCMC, 2003). During the 20th century, a *C. maximus* fishery thrived in some European temperate waters and between 1946 and 1986, these fisheries captured *c.* 77 000 *C. maximus* (Sims & Reid, 2002). The success of the fisheries varied enormously from year to year because of large variation in the abundance of *C. maximus* (Kunzlik, 1988). The Achill Island fishery captured a total of 12 360 *C. maximus* from 1947 to 1975: catches peaked in the 1950s and then fell sharply as the abundance of *C. maximus* declined (Kunzlik, 1988). The decline was originally attributed to overfishing (Parker & Scott, 1965), but Sims & Reid (2002) tentatively concluded that the decline was probably because of a distributional shift of sharks to more productive areas rather than overfishing of a local stock. However, their *C. maximus* abundance data were taken from a fishery that did not have continuous effort and from which analyses of catch per unit effort could not be made.

Cotton *et al.* (2005) showed recently that a major component of the interannual variation in relative abundance of *C. maximus* off south-west Britain was positively correlated with fluctuations in SST and the NAO. Their results indicate that climatic forcing of increased temperature through NAO fluctuations, together with SST and the density of *C. helgolandicus*, influenced *C. maximus* abundance. At a local scale (0·01–10 km), *C. maximus* distribution is determined largely by the abundance of adult *C. helgolandicus* (Sims & Quayle, 1998; Sims, 1999), with SST being less important at these small scales (Sims *et al.*, 2003*a*). However, at greater scales (10–1000 km), SST correlated significantly with *C. maximus* distribution and movement patterns (Sims & Quayle, 1998; Sims *et al.*, 2000). These observations indicate that although prey density is a key factor in determining short-term patterns of *C. maximus* distribution, 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 (Sims *et al.*, 2003*b*).

Shifts in the distribution of marine fishes in response to climate change

The recent warming of the North Atlantic has been reflected by a shift in distribution of some species, with counts of novel immigrant or vagrant species being positively correlated with increased water temperatures in the region over the last 40 years (Stebbing *et al.*, 2002). Stebbing *et al.* (2002) predict that the rate of immigration of these southern species of fish into waters around British and Ireland will accelerate with continued warming of the seas. A number of major studies have recently described long-term distributional shifts in marine fishes from areas around Britain and Ireland *i.e.* the English (1913–2002) and Bristol (1981–2001) Channels (Genner *et al.*, 2004) and the North Sea (1977–2001) (Beare *et al.*, 2004; Perry *et al.*, 2005). Although it is difficult to know how much influence spatial variation in fishing mortality has had on the shifts reported by these authors (Blanchard *et al.*, 2005), there is good evidence that climate change has had an effect on the distribution and composition of British marine fish communities. Predicting just how marine fish communities will respond to climatic change is complicated, for instance Genner *et al.* (2004) showed that within a region, spatially segregated populations of the same species may respond differently in the different areas.

Perry *et al.* (2005) demonstrated that many exploited and unexploited North Sea fishes have apparently demonstrated a marked response to recent increases in sea temperature: nearly two-thirds of species (21/36) shifted mean latitude and, or depth over a 25 year period. However, both Norway pout [*Trisopterus esmarkii* (Nilsson)] and sole (*Solea solea* L.) shifted their centre of distribution southwards. Perry *et al.* (2005) speculate that the shift in *S. solea* may be a response to improvements in water quality in the Thames Estuary (51° 30′ N; 0° 46′ E). The southern distributional shift by *T. esmarkii* may be a response to localized warming in some northern areas of the (51°30′ N; 0°46′ E) (Perry *et al.*, 2005). Approximately half of the species with a latitudinal boundary of distribution (northerly or southerly) in the North Sea showed a northerly shift in their boundary. The most significant shift was demonstrated by the blue whiting *Micromesistius poutassou* (Risso), whose southern limit moved northwards *c.* 820 km in only 25 years. Perry *et al.* (2005) speculated that if temperatures continue to increase in the North Sea, *M. poutassou* and redfishes *Sebastes* spp. will probably be lost from the North Sea, and bib *Trisopterus luscus* L. will extend their range to encompass the whole region. They also highlighted that species with 'faster' life histories, *e.g.* those with significantly smaller body sizes, faster maturation and small sizes at maturity, tended to shift their distribution and that it is these species that respond most strongly to climate change. It is unclear what influence variation in exploitation rates had on the patterns reported by Perry *et al.* (2005) and other authors examining recent biogeographical shifts in marine fishes.

Recently, Hiddink & ter Hofstede (2008) reported that a significant increase in the species richness of fish in the North Sea was related to rising water temperatures. They noted that eight times more fish species showed increased distribution ranges in the North Sea (mainly small-sized species of southern origin) compared with those whose ranges decreased (mainly large and northerly species) and explained this phenomenon by the fact that fish species richness in general decreases with latitude.

Among the fish reported by Perry *et al.* (2005) to have shifted their distribution northwards is *G. morhua*. Neat & Righton (2007) recently examined the thermal ecology of individual adult *G. morhua* at large in the North Sea and found no evidence that current temperatures constrained the distribution of adult *G. morhua* and questioned whether *G. morhua* was being forced northwards because of rising sea temperatures. Rindorf & Lewy (2006), however, suggested that a series of warm winters typified by southerly winds during the egg and larval development stage of *G. morhua* led to a northwards shift in the distribution of juvenile *G. morhua* in the North Sea the following year. These displaced recruits then tended to retain a northerly distribution throughout their lives, particularly when reaching maturity. This therefore resulted in a northerly shift in *G. morhua* distribution in the North Sea, although adult *G. morhua* did not actively shift their distribution northwards in response to rising sea temperature. Rindorf & Lewy (2006), however, did not provide any evidence from circulation modelling to support these conclusions (Heath *et al.*, 2008). Their interpretation is not supported by the work of Heath *et al.* (2008), who showed that the resulting *G. morhua* from eggs spawned from the southern North Sea since 1980 have been increasingly retained in their natal area. Beare *et al* (2004) observed that the North Sea is experiencing waves of immigration by southern species. Although concluding that these changes appeared to be part of a systematic long-term trend, Beare *et al.* (2004) could not directly relate them to temperature because of the complexity of these changes.

ESTUARINE AND COASTAL FISHES

Estuarine and coastal waters represent potentially productive habitats for fishes as they receive energetic inputs from various sources of primary production and detrital food webs (Valiela, 1991). Yet, these habitats present biota with a challenging ecophysiological environment, forcing organisms to evolve physiological and behavioural adaptations to cope with a wide range of physical and chemical variables (Horn *et al.*, 1999; Elliott & Hemingway, 2002). Inshore and estuarine areas are extremely important habitats for fish production, and many fish spend critical juvenile stages in estuarine nursery grounds (Elliott *et al.*, 1990). Under certain climatic (*e.g.* low NAO) conditions, estuarine areas may act as buffers against more severe open-sea conditions and therefore may not be directly affected by marine conditions (Attrill & Power, 2002; Sims *et al.*, 2004).

Flounder Platichthys flesus

Flounder *Platichthys flesus* L. inhabit shallow inshore areas, including brackish and freshwater environments such as estuaries and the lower reaches of rivers for much of their life (Wheeler, 1969). Their distribution ranges from southern Norway and the Baltic Sea to Morocco and includes the Mediterranean Sea (Sims *et al.*, 2004). *Platichthys flesus* have a wide tolerance for both salinity and temperature and are the only species of flatfish to be found in fresh water in Europe. Although *P. flesus* spend much of their lives in inshore, brackish waters, they migrate offshore in spring to spawn in depths of 20–40 m. Eggs and larvae develop in the pelagic environment until they drift inshore by June to July and settle in the inshore environment (Grioche *et al.*, 1997).

Sims *et al.* (2004) studied how variation in the spawning migrations of *P. flesus* in the western English Channel varied with water temperature over a 13 year period. They demonstrated that *P. flesus* migrated from colder estuarine habitats to warmer offshore spawning grounds up to 2 months earlier in years when sea temperatures were lower than average by 2° C. They also noted that during colder years, *P. flesus* arrived on the spawning grounds over a shorter period (2–6 days) than in warmer years (12–15 days). In years when the temperature difference between the inshore habitat and the spawning ground was greatest, the day of peak abundance of *P. flesus* on the spawning grounds was significantly earlier. Sims *et al.* (2004) suggested that the earlier migration to the warmer offshore waters in colder years was a response by *P. flesus* to maintain higher gonadal growth rates prior to spawning. The magnitude of the temperature difference between the two environments was related to the NAO, and during positive phases of the NAO, migration occurred earlier (Sims *et al.*, 2004).

The response of *P. flesus* to climate change has not been uniform across its distribution or even in areas of similar latitude. Attrill & Power (2002) demonstrated correlations between the NAO and *P. flesus* abundance (negative correlation) and average size (positive correlation) in the Thames Estuary. Genner *et al.* (2004) reported in the Bristol Channel (51°19′ N; 3°54′ W) that the abundance of *P. flesus* was positively correlated with increased water temperatures but were unable to demonstrate a similar relationship in the English Channel. Again, this indicates that populations of the same species inhabiting different areas may exhibit different responses to climate change.

Eelpout Zoarces viviparous

The eelpout (*Zoarces viviparous* L.) is a typical, non-migratory inhabitant of the coastal zone (Pörtner *et al.*, 2001). Its distribution ranges from the approximate latitude of the Thames Estuary in the south to the northern reaches of Scandinavia in the north (Wheeler, 1969). The thermal tolerance of *Z. viviparous* is closely correlated with the southern limits of its range (van Dijk *et al.*, 1999; Pörtner *et al.*, 2001) with an upper critical temperature limit between 21 and 24° C (van Dijk *et al.*, 1999). Pörtner *et al.* (2001) examined variation in *Z. viviparous* abundance over four decades and demonstrated a distinct relationship between hot summer events and low abundance in the following year, suggesting that *Z. viviparous* is sensitive to elevated temperatures. Recently, Pörtner & Knust (2007) provided further evidence that variation in *Z. viviparous* abundance was associated with sea temperatures. Using both field and laboratory data, they developed a model that suggests that mortality increases above threshold temperatures because of physiological constraints on oxygen transport.

The distribution of *Z. viviparous* is likely to shift northwards as a response to climate warming, with increased growth performance and fecundity at more northern latitudes as water temperatures rise (van Dijk *et al.*, 1999; Pörtner *et al.*, 2001), and as numbers fall in more southern populations (Pörtner & Knust, 2007). This shift is predicted as a direct response to the effect of rising temperature on the physiology of the fish (van Dijk *et al.*, 1999). Temperature increases may already be influencing eelpout populations as far north as the Forth Estuary in east Scotland, where Greenwood *et al.* (2002) showed recent decreases in *Z. viviparous* abundance. The shift in abundance was negatively correlated with January bottom water temperatures in the area (Greenwood *et al.*, 2002). Hiscock *et al.* (2001) warned that *Z. viviparous* could be the only commonly occurring marine fish in the Forth Estuary that could potentially disappear from Scotland. Catches of *Z. viviparous* in the young fish survey along the east coast of England were greater in the 1980s than in the 1990s (Rogers *et al.*, 1998). The shorthorn sculpin, *Myoxocephalus scorpius* (L.), is a species akin to *Z. viviparous* in that it is essential boreal and is not subject to commercial exploitation (Greenwood *et al.*, 2002). Currently, its distribution extends from the Bay of Biscay to the Barents Sea and its southern distributional limit is at a lower latitude than that of *Z. viviparous* (Wheeler, 1969). Greenwood *et al.*'s (2002) long-term study of fish community structure of the Forth Estuary showed increases in the abundance of *M. scorpius* that were positively correlated with temperature. They speculated that the increase might reflect *M. scorpius* populations shifting into northern regions as a result of climate warming or that *M. scorpius* were expanding into the niche being vacated by the declining *Z. viviparous.*

ANADROMOUS FISH

Atlantic salmon Salmo salar

Historically, Atlantic salmon *Salmo salar* L. were widely distributed in all countries whose rivers enter the North Atlantic (MacCrimmon & Gots, 1979). However, its distribution has been restricted in recent decades by anthropogenic activities, particularly man-made barriers such as dams and deterioration of water quality because of urban expansion and changes in agricultural practises (Crisp, 2000). The current distribution of *S. salar* extends from Russia, North America, Iceland, Greenland and the Baltic Sea to Iberia, and the ecology, habitat requirements and behaviour of salmon are extremely well studied (Crisp, 2000; Klemetsen *et al.*, 2003).

Salmo salar is still widespread in Britain and Ireland, occurring in suitable river systems not affected by poor water quality or barriers to migration. In England and Wales, *S. salar* is found in rivers all around the coast with the noticeable exception of the east and south-east coasts stretching from south of the Yorkshire Esk (54°30′ N; 0°40′ W) to east of the River Itchen (50°53′ N; 1°23′ W) in Hampshire (Maitland, 2004). *Salmo salar* from rivers in England and Wales have recently undergone a marked decline (Hendry & Cragg-Hine, 2003; Anon., 2005), with a *c.* 50% reduction in the number of adults returning to fresh water since the 1970s. Multi-sea winter (MSW) fish are thought to contribute most (65%) of this decline (Anon., 2005). Scotland is famous for its salmon, and in 2003 alone, >52 000 and 33 000 salmon were captured by anglers and the commercial fishery, respectively. Catch records from the recreational fishery show that catches of spring salmon (MSW salmon captured in spring) have undergone a significant decline since records began in 1952, while the numbers of grilse caught have increased (Anon., 2004*a*). In Ireland, the salmon is found in suitable river habitats throughout the island

and in particular along the Atlantic coast but is in decline, *e.g.* commercial catches fell from *c.* 250 000 fish in 2001 to <145 000 in 2004 (Anon., 2004*b*).

These declines are mirrored in three distinct modes throughout the species' natural range. In the north, populations are relatively healthy, although there have been recent declines. At intermediate latitudes, populations are in serious decline, and in the south, populations are mostly extirpated (Parrish *et al.*, 1998). Some of the causes implicated in the decline of *S. salar* include species introductions (Youngson & Verspoor, 1998), pathogens and disease (Bakke & Harris, 1998), predation (Mather *et al.*, 1998), prey availability in both freshwater and marine environments (Poff & Huryn, 1998), overfishing (Lilja & Romakkaniemi, 2003), river obstacles such as dams and weirs (MacCrimmon & Gots, 1979), pollution (Crisp, 2000), riparian deforestation (Stefansson *et al.*, 2003) and overextraction of water (Parrish *et al.*, 1998). Most of these factors act in concert to affect *S. salar* stocks (Parrish *et al.*, 1998). Accelerating climate change is likely to further compound the adverse effects from anthropogenic sources on all *S. salar* populations (Stefansson *et al.*, 2003), regardless of how well they and their environments have been managed to date.

It is likely that few North Atlantic fish species will be as intensely affected by climate change as *S. salar* (Ottersen *et al.*, 2004). The consequences of global climate change may be more profound for migratory species such as *S. salar* that depend on the timing of seasonal events and that use environmental variables as migratory cues (Friedland *et al.*, 2003), particularly as they migrate between habitats, which may be under differing climatic pressures. New and multiple challenges face *S. salar* as they are dependent on the health and environmental state of both marine and freshwater ecosystems for their survival. To understand the relationship between *S. salar* and climate variation, it is important to consider each of the key life-history stages of this fish: eggs and juveniles in fresh water, smoltification, migration of smolts to the sea, post-smolts and maturing adults in the marine environment, migration of adult salmon from estuaries upstream to spawning grounds and river occupancy of mature adults prior to spawning.

Of all the salmonids, the highest temperature limits for feeding and survival are those recorded for juvenile *S. salar* (Elliott, 1991; Crisp, 1996). For example, acclimatized parr can survive at high temperatures with an incipient mean (±S.E.) lethal level (survival over 7 days) of 27·8 ± 0·2° C and can continue to feed at temperatures as high as 22·5 ± 0·3° C and as low as 7 ± 0·3° C (Elliott, 1991). Bishai (1960) demonstrated that *S. salar* yolk-sac larvae (alevins) have an upper temperature tolerance only slightly lower than that of the parr used by Elliott (1991).

Juvenile *S. salar* begin feeding in spring at water temperatures between 6 and 7° C, with preferred temperatures between 9 and 19° C and optimal growth is exhibited between 16 and 19° C (Elliott, 1991; Elliott & Hurley, 1997). However, *S. salar* become stressed at temperatures between 22 and 24° C and respond behaviourally by seeking refugia (Cunjak *et al.*, 1993). Lund *et al.* (2002) noted that parr from the Miramichi River (47°05′ N; 65°21′ W), located towards the southern limit of the species distribution in Canada, experienced significant 'heat shock' at 23° C, as indicated by the production of mRNA and protein expression. The salmon in this catchment experience temperatures that cause significant protein damage and induce a heat-shock response for *c.* 30 days every summer (Lund *et al.*, 2002).

Future climate predictions include reduced summer precipitation for most of Britain and Ireland, especially in the south-east of England (Hulme *et al.*, 2002). Rivers and their tributaries are therefore likely to become shallower and may be less turbid because of reduced runoff. Ghent & Hanna (1999) speculated that this could increase the risk of avian predation of *S. salar* parr and could also be potentially associated with increased exposure to UV radiation (Zagarese & Williamson, 2001). Reduced precipitation will be reflected in decreased flows, increased water temperatures and decreased concentrations of dissolved oxygen, potentially exacerbating the deleterious effects of eutrophication. *Salmo salar*, like other salmonid fishes are particularly sensitive to reduced levels of dissolved oxygen (Crisp, 1993, 1996), especially when water temperatures are elevated. Fish kills, especially of sensitive life stages, *e.g.* juvenile salmonids are likely to increase in the future. In extreme cases, reduced precipitation may lead to loss of habitat for stream-dwelling salmonids.

Salmo salar show a clear relationship between body size and major life-history events, including smoltification. Fish that fail to achieve a given body size threshold within a certain time frame will not smoltify in the following spring (Thorpe *et al.*, 1998). Thorpe *et al.* (*op cit.*) suggested that the decision to smoltify is made in the previous summer following attainment of a particular growth trajectory, and the probability of smoltification therefore depends both on the size and on the rate of growth. Over the geographical range of *S. salar*, there is a strong negative association between the mean age of smoltification and an index of growth opportunity that combines both temperature and photoperiod (Metcalfe & Thorpe, 1990).

Salmo salar in the Miramichi River (Canada) are located towards the southern edge of their range, and fork lengths of Miramichi parr are negatively correlated with water temperature (Swansburg *et al.*, 2002), presumably as a result of increased metabolic costs at higher temperatures, resulting in less energy being devoted to growth. This may result in a decreasing amount of suitable habitat for juveniles in the future, as temperatures increase because of climate change and temperature thresholds not only occur earlier in the year but also for extended periods of time, resulting in decreased productivity (Swansburg *et al.*, 2002).

Studying the effects of increasing temperature on smolt production, Power & Power (1994) noted that in sites located further south, rises in summer temperature were associated with a decline in smolt production and a rise in parr density. They reported an opposite effect in more northerly populations, presumably as an effect of rising metabolic costs of growth at elevated temperatures in the south and increases towards optimal temperatures for growth in the north. Morrison (1989) reported that *S. salar* parr grew faster and smolted earlier as a result of river water temperature increasing by 1–3° C because of distillery cooling effluent entering a Scottish river. In a southern Norwegian river, the specific growth rates of *S. salar* parr during their first year of growth and the proportion of fish that smoltified after 1 year were all significantly positively correlated with the NAO during February to April during the winter of egg incubation (Jonsson *et al.*, 2005).

Smolts probably represent a life-history stage that is particularly sensitive to climatic change, as they undergo a wide range of physiological, morphological and behavioural changes as they prepare for the marine stage of their life (Stefansson *et al.*, 2003). During this transformation and transition from, freshwater to marine habitats, smolts are exceptionally vulnerable to environmental disturbances such as habitat degradation, temperature change, reduced water quality, obstacles to migration and altered estuarine habitat (McCormick *et al.*, 1998). Therefore, factors that may not have affected earlier freshwater residency could have potential effects during the short time that *S. salar* use the main stem of the river and estuaries on route to entering the ocean (Stefansson *et al.*, 2003) or during life in the ocean. Temperature has a strong effect on smoltification in *S. salar* (McCormick *et al.*, 1998; Zydlewski *et al.*, 2005). In the spring, parr smoltification rate and timing are determined by cumulative degree-days (Zydlewski *et al.*, 2005). Zydlewski *et al.* showed that smolts that experienced an earlier and more rapid increase in spring temperatures migrated downstream earlier than fishes exposed to ambient conditions. However, smolts that experienced a late and slower increase in temperature migrated over a longer period. All fish initiated and terminated downstream migration at the same number of degree-days, regardless of the temperature regimes they had experienced. Furthermore, the time frame for smolt migration experiencing cooler climates and during cooler springs is likely to last significantly longer than in warmer climates or early springs (Zydlewski *et al.*, 2005). Zydlewski *et al.*'s (2005) findings are supported by several field studies. Whalen *et al.* (1999) reported that peak migration of *S. salar* occurs later in spring for tributaries with lower temperature. Wagner (1974) demonstrated that when the temperature cycle was out of phase and behind the photoperiod cycle, the steelhead (rainbow trout) *Oncorhynchus mykiss* (Walbaum, 1792) smolt migratory period was extended, and when the reverse occurred, the migratory period was shortened. In addition, annual variation in the timing of peak migration of *S. salar* is related to variation in annual temperatures (McCormick *et al.*, 1998). Changes in precipitation patterns under future climate change scenarios (Arnell, 1998; Hulme *et al.*, 2002) may influence the ability of smolts to successfully migrate to sea.

Changes in the salinity tolerance of smolts show the same pattern of increase and decline when smolts are held in fresh water at high temperatures (McCormick *et al.*, 1997) as those demonstrated behaviourally in the study of Zydlewski *et al.* (2005). There is an optimal time frame for migration from the physiological point of view, termed the physiological smolt window (McCormick *et al.*, 1997). Zydlewski *et al.* (2005) showed that salinity tolerance follows the same pattern as the behaviour (downstream migration), showing that there is not only a behavioural limit to the timing of migration but also a physiological smolt window under various temperature regimes that may play a part in the ultimate success of migration to sea water.

At sea, *S. salar* mortality is highest during the first few months (Friedland *et al.*, 2003), and this has been shown to exert a more profound effect on the numbers of spawning fish than mortality in fresh water (Friedland *et al.*, 1993). Most fish are believed to be lost to predation during the first weeks in the ocean (Friedland *et al.*, 1998, 2000, 2003). In this phase, young salmon are sensitive to variable environmental factors such as water temperature, the NAO and to food availability (Friedland *et al.*, 1998, 2000, 2003). Marine mortality of post-smolts has increased over the past two decades, coincident with the dramatic decline in stock abundance (Friedland *et al.*, 2003). Correlations of return rates from different *S. salar* stocks suggest that common factors affect their survival rates in the critical post-smolt phase (Friedland *et al.*, 1993; Kallio-Nyberg *et al.*, 2004).

Varying ocean climates during first entry into the marine environment are critical to *S. salar* (Friedland *et al.*, 2003). Friedland *et al.* (1998) observed that thermal regimes during the first 2 weeks at sea were correlated with survival patterns of two index stocks, one migrating from southern Norway and the second from the west of Scotland. In years when warm thermal regimes existed in the North Sea and southern Norwegian coast at a time coincident with the post-smolt migration, survival was good. Similar results were also found in Baltic salmon post-smolts (Kallio-Nyberg *et al.*, 2004). Friedland *et al.* (2000) showed that when warm SSTs were prevalent as post-smolts began their ocean migrations, survival and growth were positively correlated with temperature. Hence, post-smolt survival of *S. salar* appears to be influenced by the same mechanisms hypothesized for many fishes, *e.g.* better growth during a critical period is associated with reduced predation risk and increased survival (Anderson, 1988; Sogard, 1997).

Davidson & Hazlewood (2005) demonstrated positive relationships between the post-smolt growth and the NAO winter index in four *S. salar* stocks across England and Wales. Friedland *et al.* (1993) noted that survival was positively related to growth, in both North American and European stocks of *S. salar*. Friedland *et al.* (2003) identified a negative effect of marine water temperature on post-smolt survival in spring of North American stocks, whereas in European stocks of *S. salar*, a positive relationship exists between growth and survival of post-smolts (Friedland *et al.*, 2000). This led Friedland *et al.* (2003) to conclude that in the case of the North American stocks, if food is limited, growth and therefore survival may be greater at lower temperatures. Beaugrand & Reid (2003) observed a correlation between *S. salar* catch data and phytoplankton production and zooplankton community structure in the north-western Atlantic, indicating that climate change may be affecting the growth and survival of post-smolt *S. salar* through the abundance and quality of prey.

Low water flow in rivers can have a deleterious effect on upstream migration of *S. salar* returning from the sea to spawn (Solomon *et al.*, 1999; Solomon & Sambrook, 2004). Studying radio-tagged *S. salar* in four rivers in south-western England, Solomon & Sambrook (2004) noted that when water flows were relatively high, the majority of migrating adult *S. salar* passed through estuaries and into the rivers with a minimum of delay. However, when river flow was low, most fish arriving from the sea did not pass quickly into fresh water but remained in the estuary or returned to sea for up to several months. Many fish subsequently failed to enter the river when favourable flow conditions returned, possibly as a result of lost physiological opportunity (Solomon & Sambrook, 2004). In areas located towards the southern limit of the species' range, *e.g.* Iberia and Connecticut (Garcia de Leaniz *et al.*, 1987; Juanes *et al.*, 2004), low summer flows are more common and summer running salmon are rare. The majority of adult *S. salar* migrate upstream before June, when river flows are higher and estuarine temperatures lower, and the fish spend several months before spawning in the cooler middle and upper river reaches (Garcia de Leaniz *et al.*, 1987). Variation in return timing of adult salmon to fresh waters is generally considered to reflect phenotypic responses to changes or localized differences in local flow and temperature regimes (Webb & McLay, 1996; Lilja & Romakkaniemi, 2003; Juanes *et al.*, 2004). The predicted decrease in rainfall in the south of England in summer (Hulme *et al.*, 2002) could result in earlier and later runs of *S. salar* (spring and autumn) becoming more prevalent in rivers such as the Fowey (50°20′ N; 4°38′ W) and Camel (50°33′ N; 4°56′ W) in Cornwall and Plym (50°22′ N; 4°36′ W) in Devon, where salmon return from the sea predominately in October and later (Solomon & Sambrook, 2004). A similar phenomenon was reported from the Connecticut River (41°16′ N; 72°20′ W), U.S.A., at the southern edge of the species' range (Juanes *et al.*, 2004). Following their introduction from a more northerly location, this stock responded to low summer flows by advancing the timing of migration.

Increasing marine temperature affects growth of *S. salar* at sea and can thus affect maturation and the relative contribution of grilse and MSW *S. salar* returning to natal streams to spawn (Scarnecchia, 1983; Martin & Mitchell, 1985; Jonsson & Jonsson, 2004). Martin & Mitchell (1985) associated increasing marine temperatures with larger numbers of fish returning as MSW *S. salar* and fewer as grilse in a Scottish system, with the average mass of grilse increasing with an increasing proportion of grilse. Further north, Scarnecchia (1983) showed a similar effect of smolts migrating from north Icelandic rivers into the subarctic compared with southern Icelandic stocks migrating into the warmer North Atlantic, and he concluded that warmer temperatures resulted in better growth and earlier maturation.

The proportion of *S. salar* returning as grilse to a Norwegian river was positively correlated with the NAO of the winter after smoltification (*i.e.* warmer marine conditions during positive NAO) as was the total number of returning fish (Jonsson & Jonsson, 2004). The mass increment of these grilse also positively correlated with the NAO during spring and early summer (May to July) when the smolts first enter the marine environment. A positive NAO index, and hence warmer conditions, equating to favourable survival and feeding conditions, permits salmon to develop the energy reserves necessary for gonadal development after just one winter at sea. Elevated NAO values when smolts first enter the sea promote rapid growth and therefore survival and result in an increased numbers of *S. salar* returning as grilse (Jonsson & Jonsson, 2004).

In female Atlantic *S. salar*, vitellogenesis largely takes place during summer and early autumn, when natural water temperatures tend to be relatively high. King *et al.* (2007) showed that elevated temperatures (22° C) during this period could significantly reduce reproductive fertility and subsequent survival of fertilized ova. Fertility and survival were reduced to <70 and <45%, respectively, at exposure for 6 weeks and to as low as 40 and 13%, respectively, if exposure at 22° C was maintained for 12 weeks. They also recorded significant endocrine effects within as little as 3 days of the commencement of exposure to 22° C.

There are concerns that *S. salar* may not be locally adapting quickly enough to the rate of recent climate change (Friedland *et al.*, 2003; Ottersen *et al.*, 2004). The eroding stability of those populations at the southern edge of the species' range may represent a climate-induced range contraction (Friedland *et al.*, 2003). The distributional ranges of many salmonid species are likely to be altered northwards as a result of changing temperature, rainfall and runoff because of climate change, with loss of southern populations. However, Arctic rivers, which are presently unsuitable or marginally suitable for salmonids, may become habitable and able to sustain new populations of anadromous salmonids (Stefansson *et al.*, 2003). Climate change models for eastern Canada have predicted an overall loss of juvenile *S. salar* habitat (Minns *et al.*, 1995), a view supported by the work of Lund *et al.* (2002), who suggested that any further increases in water temperature could have a profound effect for the *S. salar* in Canada. In Britain, Davidson & Hazlewood (2005) predicted that freshwater growth of *S. salar* will increase in the south-west and north of England and Wales under the UKCIP02 low emissions scenario but could fall below current growth rates under the high emissions scenario. They warn that growth rates from *S. salar* in rivers in the south-east of England are likely to decline and that this will have adverse consequences for survival and abundance.

FRESHWATER FISHES

An extensive literature search demonstrated a marked lack of studies examining the effects of climate change of freshwater fishes in Britain and Ireland, which contrasts greatly with the situation in the marine environment. Some studies have been conducted elsewhere in Europe (Lehtonen, 1996; Lappalainen & Lehtonen, 1997; Lehtonen, 1998), but the situation is in marked contrast with that of North America where for 20 years scientists have been examining the likely effects of climate change on freshwater ecosystems and fishes (Tonn, 1990; Mohseni *et al.*, 2003). It is probable that many of the predictions made for the effects of climate change on fresh waters in the continental U.S.A. are likely to hold for equivalent systems in continental Europe, as these two areas have many climatic and ecological similarities (Tonn, 1990). However, the freshwater systems of Britain and Ireland are unusual: most have been modified either physically or chemically by man, they rarely freeze as the climate is unusually mild for its latitude (Hulme & Barrow, 1997), and few regions of the world have both comparative climates and fish assemblages. Some overseas studies have included freshwater fishes found in Britain and Ireland (Shuter & Post, 1990), and these can be used to aid the understanding of the likely effects of climate change on the freshwater fishes. However, in contrast to the situation in the marine environment, the examination of freshwater fishes is notably reliant on empirical studies that detail simple relationships between aspects of individual species' ecology and temperature than on studies directly aimed at the issue of climate change.

Arctic charr Salvelinus alpinus

The Arctic charr *Salvelinus alpinus* (L.) is a holarctic salmonid with the most northerly distribution of any freshwater fish (Maitland, 1995; Klemetsen *et al.*, 2003). In the northern part of the species' distribution (>65° N), populations may include anadromous and non-anadromous individuals, but in the southern part of the distribution (including Britain and Ireland), the species is non-anadromous (Klemetsen *et al.*, 2003) and typically inhabits oligotrophic or ultraoligotrophic lakes, where some populations migrate into running water for spawning (Maitland, 1995). Britain and Ireland support *c.* 250 populations of *S. alpinus* (Maitland *et al.*, 2007), all of which are lacustrine and non-anadromous. These populations may include *S. alpinus* belonging to distinct trophic morphs or forms, where individuals of the different morphs act almost as different species, *e.g.* by segregating habitats and food resources (Adams & Maitland, 2007). It is currently unknown whether different morphs would exhibit differential responses to climate change. The understanding of the ecology of *S. alpinus* in Britain and Ireland ranges from some well-studied populations [*e.g.* Windermere (54°23′ N; 2°56′ W); Elliott & Baroudy, 1995] where a relatively good understanding of the population, and threats facing it are known, to others where little is known often beyond the actual presence (or often, the recent loss) of *S. alpinus* in a certain lake system (Igoe *et al.*, 2001). In his study of Windermere *S. alpinus*, Swift (1964) suggested that *S. alpinus* populations inhabiting Britain and Ireland may have become better adapted to warmer conditions than more northern populations.

Salvelinus alpinus are regarded as one of the most cold adapted of all salmonids: they continue to feed and grow at temperatures as low as 0·3° C (Brännäs & Wilund, 1992), and preferred temperatures are low (*c.* 12° C Larsson, 2005), even compared with other salmonids. Growth, under conditions of unlimited food, was optimal between 15 and 16° C (Larsson & Berglund, 1998); however, the relevance of this finding for natural populations that typically inhabit oligotrophic or mesotrophic system is unclear. Comparison of growth potential of *S. alpinus*, collected along a north-south gradient to examine potential adaptation to local temperatures (Larsson, 2005), showed little evidence of interpopulation thermal adaptation in *S. alpinus* and suggested that in European populations, growth is possible between 1 and 3° C, reaches a maximum between 15 and 17° C and stops at *c.* 21–22° C. Studies of upper lethal temperatures of juvenile *S. alpinus* from northern (*e.g.* Scandinavia: Lyytikainen *et al.*, 1997; Thyrel *et al.*, 1999; Elliott & Klemetsen, 2002) and southern (Windermere; Baroudy & Elliott, 1994) areas of the species' European distribution show very similar results and indicate that lethal temperatures for juvenile *S. alpinus* are in the region of 23° C.

Temperature also influences the reproductive biology of *S. alpinus*. Jobling *et al.* (1995) demonstrated that females exposed to high temperatures during summer months (*e.g.* $\geq$12° C) delayed ovulation by *c.* 3–4 weeks compared with females held at 4° C, while incubation temperatures $>$10° C were associated with increased egg mortality (Jungwirth & Winkler, 1984; Gillet, 1991). Gillet & Quétin (2006) warn that shifts in lake temperature following climatic change may reduce *S. alpinus* reproductive success in the future.

Maitland *et al.* (2007) describe a series of threats to the long-term conservation of *S. alpinus* in Britain and Ireland, including eutrophication, aquaculture and fish introductions, all of which could be predicted to continue or even increase under future climate change. Lehtonen (1998) reviewed the possible consequences of climate change for *S. alpinus* populations towards the northern extreme of their distributions. He suggested that populations most at risk would be those inhabiting shallow, low altitude lakes, which would be unable to avoid unsuitable temperatures by moving to cool hypolimnetic waters. In Britain and Ireland, these lakes may also be more likely to be nutrient enriched and at risk from invasion, *e.g.* by cyprinid fishes. In deeper, oligotrophic lakes, *S. alpinus* should still be able to utilize thermal refugia in cooler hypolimnetic waters during summer months if surface waters become unsuitable. However, any restriction in the volume of these waters or in oxygen concentrations may lead to habitat squeeze (Coutant, 1985) and a reduction in the carrying capacity of *S. alpinus* populations.

Mild increases in water temperature may lead to improved individual growth and production by *S. alpinus* in the short term, as already reported from some populations from Greenland (Kristensen *et al.*, 2006). However, it seems likely that because of the limited thermal tolerance of the species, the *S. alpinus* populations of Britain and Ireland are faced with considerable threats by the changes in climate predicted by UKCIP02, especially in shallow, productive lakes. Relatively, little is known about the status of *S. alpinus* in Britain and Ireland, and the fundamental data needed to gauge the species' response to climate change are missing. Without the instigation of robust programmes to assess and monitor *S. alpinus* populations, future biologists may simply be limited to reporting the loss of *S. alpinus* from Britain and Ireland (Igoe *et al.*, 2001).

Perch Perca fluviatilis

The perch *Perca fluviatilis* L. is a temperate mesotherm that can be considered representative of other cool-water, freshwater fishes (Hokanson, 1977). It is common and occurs in lakes, ponds and slow-flowing rivers across most of Europe and Asia, and although indigenous to much of Britain, it is absent from the extreme north-west of Scotland (Maitland, 2004). Perch are thought to have been introduced to Ireland but have been present for many centuries and are common in many lakes and rivers (Went, 1950).

Information on the effects of climate on perch mostly relate to temperature. For instance, the relationship between the temperature and the ecology of the Eurasian perch and its closely related congener, and ecological equivalent, the North American yellow perch *Perca flavescens* (Mitchill) (Thorpe, 1977; Craig, 2000) are well studied (Hokanson, 1977; Magnuson *et al.*, 1979; Craig, 1980). The optimal temperature for growth of perch in aquaculture settings is reportedly 23° C (Fiogbé & Kestemont, 2003), while Willemsen (1978) suggested a higher optimum of 26° C from a field study. In a review of the temperature requirements of percid fishes, Hokanson (1977) suggested that incipient lethal temperatures (estimated in the field and laboratory) for *P. fluviatilis* and *P. flavescens* ranged between 29·2 and 34° C. Weatherley (1963) demonstrated that when perch were exposed to temperatures $>31°$ C, interregnal tissues in the kidney became atrophied.

Thorpe (1977) reported that the southern distributional limit of both perch species corresponds with the 31° C summer isotherm. However, Willemsen (1978) noted that in a study of the effects of thermal discharge in Lake Ijssel (52°36′ N; 5°46′ E) (Netherlands), perch congregated in waters heated to

31° C and estimated a critical thermal maximum for *P. fluviatilis* of 33° C. Hokanson (1977) suggests that larval perch have a greater optimal temperature for growth (25–30° C) than adult individuals (18–27° C), a characteristic of many fishes (Coutant, 1985).

Saat & Veersalu (1996) reported that embryonic development of perch was successful between 8 and 18° C and optimal at 13° C. In an aquaculture setting, Wang & Eckmann (1994) demonstrated that the mortality, development and hatching success of *P. fluviatilis* eggs were most efficient at temperatures between 12 and 20° C, but they presented evidence that there may be adaptation at the population level. Evidence for such local adaptation is supported by observations that in Windermere, egg mortality was lowest between 6 and 10° C (Guma'a, 1978).

Climate change scenarios for Britain and Ireland predict that cloud cover will fall and exposure to solar radiation will increase (Hulme *et al.*, 2002). Experimental evidence from North America implies that this could have negative implications for *P. fluviatilis* and other littoral spawners. *Perca flavescens* eggs are extremely sensitive to UV radiation, and in a lake with low concentrations of dissolved organic carbon (which attenuates UV light), exposure to UV radiation was such that egg mortality was total (Williamson *et al.*, 1997). Although Mooij *et al.* (2005) predict that climate change will reduce transparency in shallow lakes, *Perca* spp. spawning success in shallow, clear-water lakes may decrease under future climates.

In Northern Europe, the *P. fluviatilis* reproductive cycle is closely associated with seasonal changes in climate. Oocyte development starts in August (Le Cren, 1951), and vitellogenesis typically extends from September to April to June when the fish are ripe for spawning (Guma'a, 1978). Low winter temperatures are essential for successful vitellogenesis, and Hokanson (1977) suggested that in the case of the closely related *P. flavescens*, exposure to temperatures below 6° C for a period of 6 months was optimal for gonad maturation. Studies examining the reproductive cycle of *P. fluviatilis* in waters receiving heated effluents have demonstrated that female *P. fluviatilis* are extremely sensitive to temperature during oogenesis, and elevated temperatures may lead to gonad malfunctions (Sandström *et al.*, 1997). The spread of *P. fluviatilis* in Australia may have been restricted because of temperature-related disruptions to gonadogenesis, as winter temperatures often remain >10° C (Hokanson, 1977).

Although food availability plays an important role (Persson, 1983), temperature is probably the strongest influence on the growth potential of *P. fluviatilis* (Hokanson, 1977; Craig, 1980; Wang & Eckmann, 1994). Juvenile size is linked to the probability of survival in *P. fluviatilis* (Shuter & Post, 1990) as in many fishes, and many authors have demonstrated an association between YCS and warmer temperatures (Goldspink & Goodwin, 1979; Craig, 1980; Paxton *et al.*, 2004). However, in a detailed analysis of the well-studied Windermere *P. fluviatilis* population, Paxton *et al.* (2004) revealed no discernable influences of climate change on perch recruitment.

Perca fluviatilis are carnivorous and undergo a well-described dietary ontogenetic shift from zooplankton, macroinvertebrates to piscivory (Allen, 1935). In a laboratory study, *P. fluviatilis* daily ration was maximal at 26° C (Willemsen, 1978), which is relatively close to the optimal temperature for growth (see above). Activity and foraging efficiency of perch is under the control of temperature, and it plays a role in competitive interactions between *P. fluviatilis* and other species (Persson, 1986). The well-recognized competitive interaction between *P. fluviatilis* and roach *R. rutilus* (Persson, 1986, 1990*a*) is temperature dependent, and in laboratory experiments, *R. rutilus* outperformed perch at temperatures >18° C (Persson, 1986).

To examine the possible consequences of climate change on cool-water fishes, a number of authors have used *P. fluviatilis* or *P. flavescens* as a model species (Shuter & Post, 1990; De Stasio *et al.*, 1996; Lappalainen & Lehtonen, 1997). Under climate warming, these studies typically predict an expansion in the distribution of *P. fluviatilis* because of increased scope for growth and reduced overwintering mortality (Shuter & Post, 1990), and it is likely that *P. fluviatilis* will follow a similar pattern in Britain and Ireland. Assuming that other factors (*e.g.* parasites, predators, availability of food, dissolved oxygen or the abundance of competitors) do not act as checks, *P. fluviatilis* growth, recruitment and survival is likely to improve in lakes and rivers where it is currently temperature limited. Increased growth will result in greater individual fecundity (Heibo *et al.*, 2005). Climate predictions suggest reduced precipitation during summer, so *P. fluviatilis* populations in shallow rivers, ponds and lakes could face increased risk of desiccation or oxygen stress (Alabaster & Lloyd, 1980). Climatic changes are predicted to be most extreme in the south-east of England, and during some waters, winter temperatures may rise above optimal levels for perch oogenesis (Hokanson, 1977).

Roach Rutilus rutilus

Rutilus rutilus (L.) is a common eurythermal cyprinid, characteristic of productive lakes, ponds, canals and middle and lower reaches of rivers across much of Northern Europe and Asia. They are found in much of Great Britain but are still absent from some areas of Scotland (Maitland, 2004). After their accidental introduction into Ireland during the 19th Century, *R. rutilus* rapidly dispersed (Fitzmaurice, 1981), and today, many Irish fresh waters are dominated by *R. rutilus*, an occurrence that has lead to concern on conservation and fisheries management grounds, *e.g.* Lough Neagh (Harrod *et al.*, 2001).

Rutilus rutilus is omnivorous (Michel & Oberdoff, 1995), commonly feeding on zooplankton and macroinvertebrates and is one of the few freshwater fishes of Britain and Ireland that can consume and assimilate plant and detrital materials. The generalist feeding habits of *R. rutilus* combined with their potential to reach extremely high densities means that they can directly and indirectly affect other species within a system (Brabrand *et al.*, 1986) and even the function of the ecosystem itself. *Rutilus rutilus* is potentially a strong competitor and under certain conditions has been shown to be capable of depressing populations of other fishes in lake systems, *e.g. P. fluviatilis* (Persson, 1990*a*, *b*). *Rutilus rutilus* has also been associated with declines in *Coregonus* spp. in Britain and Ireland (Harrod *et al.*, 2002) and elsewhere in Europe (Langeland & Nøst, 1994), especially following cultural eutrophication. *Rutilus rutilus* is an effective zooplanktivore, with feeding efficiency greatly increasing as temperatures reach 17–19° C (Persson, 1986), and they are able to greatly reduce zooplankton densities through predation (Brabrand *et al.*, 1986). Removal of zooplankton not only affects other fishes but can also lead to reduced grazing of phytoplankton, which combined with internal loading and recycling of nutrients by excretion and bioturbation (Horppila *et al.*, 1998) can affect water quality (Brabrand *et al.*, 1986).

Rutilus rutilus is eurythermal and can survive in temperatures from 4 to >30° C; growth, however, is restricted to water temperatures >12° C (van Dijk *et al.*, 2002). Hardewig & van Dijk (2003) suggested that this is because of reduced activities of digestive enzymes at low temperature. Experimental studies (Cocking, 1959; Horoszewicz, 1971) suggest that lethal temperatures for juvenile *R. rutilus* are in the region of 30·5–36° C but are strongly dependent on acclimation history.

From a laboratory study, van Dijk *et al.* (2002) suggested a preferred temperature for juvenile *R. rutilus* of 27° C, a temperature higher than that reached in many European lakes and rivers inhabited by *R. rutilus* (Staaks, 1996). Experimental studies by Hardewig & van Dijk (2003) indicate that in juvenile *R. rutilus* growth is maximized between 20 and 27° C. Feeding activity in the wild is positively correlated with water temperature (Hellawell, 1972), and Persson (1986) showed that the foraging ability of juvenile *R. rutilus* improved significantly at temperatures between 17 and 19° C because of increased swimming speeds, reduced handling time and increased capture rates.

As might be expected, temperature not only affects the physiology of individual *R. rutilus* but also has an effect at the population level. Recruitment (as YCS) has been positively correlated with water temperature in river [*e.g.* with degree-days above 12° C: (Grenouillet *et al.*, 2001)] and lake [*e.g.* degree-days above 14° C: (Goldspink, 1978)] populations, and it is likely that interannual variation in temperature plays a large role in the recruitment of *R. rutilus*. Reproduction is controlled both by photoperiod and by temperature in *R. rutilus* (Jafri, 1989, 1990). Published accounts of *R. rutilus* spawning vary with regard to reported water temperatures prior to spawning, *e.g.* Diamond (1985) reported spawning at 16° C and Fitzmaurice (1981) observed spawning in Irish rivers at the end of May at temperatures >15° C. Tobin (1990) reported *R. rutilus* entering various tributaries of Lough Neagh and spawning at temperatures ≥14° C, and a suspension of spawning following a reduction in water temperature to 11° C because of an abrupt weather change. *Rutilus rutilus* held in the laboratory spawned at temperatures between 18 and 20° C (Jafri, 1990).

Future warming may lead to *R. rutilus* spawning earlier in the year and hence an increased growing season for YOY fish. A series of studies examining the effects of thermal effluent on reproductive biology of *R. rutilus* implies that a small (+2–3° C) increase in temperature over ambient conditions simply resulted in an advanced spawning date (Mattheeuws *et al.*, 1981), while more significant increases above ambient temperatures (+8–10° C) are likely to lead to interrupted gametogenesis, poor spawning success and subsequent recruitment (Luksiene & Sandström, 1994; Luksiene *et al.*, 2000). From a long-term study (1983–2000) of *R. rutilus* reproductive biology in Lake Geneva, Gillet & Quétin (2006) describe a 15 day advancement in the date on *R. rutilus* spawning was initiated. This shift was further associated with a 2° C increase in mean May water temperature over the same period. In a similar study in the Narva River (Estonia: 59°28′ N; 28°02′ E), Nõges & Järvet (2005) reported that the temperature at the onset of *R. rutilus* spawning increased by 3° C because of warming of average water temperature between 1951 and 1990, but they found no evidence that *R. rutilus* advanced the date of spawning over the same period.

Currently, water temperatures in some parts of Britain and Ireland may be such that small *R. rutilus* are susceptible to overwinter size-selective mortality (Sogard, 1997) following poor summer growth and failure to develop sufficient energy reserves (Griffiths & Kirkwood, 1995), particularly in the first summer of life. Juvenile *R. rutilus* are likely to have an increased scope for growth and assimilation of energy reserves in future as water temperatures rise, and this could reduce overwintering mortality.

Nunn *et al.* (2007) showed that *R. rutilus* YCS was positively correlated with the position of the North Wall of the Gulf Stream in both the rivers Ouse (53°42′ N; 0°45′ W) and Trent (53°41′ N; 0°41′ W). However, they also showed that river discharge had a greater impact on roach growth than on temperature in the Ouse.

As a eurythermal generalist, it can be expected that *R. rutilus* will benefit from many aspects of predicted climate change in Britain and Ireland, as predicted elsewhere in Europe (Lehtonen, 1996). Warmer water temperatures throughout the year, with an earlier spring and extended summer and autumn, will increase the scope for recruitment, assuming that other limiting factors do not come into play (*e.g.* food, predation, disease or parasitism). *Rutilus rutilus* is likely to spawn earlier in the year (Gillet & Quétin, 2006), and YOY fish will forage with greater efficiency (Persson, 1986) over an extended growing season. If *R. rutilus* growth increases during the sensitive first summer of life, the risk of predation (Nilsson & Bronmark, 2000) and overwinter mortality (Griffiths & Kirkwood, 1995) will decrease. Assuming that YOY *R. rutilus* do respond to climate warming in this way, there is considerable scope for predation on zooplankton to intensify, with subsequent community (*e.g. R. rutilus–P. fluviatilis* competition) and ecosystem (*e.g.* reduced grazing of phytoplankton) effects. However, if food resources prove limiting, increased recruitment may lead to increased frequency of stunting in *R. rutilus* populations (Linfield, 1980). Adult *R. rutilus* may respond to increased temperatures by increasing growth, with associated increases in fecundity in female fish (Lappalainen *et al.*, 2008). *Rutilus rutilus* can withstand low dissolved oxygen concentrations (*c.* 1 mg l^{-1} Doudoroff & Shumway, 1970) for short periods, even if water temperatures reach *c.* 30° C (Cocking, 1959). Although clearly at risk if water levels fall significantly or if small rivers, shallow lakes and ponds dry out compared with many other fishes, *R. rutilus* should be relatively resistant to drought conditions. Riverine *R. rutilus* populations will face particular changes under predicted climate change scenarios: flow regimes will change with shifts in precipitation patterns and water temperatures will increase (Arnell, 1998; Hulme *et al.*, 2002). Reduced summer flows and warmer water temperatures (if not too extreme) could lead to improved recruitment (Grenouillet *et al.*, 2001). Extreme precipitation events are predicted to increase in frequency, which may lead to the loss of juvenile *R. rutilus* if suitable refugia are not available (Mann, 1996; Mann & Bass, 1997). However, on a larger scale, climate change represents a clear opportunity for *R. rutilus* in Britain and Ireland: warmer waters will result in increased recruitment because of earlier spawning, improved growth and survival of juvenile *R. rutilus*, and it is extremely likely that *R. rutilus* will expand its distribution and intensify its influence on those habitats where it is found (Brabrand *et al.*, 1986).

Responses of freshwater fishes to climate change

Although some populations of cold-adapted fishes may currently encounter temperature conditions close to their thermal limits, the majority of freshwater fishes found in Britain and Ireland will probably respond positively to predicted increases in temperature. Assuming that other limiting factors such as food, predation, disease or competition do not act, this is likely to lead to increased reproductive success, growth and production. Increased temperatures are likely to favour fishes whose current distribution and reproductive success may be constrained by low temperatures, *e.g. P. fluviatilis*, *R. rutilus*, bream *Abramis brama* (L.) and carp *Cyprinus carpio* L. (Goldspink, 1978, 1981; Lehtonen & Lappalainen, 1995; Lappalainen & Lehtonen, 1997). Following climate change, some lake-dwelling cold-water stenothermal fishes may be exposed to conditions beyond their thermal limits, *e.g. S. alpinus* and the three *Coregonus* spp. found in Britain and Ireland, and climate change must be considered as a further threat to the long-term preservation of these conservationally important species (Maitland & Lyle, 1991; Winfield *et al.*, 1996; Harrod *et al.*, 2001). The response of other, more widely distributed stenothermal freshwater fishes, *e.g.* brown trout *Salmo trutta* L., is likely to be variable and a function of their location. For instance, increased water temperatures may increase the scope for growth and production in northern or upland populations (Weatherley *et al.*, 1991), while southern or lowland populations may face conditions that restrict growth because of elevated temperatures, reduced dissolved oxygen concentrations or loss of habitat.

CONCLUSIONS

There is a growing scientific consensus that human activities have modified the composition of the atmosphere and that these changes have caused, and will continue to cause, significant shifts in the climate of Britain and Ireland (Hulme *et al.*, 2002; Sweeney *et al.*, 2003). Many studies discussed here have demonstrated the often strong influence climate can have on the ecology and distribution of fishes. As might be expected, climate change has and will continue to affect the fishes of Britain and Ireland. Humans rely heavily on aquatic systems for many goods and services, *e.g.* food production, recreation, nutrient recycling and gas regulation. Effects of climate change on aquatic systems and their inhabitants (*e.g.* fishes) are therefore likely to have widespread implications for future human populations of Britain and Ireland. The likely consequences of climate change on the fishes in the British Isles include:

1. Continued shifts in the distribution of fishes, and future climates will theoretically favour mesothermal and eurythermal fishes, which are likely to

extend their distribution, and increase their growth and production, assuming that other limiting factors, *e.g.* availability of food, do not come into play.

2. In fresh waters, fish communities will be increasingly dominated by warm-adapted cyprinid and percid species and cold-adapted salmonids will face temperature stress. In extreme circumstances, some populations of extreme cold-adapted salmonid fishes may become extirpated, *e.g. S. alpinus* and *Coregonus* spp. Diadromous species face particular uncertainties because of their utilization of fresh, estuarine and marine waters, all of which potentially face different and complex responses to climatic change. Whatever the outcome of climate change, it will lead to new selection pressures on fishes and indeed all organisms.
3. Climate warming may increase the probability that non-native taxa become successfully established in Britain, Ireland and surrounding waters (Dukes & Mooney, 1999) with complex ecological implications (Chapin *et al.*, 2000), such as changes in ecosystem function (Vander Zanden *et al.*, 1999) or the introduction of novel parasites and pathogens that challenge the immunological capacity of native fishes.
4. The exploitation of fishes, *via* both wild capture and aquaculture, is likely to be affected by climate change, and adaptation strategies should be developed (*e.g.* targeting or culturing new species) to enhance the sustainable use of marine resources (Troadec, 2000; McCarthy *et al.*, 2001). It is likely that commercial fisheries in Britain and Ireland will respond rapidly to shifts in the distribution of fishes following climate change.
5. The inclusion of environmental data is essential in the assessment of exploited stocks, particularly on stock-recruitment relationships (Axenrot & Hansson, 2003; Clark *et al.*, 2003). Failure to include environmental factors can result in overestimates of stock biomass, increasing overexploitation and probable collapse of stocks, given the forecasted trends in climate and the uncertainty of the effects (Brander, 2007). Reducing fish mortality of stocks that are already fully or over exploited is the principal feasible method of reducing the effects of climate change (Brander, 2007).
6. Throughout Britain and Ireland, aquaculture has become increasing important since the 1950s, producing 240 000 t of fish and providing employment to *c.* 10 000 people. Temperature increases may be beneficial for aquaculture, with the likely diversification to novel species or increased production from cultured species that are currently temperature limited (Troadec, 2000; McCarthy *et al.*, 2001). However, predicted reductions in summer precipitation in some parts of Britain and Ireland indicate that aquaculture facilities and hatcheries may face restricted water supplies, affecting inland aquaculture systems particularly through lower dissolved oxygen levels.
7. Currently, temperatures restrict the range of many fish pests and parasites, and warmer waters are likely to lead to an increase in the incidence of outbreaks of unwelcome infections (Lafferty & Kuris, 1999; Marcogliese, 2001). Temperature increases of only a few degrees could have indirect implications for aquaculture facilities, *e.g.* increased incidence of harmful algal blooms that release toxins into the water and generate fish kills (Shumway, 1990). Caged fish will be particularly susceptible to such occurrences, unlike wild

fishes that may have the opportunity to avoid contaminated waters (Kent & Poppe, 1998).

It is very difficult to rank or determine the relative importance of the different effects of climate change on the fishes of Britain and Ireland, as they vary greatly by species, and even populations, and climate change will affect all aquatic habitats. Changes in temperature are predicted to exceed any seen in the past 10 000 years (Houghton *et al.*, 2001) and this probably represents the greatest threat to fish. For instance, throughout this review, the influence of temperature on recruitment and therefore YCS has been described for several fishes, largely though its influence on mortality of early life stages. The authors suggest that climate based shifts in the phenology of these sensitive early life stages are likely to be the principle means by which climate change affects the fishes of Britain and Ireland. Current studies indicate that this effect will be particular apparent in the marine environment.

The effect of climatic change cannot be considered alone, for instance climate change is and will continue to be a very important driver for several commercially important fishes, but the detrimental effect of continued overfishing is almost certainly greater. Recent studies have highlighted the importance of including environmental variation as a model input when assessing fish stocks, *e.g.* determination of total allowable stocks. For instance, assuming that exploitation rates do not fall, the combined product of climate change (reduced recruitment) and high fishing mortality (reduced SSB) are likely to drive *G. morhua* to dangerously low numbers around the British Isles.

Existing international agreements and legislation, *e.g.* the Ramsar convention (UNESCO, 1971), various European directives (EC, 1979, 2000), and the International Convention on Biological Diversity (UNCED, 1992) provide a clear obligation for governments and managers to respond to the challenge of climate change. In order for governments to react, they rely on scientists to provide them and other interest groups with reliable information regarding the responses of natural systems to climate change. Clearly, this means that funding will have to be provided by Government to support basic science, including monitoring explicitly designed to examine the influence of environmental change. Much of the current understanding of the likely consequences of climate change on aquatic ecosystems and fishes has resulted from routine monitoring of environmental and ecological data. Such routine monitoring should be continued and extended to data-deficient areas (*e.g.* lakes and rivers) to demonstrate how the aquatic ecosystems and fishes of Britain and Ireland respond to climate change. Although these studies have proved very valuable in identifying climate-induced changes in fish populations and communities, focused research is needed to specifically investigate the effects of climate change and the processes through which the changing climate is exerting its influence.

If the U.K. and Irish Governments are to fulfil their obligations under international and national conventions and legislation to conserve and protect aquatic biodiversity, they need to ensure funding is available for basic monitoring as well as modelling and laboratory studies. However, ecologists must consider the role of climatic change as a potential confounding variable in their analyses of existing data. For instance, the forthcoming implementation of the European Water Framework Directive has prompted attempts to determine the ecological status of aquatic ecosystems (EC, 2000; Pont *et al.*, 2006) including studies to determine reference conditions in fresh and transitional waters. Workers involved in these and similar studies should be aware that the shifting climate signals over recent decades might influence results (Kristensen *et al.*, 2006), and if not considered, may lead to erroneous conclusions (Carvalho & Kirika, 2003).

As noted by Carpenter *et al.* (1992) and Magnuson (1991), the fisheries, aquaculture and aquatic ecology literature have great relevance to those trying to understand large-scale issues in ecology, including the likely ecological consequences of climate change. However, there is still much to be done, and fisheries scientists, aquatic scientists (*e.g.* limnologists, hydrologists and oceanographers) and climate scientists need to combine their efforts. If climate models are going to be useful for evaluating the consequences of global change on ecological systems, the ecological community needs to make a case for climate modellers to address the relevant ecological scale (Wilby *et al.*, 1998; Kapetsky, 2000; Brander, 2005). For example, Elliott *et al.* (2005) utilized a regional climate model to predict phytoplankton community dynamics under future climate conditions at a single lake level. A suitable regional scale for future climate models may be at the level of Water Framework Directive River Basin Districts (EC, 2000).

Although controls have been proposed on atmospheric emissions (United Nations, 1997), these have not been effective, and emissions continue to rise worldwide. The U.K. and Irish Governments are aware of the huge implications of climate change to human populations and to the natural systems they rely on for life and have attempted to respond to these threats (DEHLG, 2000; DEFRA, 2006) to limit emissions of the gases associated with climate change. However, the residual inertia in climate systems is such that even a total cessation of emissions tomorrow would leave fishes exposed to continued climate change for *c.* 50 years (Hulme *et al.*, 2002). Hence, regardless of the success or failure of programmes aimed at curbing climate change, the authors and the fish biologists of tomorrow can expect major changes in fish communities.

We would like to acknowledge Fisheries Society of the British Isles funding for this review. We would like to thank the following for useful comments and constructive criticism of earlier forms of this article: Felicity Huntingford, David Griffiths, David Fraser, David Righton, David Sims, Graeme Peirson, Jyrki Lappalainen, Per Jacobson and Ross Gardiner. Many thanks to Jennie Mallela and to Brigitte Lechner. The authors thank two anonymous referees for comments that improved the manuscript.

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